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Age and sex influence marmot antipredator behavior during periods of heightened risk

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Abstract Animals adjust their antipredator behavior according to environmental variation in risk, and to account for their ability to respond to threats. Intrinsic factors that influence an animal's ability to respond to predators (e.g., age, body condition) should explain variation in antipredator behavior. For example, a juvenile might allocate more time to vigilance than an adult because mortality as a result of predation is often high for this age class; however, the relationship between age/vulnerability and antipredator behavior is not always clear or as predicted. We explored the influence of intrinsic factors on yellow-bellied marmot (*Marmota flaviventris*) antipredator behavior using data pooled from 4 years of experiments. We hypothesized that inherently vulnerable animals (e.g., young, males, and individuals in poor condition) would exhibit more antipredator behavior prior to and immediately following conspecific alarm calls. As expected, males and yearlings suppressed foraging more than females and adults following alarm call playbacks. In contrast to predictions, animals in better condition respond more than animals in below average condition. Interestingly, these intrinsic properties did not influence baseline time budgets; animals of all ages, sexes, and condition levels devoted comparable amounts of time to foraging prior to alarm calls. Our results support the hypothesis that inherent differences in vulnerability influence antipredator behavior; furthermore, it appears that a crucial, but poorly acknowledged, interaction

exists between risk and state-dependence. Elevated risk may be required to reveal the workings of state-dependent behavior, and studies of antipredator behavior in a single context may draw incomplete conclusions about age- or sex-specific strategies.

Keywords State-dependence · Antipredator behavior · Vigilance · Alarm call

Much attention has been paid to environmental variables that influence antipredator vigilance. Factors such as time of year (Metcalfé and Furness 1984), distance to cover (Burger et al. 2000), group size (Beauchamp 2008), visibility (Bednekoff and Blumstein 2009), position within the group (di Blanco and Hirsch 2006), and temperature (Pravosudov and Grubb 1995) affect the amount of time an animal devotes to predator detection. Additionally, intrinsic attributes (e.g., stress levels (Mateo 2007), body size (Caro 2005), and body condition (Bachman 1993)) also explain variation in vigilance. Animals allocate their antipredator effort in accordance with the level of risk experienced (Lima and Bednekoff 1999), and vulnerability as a result of an individual's state or attributes (e.g., age, sex, or body condition) should therefore influence antipredator behavior.

Previous studies of age and sex differences in mammalian antipredator vigilance have reported conflicting results, even though predation is generally a major source of mortality for juveniles of most species within the taxon (e.g., Rongstad 1965; Ozgul et al. 2006; Borrego et al. 2008). In a recent review, Arenz and Leger (2000) found that juveniles were reported as the more vigilant age class in only two of 22 mammalian species. Juveniles were found to be *less* vigilant than adults in 11 species, and the authors concluded that young mammals typically devote less time to predator detection. Considering that increased predation risk typically

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results in increased vigilance (Elgar 1989), it is rather surprising that juveniles (who are often more vulnerable) tend to be less vigilant than adults.

One possible, and often overlooked, explanation is that age-specific strategies may be differentially expressed during periods of imminent danger. While past studies have considered the influence of age and sex on time allocated to vigilance, few have considered how these factors influence antipredator behavior during heightened periods of risk. Factors affecting an animals' general tradeoff between foraging and vigilance will most likely act in distinct, though not dissimilar, ways when individuals respond to an immediate indication of danger, such as hearing conspecific alarm calls. Arenz and Leger's (2000) review included 17 studies, only two of which examined how animals respond to an immediate indication of danger (alarm call or predator model). One of these studies (Loughry and McDonough 1989) found that age differences were more pronounced during non-calling or baseline periods than in the 5 min following a naturally occurring conspecific alarm call, while sex differences in behavior followed the opposite trend (i.e., males and females responded in significantly different ways immediately following alarm calls). The results of Loughry and McDonough (1989) emphasize the possibility that age and sex differences in anti-predator behavior may vary across risk levels. Certain insight into state-dependent antipredator response may only emerge during periods of heightened risk, and conclusions drawn from studies addressing baseline or heightened risk levels alone may misrepresent the relationship between vulnerability and antipredator behavior.

We focused on age, sex, and condition-dependent behavior in yellow-bellied marmots (*Marmota flaviventris*) prior to and immediately following conspecific alarm calls. We pooled data from alarm call studies conducted over a 4-year period (Blumstein and Daniel 2004; Blumstein et al. 2008a, b; Blumstein and Recapet 2009), to examine variables that may have small, but potentially significant, effects on antipredator response. These initial studies were not designed to specifically address state-dependence, but all studies used similar protocols and recordings as controls (see [Methods](#)). In other words, original studies used experimental (e.g., manipulated) vocalizations, but always included playbacks of unfamiliar adult females alarm calls (four calls per 2 s) as the control. Therefore, we were able to pool control playbacks from each study and create a data set that allowed us to examine previously unaddressed variables (see also Rainey et al. 2004).

