

Costly calling: Marmots who alarm call at higher rates are less likely to survive the summer and live shorter lives

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Abstract

Emitting alarm calls may be costly, but few studies have asked whether calling increases a caller's risk of predation and survival. Since observing animals calling and being killed is relatively rare, we capitalized on over 24,000 h of observations of marmot colonies and asked whether variation in the rate that yellow-bellied marmots (*Marmota flaviventris*) alarm called was associated with the probability of summer mortality, a proxy for predation. Using a generalized mixed model that controlled for factors that influenced the likelihood of survival, we found that marmots who called at higher rates were substantially more likely to die over the summer. Because virtually all summer mortality is due to predation, these results suggest that calling is indeed costly for marmots. Additionally, the results from a Cox survival analysis showed that marmots that called more lived significantly shorter lives. Prior studies have shown that marmots reduce the risk by emitting calls only when close to their burrows, but this newly quantified survival cost suggests a constraint on eliminating risks. Quantifying the cost of alarm calling using a similar approach in other systems will help us better understand its true costs, which is an essential value for theoretical models of calling and social behavior.

Key words: alarm calling, predator deterrence, predation, longevity.

Alarm calls are produced when prey detect predators (Klump and Shalter 1984). Yet by producing loud vocalizations, animals may attract the attention of predators (Ryan et al. 1982; Haff and Magrath 2011). In response to this potential risk, the structure of alarm calls have, in some species, been hypothesized to have evolved to be less conspicuous to predators. For instance, a number of birds produce relatively high frequency and more tonal calls which fade in and out and making them difficult for raptors to detect and locate callers (Marler 1955, 1957). Indeed, some species dynamically vary the structure of their alarm calls in ways that reduce their conspicuousness (Bayly and Evans 2003), modify emission based on social context (Townsend et al. 2012), and modify call type based on predation risk (Rauber and Manser 2017). Regardless, predators may locate vocalizing individuals and thus it is generally assumed that calling is a potentially altruistic behavior that benefits the receivers at a cost to the signaler (Maynard 1965).

Although widely assumed to be risky, like “selfish” sentinel behavior (Clutton-Brock et al. 1999; Wright et al. 2001), animals may reduce the risk of calling by only emitting alarm calls once they have reached a secure location. Thus, by doing so, they may not really increase their exposure to risk. Indeed, great gerbils (*Rhombomys optimus* [Randall et al. 2000]), black-tailed prairie dogs (*Cynomys ludovicianus* [Hoogland 1995]), and yellow-bellied marmots (*Marmota flaviventris* [Blumstein et al. 1997; Collier et al. 2010]) call mostly from positions of safety. With minimal costs, calling may only

require minimal benefits to be maintained or, if there is no cost, calling may not be altruistic in any sense.

Most hypotheses to explain the evolution and maintenance of alarm calling, however, focus on the benefits accrued to the caller (reviewed in Blumstein 2007b). For instance, callers may directly benefit themselves if they increase their chance of survival by discouraging pursuit or by creating pandemonium (Neill and Cullen 1974) which facilitates their escape. Thus, if individuals directly benefit, it is straightforward to envision how potentially costly calling is maintained by selection. In addition, calling may also increase an individual's indirect, and hence inclusive fitness, if by emitting alarm calls relatives are warned and are more likely to survive (Sherman 1977).

Although conspicuous sexual signals (Zuk and Kolluru 1998), and specifically other sorts of vocalizations (e.g., Cade 1975; Bellwood and Morris 1987; Hale 2004; Kleindorfer et al. 2016), have been shown to increase vulnerability to predators and parasitoids, we are aware of only one study that showed that alarm calling increased a caller's vulnerability to predation (Sherman 1985). This lack of previously reported studies quantifying the predation costs of calling is likely because it is remarkably difficult to quantify the survival value of emitting a bout of alarm calls.

In the only study we are aware of that directly quantified predation in response to predator attacks, Sherman (1985) found that in over nine years of detailed behavioral observations on Belding ground squirrel (*Urocitellus beldingi*) colonies, only 2% ground squirrels that produced alarm calls in

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response to the sight of a raptor were killed whereas 28% of non-callers were killed. He also reported that in response to terrestrial predators, 8% of alarm callers were killed although 4% of non-callers were killed. He noted that most squirrels alarm called whereas running from hawks. However, in response to terrestrial predators, squirrels only called once at their safe burrows. These findings illustrate the relative risk of these different types of predators.