Marmots are moderately social hibernating sciurid rodents that live in matrilineal groups composed of one or more breeding adult females and their offspring or close kin (Armitage 1991). Marmots are prey to numerous predators,

including coyotes (*Canis latrans*), American badgers (*Taxidea taxus*), American martens (*Martes americana*), black bears (*Ursus americanus*), and golden eagles (*Aquila chrysaetos*; Van Vuren 2001). Predator-related deaths are the main cause (98%) of mortality during the active season (Van Vuren 2001), and marmots therefore possess a collection of evolved antipredator behaviors.

For example, alarm vocalizations are given in response to predators and function to warn conspecifics of imminent danger (Klump and Shalter 1984; Blumstein 2007). Due to their acute predation pressure, we expect selection for effective alarm call responses in marmots, including behavioral strategies that are sensitive to age, sex, and body condition. Marmot survival rates vary by age (yearlings experience higher mortality than adults; Ozgul et al. 2006; Borrego et al. 2008) and sex (adult males experience higher mortality than adult females; Borrego et al. 2008), and we therefore predicted that marmot antipredator behavior would reflect this variation in survival. The age- and sex-specific mortality rates experienced by this species allowed us to test the hypothesis that selection favors increased antipredator behavior in inherently vulnerable animals. Furthermore, we wished to examine the interaction between such state-specific behavior and risk level, in an effort to understand why the relationship between vulnerability and antipredator behavior is often unclear.

Methods

General methods

All data were collected at the Rocky Mountain Biological Laboratory (RMBL) in Gunnison County, Colorado, USA. Marmots at RMBL are part of a long-term study (Armitage 1991), and individuals who remain at the study site are monitored from birth to death. Marmots are regularly trapped (following protocols in Armitage 1982), marked with non-toxic dye (Nyanzol-D, Albanil Dyestuff Corp., Jersey City, NJ, USA), and observed throughout the active season (mid-April to September). Marmots are observed from a distance (to minimize stress and avoid influencing behavior) and handled minimally during trapping procedures. Body mass is measured at each trap event (accurate to within 50 g) and fecal samples are collected non-invasively from identified animals throughout the season for glucocorticoid analyses.

Recordings and playbacks

Alarm calls were recorded from trapped individuals using Audix OM-3xb microphones (frequency response=40 Hz–20 kHz) placed 20–40 cm from calling marmots. Calls were

recorded onto digital audio tape decks (Sony PCM-M1 or Tascam DA-P1) at a sampling rate of 44.1 kHz and resolution of 16-bits. Yellow-bellied marmot alarm calls communicate degree of risk (Blumstein and Armitage 1997), and we therefore controlled for potential variation by using calls obtained in identical contexts (i.e., at trapping events). Furthermore, playback tracks were created using calls from a single age sex class (adult females) to control for additional variation; age and sex influence properties of the alarm vocalization (Blumstein and Munos 2005) and marmots may differentiate between calls from the various age sex classes and adjust their response accordingly (Blumstein and Daniel 2004).

Recorded calls were transferred to a Macintosh computer (Apple, Cupertino, CA, USA) and normalized to match peak amplitudes in SoundEdit 16 (Macromedia, San Francisco, CA, USA). Playback tracks were created to include 1 min of silence (for assessment of baseline behavior) followed by four alarm calls (from the same individual) broadcast over a 2-s period and 2 min of silence. Each experiment incorporated exemplars from at least four adult females (Blumstein and Daniel 2004, $N=4$; Blumstein et al. 2008a, $N=8$, b, $N=4$; Blumstein and Recapet 2009, $N=8$); each track included vocalizations from a single individual and multiple tracks were therefore used in each experiment to avoid the problem of pseudoreplication. Tracks were transferred to an iPod (Apple, Cupertino, CA, USA) and broadcast through a playback speaker (Advent AV570; frequency response=40 Hz–20 kHz). Playback tracks were calibrated to 95–100 dB SPL as measured by a digital sound level meter (SPER Scientific 840029) 1 m from the speaker. Detailed descriptions of recording and editing procedures are discussed elsewhere (Blumstein and Daniel 2004; Blumstein and Recapet 2009).

All playbacks were conducted in the morning during peak hours of marmot activity (06:30–10:30). We used bait (Omlene 300 horse feed, Ralston Purina Inc, ST. Louis, MO, USA) to entice marmots from their burrows. We began the playback track when a marmot emerged from its burrow and began feeding 8–12 m from the speaker. Calls from unfamiliar (i.e., acoustically isolated) adult females were broadcast to each subject to control for response variation due to identity or age sex class. Playbacks were video recorded (Canon G1-1 mini-DV digital video recorder) by observers at a distance that did not obviously affect the animals' behavior (range, 20–120 m depending on habitat features). Additional variables such as the number of conspecifics within 50 m, the presence of pups (i.e., had pups emerged at this site by the playback date?), and days since 1 January were also recorded. Furthermore, we noted the identities of nearby individuals and tallied the number of previous playbacks each individual heard that year. This

allowed us to explore the effects of conspecific presence, season, and possible habituation in later analyses.

All playbacks were scored in JWatcher 1.0 (Blumstein and Daniel 2007) with the following ethogram: vigilance (looking in a quadrupedal, bipedal, or lying position), hiding (time spent in burrow), locomotion, foraging, self-grooming, social interactions, and out of sight. We calculated the proportion of time in sight devoted to each behavior in the 60 s prior to and 15 s immediately following alarm call playbacks, with all proportions arcsine square root transformed for analysis. We focused on time allocated to foraging as our dependent measure; marmots typically tradeoff between foraging and vigilance within a foraging bout, and this measure therefore captures information about perceived risk. For all described analyses, we explored time allocated to vigilance as an additional dependent variable, and while results were similar, time allocated to foraging was the more sensitive measure. This finding is consistent with previous studies of antipredator response in yellow-bellied marmots (Blumstein and Daniel 2004; Blumstein et al. 2004; Blumstein et al. 2008a).

Measuring glucocorticoid concentration

We collected fecal samples throughout the active season at regular trapping events because stress profiles may reflect variation in seasonal, social, or reproductive pressures. For analysis, we selected the fecal glucocorticoid metabolite concentration measured closest to the playback date. Samples were never collected on the same day an alarm call playback was conducted, and our data set contains a range of days between collection/trapping events and playbacks (range –64 to 58 days, $X \pm SD = -1.20 \pm 19.49$). This measure was therefore representative of an individual's baseline or inherent stress level and was not meant to capture any immediate endocrine response to playback. Collection dates (in relation to playbacks) were similar among age (t test, $t=0.397$, $P=0.475$, $N=71$) and sex (t test, $t=0.561$, $P=0.686$, $N=71$) classes, as well as between the four age sex classes (ANOVA, $F=2.223$, $P=0.192$, $N=71$).

Fecal samples were immediately placed on ice and stored at -20°C within 2 h of collection. We used a double-antibody I radioimmunoassay kit (MP Biomedicals, Costa Mesa, CA) to measure fecal glucocorticoid metabolites (for further details of sample preparation and assay procedures see Blumstein et al. 2006). This assay detects mammalian corticosterone and cortisol (Wasser et al. 2000), two hormones secreted by the adrenal cortex in response to stress. Glucocorticoid concentrations reflect physical and psychosocial arousal and anxiety (Reeder and Kramer 2005) and have been shown to potentiate alarm calling in adult female marmots (Blumstein et al. 2006).

Statistical analyses

In total, 92 playbacks (41 in 2004, 29 in 2005, and 22 in 2007) were broadcast to 53 adult and 39 yearling marmots. Our data set included 61 unique individuals (37 females, 24 males), with some individuals observed across multiple years and age classes. These data were used to examine the effects of age class, sex, and body condition on antipredator behavior during periods of baseline (prior to playback) and heightened risk (immediately following playback). Body condition was calculated as the standardized residual from a univariate general linear model. This model included every recorded weight (obtained at trap events) for all adults and yearlings during the study period (2003–2007, $N=2601$ trap events). Variation in body mass was explained by age and a covariate of days since 1 January. We then identified the mass recording for each subject that was closest to the playback date and used the residual from this data point as an index of body condition.

We tested for effects of age class, sex, and body condition on baseline foraging behavior (i.e., 60 s prior to alarm call playback) by fitting a linear mixed effects model with maximum likelihood estimation (West et al. 2006) and individual identity specified as the repeated subject measure. We found that marmots did not significantly differ in the proportion of time spent foraging during the baseline period (age class type III $F=1.472$, $P=0.226$; sex type III $F=0.000$, $P=0.995$; body condition type III $F=0.000$, $P=0.989$) and therefore focused our analyses on foraging behavior in the 15 s immediately following the playback to understand variation in immediate response to alarm call playbacks.

Further analyses considered the influence of the age, sex, and body condition, as well as the number of conspecifics within 50 m, the presence of pups, a binomial variable indicating whether or not the individual reproduced, glucocorticoid concentration, the number of previous playbacks heard, year, and days since 1 January. Playbacks were conducted on a range of dates (days since 1 January ($X\pm SD$) for 2004 playbacks, 163.488 ± 18.373 ; 2005, 191.103 ± 7.943 ; 2007, 177.682 ± 11.000) but were all completed at least 2 months prior to hibernation (latest playback date=14 July). Animals therefore experienced similar pressures in terms of approaching hibernation and foraging/mass gain demands. Glucocorticoid metabolite concentration was log-10 transformed, and the number of previous playbacks heard was log-10 ($x+1$) transformed to homogenize variances and better approximate normal distributions.