The yellow-bellied marmots are an ideal species to study both the benefits and costs of alarm calling. They are a facultatively social ground-dwelling sciurid rodent that may (or may not) emit alarm calls upon detecting a predator (Blumstein 2007a) which means that there is variation in the propensity to call that can be explained. However, and unlike some ground squirrels and prairie dogs, marmots do not seem to have contagious calling, and calling does not create pandemonium in the colony which eliminates at least one putative hypothesis for why they may emit alarm calls. Indeed, prior work has shown that marmot alarm calling may be a form of maternal care because only females with newly emerged young increase rates of calling after pups emerge (Blumstein et al. 1997). But because other animals occasionally emit alarm calls, calls may also be directed to the predator, which means that calling might be directly associated with enhanced survival if by calling predators are deterred. Additionally, because socially isolated animals are more likely to emit calls (Fuong et al. 2015), calling may increase the caller's status among conspecifics, or be directed to the predator to discourage pursuit. Thus, it remains an open question as to whether marmots directly benefit from producing alarm calls and whether or not alarm calling is costly. Our aim was to determine whether individuals who called relatively more than others were more likely to die during the summer. Because essentially all summer mortality in our system is associated with predation (Armitage 2014), we can therefore indirectly determine whether alarm calling is costly.

Materials and Methods

We studied alarm calling yellow-bellied marmots in the upper East River valley, in and around the Rocky Mountain Biological Laboratory, near Crested Butte, Colorado, USA between 2002 and 2022. The individually-marked population has been studied since 1962 (Blumstein 2013; Armitage 2014). All subjects are trapped regularly during the summer active season, permanently marked with unique ear tags, and individually identified for observations from afar with a unique Nyanzol dye mark on their dorsal pelage (Blumstein et al. 2009). Marmots were studied under annual permits issued by the Colorado Division of Wildlife (TR-917). All procedures were approved under research protocol ARC 2001-191-01 by the University of California Los Angeles Animal Care Committee on 13 May 2002, and renewed annually.

We study marmots at up to 11 geographically distinct colony sites (some areas contain no residents in some years) along a 5 km elevational gradient (Blumstein 2013; Armitage 2014). Colonies are observed most days, weather permitting, between mid-April and early September during periods of peak marmot activity (0700–1000 h and 1600–1900 h) (Armitage 1962). During these observations, multiple trained observers (the numbers varied by year and month but we typically logged about 1000 h of observations annually) noted the occurrence of all alarm calls during observation sessions

and attempted to identify the caller. Based on the number of observers, observers may have moved one or more times during their daily observations or have remained in a single location. Observation efforts varied based on the number of marmots at a site which varied annually. When there were more marmots, we allocated proportionally more time to observing the colony site.

Despite our efforts, we were not always certain who called or what the calls were elicited by. In many cases we were unable to identify the exact caller because many calling bouts have only one or a few calls, and although we know that some individual called, we could not identify the caller with certainty. We do not believe that these unattributed calls resulted in a significant bias. We also included all calls regardless of what elicited the call. Some calls were obviously produced in response to detecting a predator (e.g., these included several terrestrial and aerial predators—see below) but observers were not certain in all situations and in some cases an ungulate moving through the area elicited alarm calls. Here too we suggest that this uncertainty should not bias our results.

For these analyses, we focused on well-studied sites where we also were able to estimate the relative predation risk by quantifying predator visits. Because young emerged in late June or July, and because many yearlings dispersed around the time of pup emergence, these age cohorts are not present the entire year. Thus, we focused on adults (≥ 2 -year old) who were resident in their colony the entire summer active season where we could more confidently equate disappearance with likely predation.