We fitted a linear mixed effects model to explain variation in time allocated to foraging immediately following a conspecific alarm call playback. We began with a global model including all available explanatory variables

(see above list). We then systematically excluded non-significant variables ($P>0.05$) from the global model until the Akaike Information Criterion (AIC) and second-order Akaike Information Criterion (appropriate for small sample sizes, AIC_c) were optimized (Burnham and Anderson 2002). We computed the delta AIC_c for all models as the difference between each model and the model with the lowest AIC_c . We ultimately selected the model with the lowest AIC_c , but models that differ by <2 (i.e., delta $AIC_c<2$) still have some support (Burnham and Anderson 2002). All candidate models are presented in Table 1.

We used several techniques to understand the relative influence of each fixed effect on alarm call response. First, we regressed the model fitted predicted values against our observed data and repeated this procedure after removing each fixed effect from the model. We also computed the Akaike weights for all models, which indicate the probability that a given model is the best among the candidate models. For models excluding a given variable, a low weight therefore indicates the excluded variable is of high importance (i.e., a model without that variable is highly unlikely; Burnham and Anderson 2002). Finally, we used pair-wise comparisons (post hoc Tukey's HSD test) of estimated marginal means to compare age classes and sexes between and within levels; this analysis allowed us to test for significant differences between age sex classes and further understand the interaction between these variables. All analyses were performed in SPSS 18.0 (SPSS Inc. 2009, Chicago, IL, USA).

Results

Age class, sex, age class*sex, pup presence, body condition ($X\pm SD=0.595\pm 1.011$, $N=91$), and number of previous playbacks heard ($X\pm SD=0.461\pm 0.294$, $N=91$) significantly explained variation in time allocated to foraging following playbacks (Table 2). The effect of glucocorticoid concentration ($X\pm SD=2.053$ ng/g ± 0.197 , $N=71$) was not significant, but models without this variable produced higher (difference >6) AIC_c s. Many factors may influence glucocorticoid levels on a given day, and this variability may account for insignificant results regarding this measure. Though the influence of glucocorticoid concentration on model fit is small (Table 3) and the effect of the variable is not significant, we wished to remain true to our data and a priori model selection procedures (i.e., retention of variables that produced models with the lowest AIC_c s); we therefore included this variable in the final model, though we acknowledge its limitations.

Individuals in poorer body condition foraged more than individuals in better body condition following alarm call playbacks. A slight habituation effect was observed;

Table 1 Akaike Information Criterion (AIC), second-order Akaike Information Criterion (AIC_c), and number of parameters (including the model intercept, K) for each candidate model

Fixed effects	K	AIC	AIC _c	Delta AIC _c
Null model		82.792	82.815	36.383
Best model–pup presence	6	64.328	64.828	18.396
Best model–sex	6	53.478	53.978	7.546
Best model–age class	6	52.305	52.805	6.373
Best model–glucocorticoid concentration	6	52.211	52.711	6.279
Best model–number of previous playbacks heard	6	50.577	51.077	4.645
Best model–body condition	6	49.742	50.242	3.810
Best model	7	45.837	46.432	0.000
Best model+days since 1 January	8	47.218	47.912	1.481
Best model+number of conspecifics within 50 m	8	47.205	47.890	1.468
Best model+reproduction	8	46.746	47.440	1.009
Best model+year	8	48.677	49.371	2.940
Best model+year+days since 1 January	9	50.428	51.228	4.796
Best model+year+reproduction	9	50.644	51.444	5.012
Best model+year+number of conspecifics within 50 m	9	50.625	51.425	4.993
Best model+reproduction+number of conspecifics within 50 m	9	48.746	49.546	3.114
Best model+reproduction+days since 1 January	9	48.726	49.526	3.094
Best model+number of conspecifics within 50 m+days since 1 January	9	49.180	49.98	3.548
Best model+year+days since 1 January+reproduction	10	52.379	53.291	6.859
Best model+year+number of conspecifics within 50 m+reproduction	10	52.597	53.509	7.077
Best model+year+number of conspecifics within 50 m+days since 1 January	10	52.421	53.332	6.901
Best model+number of conspecifics within 50 m+days since 1 January+reproduction	10	50.718	51.623	5.198
Best model+year+number of conspecifics within 50 m+days since 1 January+reproduction	11	54.375	55.4053	8.974

The null model included only the individual random factor without the addition of fixed effects. The best model (providing the lowest AIC and AIC_c) included fixed effects of age class, sex, pup presence, glucocorticoid concentration, number of previous playbacks heard, and body condition. Delta AIC_c was calculated as the difference between a given model and the best model

marmots exposed to higher numbers of previous playbacks foraged more than those individuals less familiar with alarm call playbacks. Marmots responded more (i.e., foraged less) to playbacks before pups emerged. Condition and the number of previous playbacks heard influenced overall model fit the least, while pup presence appears to be the most influential fixed effect (Table 3).