For known adult callers, we calculated the rate of alarm calling as the number of calling bouts emitted by an individual in a given year as a fraction of the total time that an animal could be observed calling. Bouts could contain a single to >1000 alarm calls in response to some disturbance, but most bouts consisted of only a single alarm call which made it difficult to accurately identify the caller. Total time was calculated by summing the duration of a year's near daily observation sessions during which a given subject was seen at any time (we do not see all individuals during all observation periods; particularly later in the year when the vegetation grows, and at a few difficult to observe sites). Because the majority of individuals were never identified calling, analyses using all subjects would be extremely zero inflated. Thus, we focused only on positively identified callers. With these data we asked how was calling rate associated with the probability of surviving the summer that is a proxy for predation.

Marmots emerge from hibernation starting in mid-April and begin to disappear into their hibernacula starting in early September (Blumstein 2009; Armitage 2014). Summer survival was determined through regular observations and trapping. Virtually all individuals are captured at least once annually (Ozgul et al. 2006, 2007), most individuals were seen every week, and many were captured every other week. For our purposes, if an animal was detected between 10 August and 10 September, we scored the animal as having survived the summer. A few individuals were not seen then, but were seen or captured within the next four years. These animals were scored as surviving the previous summer.

By focusing on adults, we could be certain that missing individuals had died and not dispersed. Although we have directly observed relatively little predation on adults, with only a few exceptions (which did not include any of these animals from which we had calling data), failing to survive

the summer can be attributed to predation (Armitage 2014). Adults do not disperse and obvious disease-related mortality in adults is essentially non-existent during the summer. We note that some older animals are occasionally hit by cars or climb into cars and are moved out of the valley, but these are relatively rare events.

Variation in predator pressure could explain variation in calling. During each morning or afternoon observation period we quantified relative predator pressure by noting whether we detected any predator. Coyotes (*Canis latrans*), badgers (*Taxidea taxus*), American martens (*Martes americana*), black bears (*Ursus americanus*) and raptors—mostly golden eagles (*Aquila chrysaetos*) are key adult predators (Van Vuren 2001), but we also noted visits by red foxes (*Vulpes vulpes*), and smaller raptors such as red-tailed hawks (*Buteo jamaicensis*). For each colony, and for each year, we then calculated the proportion of observation periods where at least one predator was detected. Using a median split, we assigned colony years with rates of predator detection below the median as “low predation pressure” and those with rates above the median as “high predation pressure.”

Analyses were conducted in R (R Core Team 2024). To ask whether calling rate explained variation in summer survival we fitted a generalized linear mixed model in the R package lme4 (Bates et al. 2015). We used the package sjPlot (Lüdecke 2024) to estimate the conditional R^2 , which includes only fixed effects, and the marginal R^2 , which includes fixed and random effects. We included the \log_{10} rate of alarm calling, sex (M/F), the position in the valley, the exact age of each individual, and relative predation risk as predictors of summer survival. Because marmots at our study site can live up to 16 years, many individuals were observed for more than a single year and we included random effects of marmot identity, colony, and year. We checked assumptions using the package performance (Lüdecke et al. 2021); all VIFs were <2.0; random effects were normally distributed.

To ask whether calling rate explained variation in longevity, we fitted a mixed effects Cox survival model in the R package coxme (Therneau 2015). We included the following main effects: \log_{10} transformed calling rate (to normalize its distribution), sex (M/F), the position in the valley (scored as up or down valley because valley position has a variety of effects on life history traits [Kroeger et al. 2018]), and the relative predation risk (categorized as low or high). Please note that age was not included as a separate predictor because survival analyses explicitly include age in the analysis. We included individual ID and colony ID as random effects in this model. To check assumptions of the Cox survival model we used the “cox.zph()” function from the ‘survival’ package (version 3.5.8; Therneau 2024); all P -values > 0.05. To illustrate the results, we plotted annual survival for the 25th (i.e., those individuals who called the most) and 75th (i.e., those individuals who called the least) caller percentiles.

Results

Between 2002 and 2021 marmots were observed for 24,388 h. Of marmots ≥ 2 years old, 355 were observed to alarm call during at least one year and were therefore retained for analysis which left us with a full data set containing 837 annual rate estimates from 328 marmots that lived between 2 and 14 years. These data were used to fit a generalized linear mixed effects model to study annual survival (see below). In this data set,

annual individual call rates averaged 0.137 ± 0.02 SEM calling bouts per hour. The 25th percentile calling rate was 0.02 calling bouts per hour and the 75th percentile calling rate was 0.09 calling bouts per hour. Because many individuals were still alive at the time of this study our final Cox survival model included 837 annual rate estimates from 275 individuals with known longevities. Both datasets spanned 20 years.

Is calling rate associated with summer survival?

Individuals who called more were less likely to survive the summer (Table 1; Figure 1). The full model of the variation in survival had a marginal $R^2 = 0.189$ and a conditional $R^2 = 0.344$. When the rate of alarm calling was removed, the marginal R^2 dropped to 0.074. This suggests that calling alone explained about 12% of the variation in summer survival. The only other significant effect was that males were less likely to survive the summer (Table 1).

Is calling rate associated with longevity?

Marmots who called more lived shorter lives (Table 2; Figure 2). In the full dataset, \log_{10} Rate of Alarm Calling was found to be significant ($P < 0.0001$) with an exponentiated coefficient, or hazard ratio, of 1.87. A hazard ratio value greater than 1 indicates a decreased likelihood of survival over time, indicating that individuals who called more increased their annual risk of death by 1.87. Here too, males lived significantly shorter lives with an increased annual risk of death of 1.51 (Table 2). No other fixed effects explained significant variation in longevity. The full survival model had an R^2 of 0.18, but when the rate of alarm calling was removed, the R^2 dropped to 0.07, suggesting that about 11% of the variation in survival was attributable to calling rate.

Discussion

Although it is often assumed that emitting alarm calls increases predation risk because calling advertises the caller’s exact location, few data actually support this cost (Sherman 1985).

Table 1. Results from the generalized linear mixed model explaining variation in adult yellow-bellied marmot (*Marmota flaviventris*) summer survival. Bolded results are considered statistically significant ($P < 0.05$). The model includes 328 individuals and a total of 837 unique observations that were collected over 20 years

Predictors	Estimate	Std. error	P
(Intercept)	-0.061	0.546	0.912
\log_{10} rate alarm calling	-1.630	0.227	<0.001
Sex (M)	-0.683	0.254	0.007
Age	-0.016	0.057	0.780
Valley position (up)	-0.111	0.549	0.840
Predator index (low)	0.040	0.258	0.877
Random effects		Variance	
Marmot ID		0.245	
Year		0.117	
Colony		0.418	
Marginal R^2		0.189	
Conditional R^2		0.344	