Male marmots responded more to alarm call playbacks than female marmots (mean difference±SE=0.224±0.073,

$P=0.005$), and yearlings responded more than adults (mean difference±SE=0.300±0.066, $P<0.001$). Among males, yearlings responded more than adults (mean difference±SE=0.508±0.112, $P<0.001$, Fig. 1); however, among females, yearlings and adults did not differ significantly in their responses (mean difference±SE=0.093±0.071, $P=0.202$, Fig. 1). Within age classes, yearling males responded significantly more than females (mean difference±SE=0.431±0.101, $P<0.001$, Fig. 1), but adult males

Table 2 Summary of fixed effects (in a linear mixed effects model) that explained variation in proportion of time allocated to foraging following playbacks

Fixed effect	Coefficient	SE	Type III <i>F</i>	<i>P</i>
Age class	0.093	0.071	20.744	<0.001
Sex	−0.017	0.097	9.367	0.004
Age class*sex	−0.415	0.133	9.691	0.004
Pup presence	−0.341	0.061	31.327	<0.001
Glucocorticoid concentration	−0.041	0.174	0.054	0.817
Body condition	−0.075	0.026	8.135	0.009
Previous playbacks heard	0.306	0.100	10.073	0.004
Intercept	0.613	0.363	0.667	0.418

Table 3 Equations and variation explained (R^2) by regressing model predicted values vs. observed values

Model description	Linear regression summary	Akaike weights
Best model		
Age class, sex, age class*sex, pup presence, glucocorticoid concentration, body condition, previous playbacks heard	$y = 0.809x + 0.089$ $R^2=0.318$	0.739
MODEL excluding age class and age class*sex	$y = 0.777x + 0.130$ $R^2=0.252$	0.030
MODEL excluding sex and age class*sex	$y = 0.777x + 0.118$ $R^2=0.247$	0.017
MODEL excluding pup presence	$y = 0.794x + 0.031$ $R^2=0.202$	0.000
MODEL excluding glucocorticoid concentration	$y = 0.863x + 0.080$ $R^2=0.269$	0.032
MODEL excluding body condition	$y = 0.855x + 0.073$ $R^2=0.307$	0.110
MODEL excluding previous playbacks heard	$y = 0.846x + 0.070$ $R^2=0.299$	0.072

Each fixed effect (along with related interactions) was systematically excluded from the best model and only one effect was removed at a time. Akaike weights are provided for each model

did not significantly differ from adult females (mean difference \pm SE=0.017 \pm 0.097, $P=0.864$, Fig. 1).

Discussion

As predicted, age and sex influenced how yellow-bellied marmots responded to alarm calls. In general, males responded more than females and yearlings responded more than adults. Previous studies of marmot antipredator behavior have not reported significant effects of age or sex on time allocated to foraging following alarm calls (Blumstein et al. 2008a, b; Blumstein and Recapet 2009; a small effect was detected in Blumstein and Daniel 2004). However, by pooling results from previous experiments, we

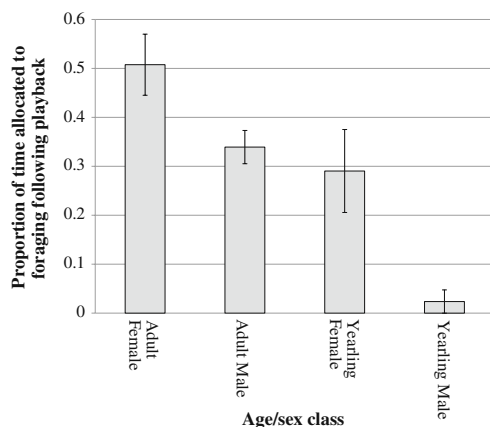


Fig. 1 Proportion of time allocated to foraging (angularly transformed) following playbacks. Means for each age/sex class are presented with standard error bars

were able to detect additional patterns and sources of variation.