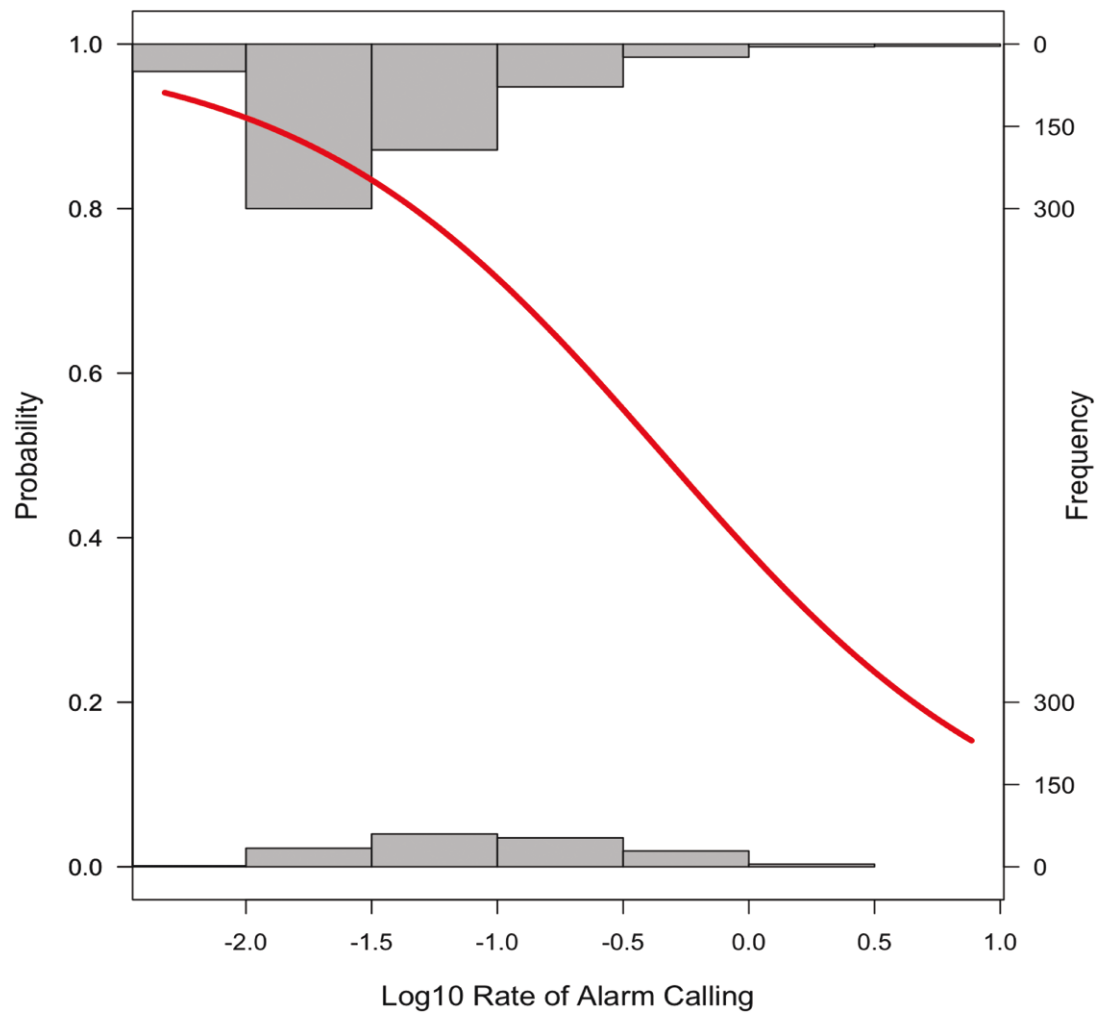


Figure 1. The relationship (thick red line) between \log_{10} rate of alarm calling (x-axis) and the probability of summer survival in yellow-bellied marmots (*Marmota flaviventris*) (left y-axis) with the frequency of callers (right y-axis) that survived (top) and died (bottom) illustrated with the histograms. The data consist of 328 individuals and 837 unique observations collected over 20 years.

This is because it is often difficult to detect predation in the field and attribute it to calling. Thus, rather than looking at the immediate consequence of producing alarm calls (we have not seen calling marmots subsequently killed), we asked whether variation in calling rate was associated with surviving the summer. Capitalizing on a long-term study, we found that marmots that called at higher rates were less likely to survive the summer and lived shorter lives. Because of our knowledge of sources of mortality in this well-studied system, we infer this was a function of predation. Thus, we infer that marmots who called more were more likely to be killed. Importantly, this finding emerged after controlling for relative predation pressure quantified annually at the colony level. Why should alarm calling be maintained if there is this increased mortality risk?

One solution to the problem of marmots paying a direct cost may be that calling may enhance indirect fitness. Indeed, because marmots live in female-dominated matrilineal groups comprised of relatives (Armitage 2014), calls warn related individuals and thus calls may be broadly described as being kin selected. Marmots who have relatives living within audible range inevitably gain indirect fitness by emitting alarm calls. Although prior work in our system suggested that calling is a form of maternal care where mothers warn vulnerable

offspring (Blumstein et al. 1997), this work which is based on a larger data set implies that it might be profitable to reexamine this conclusion with another two decades of data because our analysis shows that the more animals times adults (both males and females, reproductive or not) emit calls, the less likely they are to survive the summer and the less likely they are to live relatively long lives.

Prior work in our system has shown that individuals which are less socially connected with conspecifics are less secure (Mady and Blumstein 2017) and are also more likely to emit calls (Fuong et al. 2015). These findings are consistent with the idea that vulnerable animals rely more on their own actions to manage predation risk.