Our results are consistent with the hypothesis that variation in risk drives the evolution of age- and sex-specific responses to predator warnings. Yearlings and males are more vulnerable than adults and females, and age- and sex-specific responses appear to reflect differential survival rates. It is interesting to note that our study, as well as previous studies (Blumstein et al. 2004) of the foraging vs. vigilance tradeoff in marmots, found no effect of age or sex on *baseline* foraging behavior. However, Bednekoff and Blumstein (2009) found that marmots of various age and sex classes differed in their responses to experimental manipulations of peripheral vision. In this experiment, adults and males responded more (than juveniles and females) to lateral obstructions by increasing their vigilance when the obstruction was no longer present; the authors suggest that the nutritional demands of juveniles and a male's need to monitor potentially rival conspecifics may explain differences among age/sex classes. Age and sex appear to influence antipredator behavior more acutely during periods of heightened, or experimentally manipulated, risk. We would expect stronger selection for appropriate antipredator decisions in high-risk situations, and it is therefore not surprising that age- and sex-specific differences are more pronounced following conspecific alarm calls. This interaction between risk and state-dependence is not generally acknowledged, yet it may be crucial to our understanding of age- and sex-specific behavioral strategies.

Though Arenz and Leger (2000) concluded that juvenile mammals are typically *less* vigilant than adults, a recent

meta-analysis (Lea and Blumstein, in review) found that, on average, young are more responsive to alarm calls than adults (Hedge's $d \pm SE = 0.328 \pm 0.120$, $N = 33$ experiments; d indicates the magnitude of difference in alarm call response between age classes), and males are more responsive to alarm calls than females (Hedge's $d \pm SE = 0.164 \pm 0.083$, $N = 17$). Clearly, risk levels influence our conclusions about age differences in antipredator behavior across species, and more attention should be paid to this idea during discussions of state-dependence and age-specific behavioral strategies. It may be that differential mortality rates (as a result of predation) encourage selection for increased vigilance in more vulnerable animals (e.g., males or juveniles) during periods of heightened predation risk. However, other pressures (e.g., increased nutritional need among juveniles; Arenz and Leger 2000) may govern the vigilance vs. foraging tradeoff in low-risk environments.

Trends reported from the meta-analysis are based on a weighted average of effect sizes reported across mammalian studies, and we must note that some studies report opposing trends. For example, Swan and Hare (2008) found that adult Richardson's ground squirrels (*Spermophilus richardsonii*) were more vigilant than juveniles prior to alarm calls; however, both age classes responded similarly to playbacks. Experimental or environmental factors, as well as population-specific predation rates, may influence age- or sex-specific responses to alarm calls. Furthermore, young of quickly maturing mammalian species generally display more adult-like antipredator behavior than young of slowly maturing species following alarm calls (for species reaching sexual maturity at one year of age: Hedge's $d \pm SE = -0.032 \pm 0.150$; ages 1–3 years, -0.923 ± 0.209 ; age >3 years, -0.592 ± 0.203 ; Lea and Blumstein, in review). In species that reach sexual maturity or disperse after their first year of life (e.g., Belding's ground squirrel (*Spermophilus beldingi*), California ground squirrel (*Spermophilus beecheyi*), meerkat (*Suricata suricatta*)), juveniles are expected to cope independently with predation risks at a young age, and adult-like responses may be expected early in life. Conversely, young of slowly maturing species (e.g., Bonnet macaque (*Macaca radiata*), Vervet monkey (*Cercopithecus aethiops*)) may develop behavior during their extended ontogenetic period, or, they may experience different age-specific selection pressures resulting in dissimilar age-specific strategies. Our discussion of the interaction between risk and sex- or age-related differences in responsiveness are meant to broaden current views on antipredator behavior, not to discount the influence of additional extrinsic and intrinsic factors.

In addition to the effects of age and sex, we found that body condition influences how an individual responds to alarm calls. Marmot baseline foraging behavior is not condition-dependent, but body condition has a moderate effect (Table 3) on antipredator behavior in high-risk

contexts. Though we expected more vulnerable animals to display heightened antipredator responses, individuals in better body condition suppressed foraging more than individuals in poorer body condition. Previous studies of Arabian babblers (*Turdoides squamiceps*, Wright et al. 2001) and meerkats (*S. suricatta*, Clutton-Brock et al. 1999) have reported similar effects of superior condition (as a result of food-supplementation) on sentinel behavior during non-calling periods, and these authors suggest that, when animals are satiated or have adequate energy reserves, it is in their best interest to devote more time to predator detection (Wright et al. 2001). However, this explanation was proposed for cooperative sentinel species (where some gain is associated with performance of this social duty) and does not account for the counterintuitive relationship between vulnerability and antipredator behavior observed in marmots.

Condition-dependent alarm call responses have also been reported in Belding's ground squirrels (*S. beldingi*) with individuals decreasing their responsiveness to alarm calls following supplementation and weight gain (Bachman 1993). While we may expect hibernating animals in sub-optimal body condition to devote ample time to foraging, these animals are not in immediate danger of starvation. Animals that fail to gain sufficient mass during the active season may perish overwinter (Murie and Boag 1984), but those that ignore current predation threats are in imminent danger. We generally assume that animals should respond to immediate more than future risk (Lima and Dill 1990); yet, sciurid behavior appears to follow the opposite trend. The positive relationship we observed between responsiveness and body condition suggests that animals in superior condition can afford to allocate time to antipredator behavior, while those in poor condition may continue foraging to increase their overwinter survival probability. Hibernating sciurids may therefore evaluate risk on a long-term time scale, adjusting their behavior according to the probability of surviving hibernation (Bachman 1993).

The presence of pups had a profound effect on how individuals responded to alarm calls (Table 2), with marmots (of all age and sex classes) responding more to alarm calls prior to pup emergence. Mothers with juveniles are often more alert than non-reproductive females (during non-calling periods; Burger and Gochfield 1994; Hunter and Skinner 1998), presumably because naïve juveniles are highly vulnerable to predators. We observed the opposite trend in yellow-bellied marmots, and our results are more consistent with those reported for adult California ground squirrels (*S. beecheyi*). Loughry and McDonough (1989) observed a decrease in adult alarm call response following pup emergence, with seasonal differences possibly due to habituation. Calling (total number of call bouts recorded at the study site) is more frequent following pup emergence, and adults may decrease their responsiveness accordingly

(Loughry and McDonough 1989). Furthermore, as the season progresses and hibernation approaches, animals may experience heightened nutritional demands and devote more time to foraging.

We detected some relationship between the number of previous playbacks an animal heard and its antipredator response. Marmots appear to habituate to alarm call playbacks, though the overall effect is small (Table 3). Such habituation may be considered as an adaptive form of learning, where animals decrease their responsiveness after a stimulus is repeatedly presented without reinforcement (Zucchi and Bergmann 1975). Antipredator behavior is costly in that time and energy devoted to vigilance will be unavailable for other activities (e.g., foraging, social behavior, and mating); therefore, animals should assess the level of risk posed by a particular situation and quickly learn to decrease their response to unthreatening stimuli.

While body condition, age, and sex do not influence general time budgets in yellow-bellied marmots, these factors explain some variation in alarm call response. Our results emphasize the importance of distinguishing between periods of baseline and heightened risk, as the relationship between inherent vulnerability (as a result of age, sex, or condition) and antipredator behavior may vary across contexts. Animals should vary their antipredator behavior according to the level of risk experienced, and many studies have found this to be true (reviewed in Lima and Dill 1990). However, we must also acknowledge that intrinsic and environmental factors will interact, and animals may only exhibit certain state-dependent behaviors in high-risk contexts.

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References

- Arenz CL, Leger DW (2000) Antipredator vigilance of juvenile and adult thirteen-lined ground squirrels and the role of nutritional need. *Anim Behav* 59:535–541
- Armitage KB (1982) Yellow-bellied marmot. In: Davies DE (ed) CRC handbook of census methods for terrestrial. CRC Press, Inc, Boca Raton, pp 148–149
- Armitage KB (1991) Social and population dynamics of yellow-bellied marmots: results from long-term research. *Ann Rev Ecol Evol Syst* 22:379–407
- Bachman GC (1993) The effect of body condition on the trade-off between vigilance and foraging in Belding's ground squirrels. *Anim Behav* 46:233–244
- Beauchamp G (2008) What is the magnitude of the group size effect on vigilance? *Behav Ecol* 19:1361–1368
- Bednekoff PA, Blumstein DT (2009) Peripheral visibility influences marmot vigilance. *Behav Ecol* 20:1111–1117
- Blumstein DT (2007) The evolution, function, and meaning of marmot alarm communication. *Adv Stud Behav* 37:371–401
- Blumstein DT, Armitage KB (1997) Alarm calling in yellow-bellied marmots: I. The meaning of situationally-specific calls. *Anim Behav* 53:143–171
- Blumstein DT, Daniel JC (2004) Yellow-bellied marmots discriminate between the alarm calls of individuals and are more responsive to the calls from juveniles. *Anim Behav* 68:1257–1265
- Blumstein DT, Daniel JC (2007) Quantifying behavior the JWatcher Way. Sinauer, Sunderland
- Blumstein DT, Munos O (2005) Individual and age/sex class variation in marmot alarm calls. *Anim Behav* 69:353–361
- Blumstein DT, Recapet C (2009) The sound of arousal: the addition of novel non-linearities increases responsiveness in marmot alarm calls. *Ethology* 115:1074–1081
- Blumstein DT, Runyan A, Seymour M, Nicodemus A, Ozgul A, Ransler F, Im S, Stark T, Zugmeyer C, Daniel JC (2004) Locomotor ability and wariness in yellow-bellied marmots. *Ethology* 110:615–634
- Blumstein DT, Patton ML, Saltzman W (2006) Faecal glucocorticoid metabolites and alarm calling in free-living yellow-bellied marmots. *Biol Lett* 2:29–32
- Blumstein DT, Cooley L, Winternitz J, Daniel JC (2008a) Do yellow-bellied marmots respond to predator vocalizations? *Behav Ecol Sociobiol* 62:457–468
- Blumstein DT, Richardson DT, Cooley L, Winternitz J, Daniel JC (2008b) The structure, meaning and function of yellow-bellied marmot pup screams. *Anim Behav* 76:1055–1064
- Borrego N, Ozgul A, Armitage KB, Blumstein DT, Oli MK (2008) Spatiotemporal variation in survival of male yellow-bellied marmots. *J Mammal* 89:365–373
- Burger J, Gochfeld M (1994) Vigilance in African mammals: differences among mothers, other females and males. *Behaviour* 131:153–164
- Burger J, Safina C, Gochfeld M (2000) Factors affecting vigilance in springbok: importance of vegetative cover, location in herd, and herd size. *Acta Ethol* 2:97–104
- Burnham KP, Anderson DR (2002) Model selection and inference: a practical information-theoretic approach. Springer, New York
- Caro T (2005) Antipredator defenses in birds and mammals. University of Chicago Press, Chicago
- Clutton-Brock T, O'Riain MJ, Brotherton PNM, Gaynor D, Kansky R, Griffin AS, Manser MB (1999) Selfish sentinels in cooperative mammals. *Science* 284:1640–1644
- di Blanco Y, Hirsch BT (2006) Determinants of vigilance behavior in the ring-tailed coati (*Nasua nasua*): the importance of within-group spatial position. *Behav Ecol Sociobiol* 61:173–182
- Elgar MA (1989) Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol Rev Camb Philos Soc* 64:13–33
- Hunter LTB, Skinner JD (1998) Vigilance behaviour in African ungulates: the role of predation pressure. *Behaviour* 135:195–211