It is important to realize that alarm calls can be directed to both conspecifics and to predators (Blumstein 2007b), and calls directed to predators may discourage pursuit (Hasson 1991). Indeed, we routinely observe foxes and coyotes walking away once a marmot emits an alarm call. In rodents, the initial target of alarm calls seems to have been predators, not conspecifics. This is because although there was no association between the evolutionary origin of sociality and the evolutionary origin of emitting alarm calls, rodents that evolved to be active during the day (most rodents are nocturnal) were more likely to subsequently evolve alarm calling (Shelley and

Table 2. Results from the mixed effects Cox survival model explaining variation in adult yellow-bellied marmot (*Marmota flaviventris*) summer survival. Bolded results are considered statistically significant (P -value < 0.05). The model includes 275 individuals and a total of 837 unique observations that were collected over 20 years

	Variable	coef	exp(coef)	se(coef)	P -value
Fixed effects	\log_{10} rate AC	0.628	1.87	0.101	<0.001
	Sex (male)	0.413	1.51	0.138	0.003
	Valley position (up)	0.084	1.09	0.130	0.519
	Predation index (low)	0.040	1.04	0.131	0.758
Random effects	Variable	Variance	SD		
	Marmot ID	1.55×10^{-4}	0.012		
	Colony ID	1.30×10^{-5}	0.004		

Blumstein 2005). Once animals can properly assess risk by looking around during the day, they can produce calls only when it is safe to do so.

Thus, our findings are consistent with a somewhat ineffective predator-deterrent function of calling. From this perspective, our results suggest that on average, predator-directed calling may be costly because those who call more are more likely to be killed. We recognize that different predators may pose different risks and thus marmot vulnerability may vary with predator hunting style. Although marmots are safe from canids once they are in a burrow, badgers may dig animals out of their burrows. Raptors may strike and kill animals before they have even been detected. Future work with observations on the specific predator that elicited the calls may be required to understand the potential for calling to be costly for specific predators and such analyses may explain more variation in the rate of calling.

The present results permit us to conclude that, regardless of its target (conspecific or predator), emitting alarm calls has a direct cost. But how costly is calling? Our estimate of the cost of calling is relatively small; only about 12% of the variation