- Klump GM, Shalter MD (1984) Acoustic behavior of birds and mammals in the predator context. II: The functional significance and evolution of alarm signals. *Z Tierpsychol* 66:189–226
- Lima SL, Bednekoff PA (1999) Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *Am Nat* 153:649–659
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640
- Loughry WJ, McDonough CM (1989) Calling and vigilance in California ground squirrels: age, sex, and seasonal differences in responses to calls. *Am Midl Nat* 121:312–321
- Mateo JM (2007) Ecological and hormonal correlates of antipredator behavior in adult Belding's ground squirrels (*Spermophilus beldingi*). *Behav Ecol Sociobiol* 62:37–49
- Metcalfe NB, Furness RW (1984) Changing priorities: the effect of pre-migratory fattening on the trade-off between foraging and vigilance. *Behav Ecol* 15:203–206
- Murie JO, Boag DA (1984) The relationship of body weight to overwinter survival in Columbian ground squirrels. *J Mammal* 65:699–690
- Ozgul A, Armitage KB, Blumstein DT, Oli MK (2006) Spatiotemporal variation in age-specific survival rates: implications for population dynamics in yellow-bellied marmots. *Ecology* 87:1027–1037
- Pravosudov VV, Grubb TC (1995) Vigilance in the tufted titmouse varies independently with air temperature and conspecific group size. *Condor* 97:1064–1067
- Rainey HJ, Zuberbuhler K, Slater JB (2004) The responses of black-casqued hornbills to predator vocalizations and primate alarm calls. *Behaviour* 141:1263–1277
- Reeder DM, Kramer KM (2005) Stress in free-ranging mammals: integrating physiology, ecology, and natural history. *J Mammal* 86:225–235
- Rongstad OJ (1965) A life history study of the thirteen-lined ground squirrels in southern Wisconsin. *J Mammal* 46:76–87
- Swan DC, Hare JF (2008) Signaler and receiver ages do not affect responses to Richardson's ground squirrel alarm calls. *J Mammal* 89:889–894
- Van Vuren D (2001) Predation on yellow-bellied marmots (*Marmota flaviventris*). *Am Midl Nat* 145:94–100
- Wasser SK, Hunt KE, Brown JL, Cooper K, Crockett CM, Bechert U, Millsaugh JJ, Larson S, Monfort SL (2000) A generalized fecal glucocorticoid assay for use in a diverse array of nondomestic mammalian and avian species. *Gen Comp Endocrinol* 120:260–275
- West B, Welch KB, Galecki AT (2006) Linear mixed models: a practical guide using statistical software. Chapman and Hall/CRC Press, Inc, Boca Raton
- Wright J, Berg E, de Kort SR, Khazin V, Maklakov AA (2001) Cooperative sentinel behaviour in the Arabian babbler. *Anim Behav* 62:973–979
- Zucchi H, Bergmann HH (1975) Long-term habituation to species-specific alarm calls in a songbird (*Fringilla coelebs*). *Cell Mol Life Sci* 31:817–818