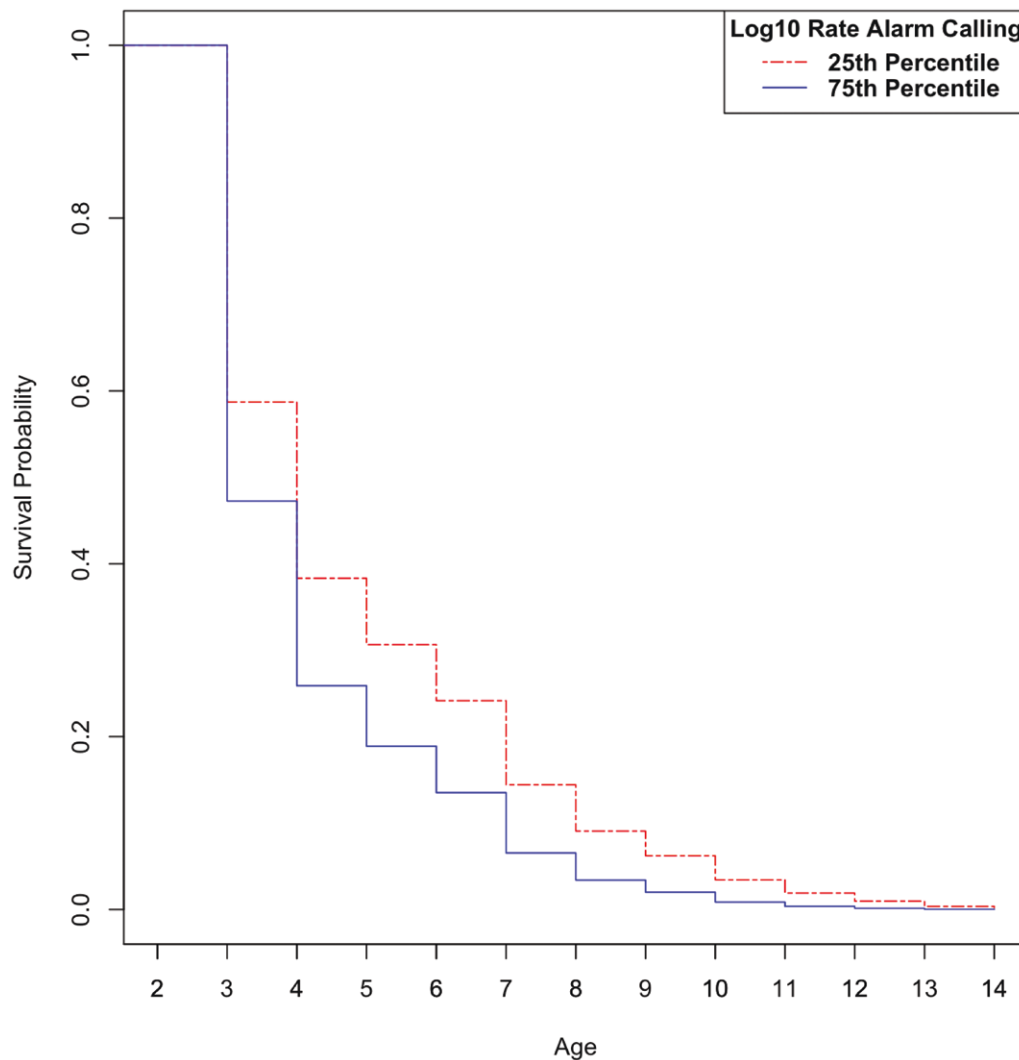


Figure 2 Survival probability of yellow-bellied marmots (*Marmota flaviventris*) based on the rate that they emitted alarm calls as an adult. We illustrate the 25th and 75th percentiles of \log_{10} rates of alarm calling. Results were based on 275 individuals collected over 20 years and were analyzed using a Cox proportional hazards model after removing individual as a random effect.

in survival for those animals we could identify calling was explained by calling rate. Despite over 24,000 h of observations, calling is rare and it was difficult to identify callers with certainty, in part because the modal number of alarm calls in a bout was one. Thus, we elected to analyze only those animals that were positively identified calling. Had we included all animals every year, whether observed calling or not, our zero inflated results would be misleading because some of these animals certainly called but we were unable to detect those calls. Because a substantial amount of the variation in summer survival is explained by other factors, these zero-inflated results would obscure any effect of calling on survival.

Can marmots compensate for these risks? Given that the modal number of alarm calls is one, that marmots do not engage in contagious calling, and that marmots mostly emit calls from the safety of their burrows (Collier et al. 2010), marmots seem to be doing the best they can to reduce the costs of calling. That they continue to call implies that they receive benefits from doing so but these benefits may vary based on the type of predator. For instance, it's possible that calling away from a burrow may be better strategy if calling has a deterrent function, whereas calls from a burrow may have a conspecific warning function. Future studies, with better resolved data on where animals were when they called, will be required to tease apart the conspecific warning versus pursuit deterrent functions of calling in marmots and other species.

More generally, quantifying the true costs of alarm calling are essential for models aiming to understand the evolution and maintenance of alarm calling (Bergstrom and Lachmann 2001), as well as for models of social behavior and organization (Maynard 1965). It is notable that long-term data from individually-marked animals (Clutton-Brock and Sheldon 2010) may be required to estimate predation risks of alarm calling. Such studies are relatively rare. Sherman's previous study analyzed a 9-year dataset (Sherman 1985) and included staged predator encounters. We analyzed a 20-year dataset of entirely natural encounters. Despite long-term data collection, at least one other notable multi-year study, did not reveal costs of alarm calling (Hoogland 1995). Animals seemingly reduce these costs whenever possible, but emitting alarm calls may nevertheless modestly increase mortality risk.

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Ethics Statement

Data were collected under the UCLA Institutional Animal Care and Use protocol (2001-191-01, renewed annually) and with permission from Colorado Parks and Wildlife (TR917, renewed annually).

Data Availability

Data and code are archived at OSF: <https://osf.io/7ytpn/>

Authors' Contributions

D.T.B. conceived idea, collected data, analyzed and interpreted data, and wrote the paper. K.A. collated data, analyzed data, and contributed to manuscript writing/editing. J.U. collated data and contributed to manuscript writing.

Conflict of Interest

The authors declare that they have no competing interests.

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