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ORIGINAL ARTICLE

Assessing the sensitivity of foraging and vigilance to internal state and environmental variables in yellow-bellied marmots *(Marmota flaviventris)*

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Abstract
Both internal and environmental factors influence the trade-offs animals make between foraging and antipredator vigilance. However, few studies examine both internal and environmental factors simultaneously, preventing us from drawing inferences about their relative importance during foraging. We capitalized on a long-term study of yellow-bellied marmots (*Marmota flaviventris)* to compare the relative importance of internal state-based factors versus external environmental factors in explaining variation in marmot foraging and vigilance behavior. Results indicate that while internal factors such as baseline fecal glucocorticoid metabolites, parasite infection, and body condition influence the time allocated to both foraging and vigilance, environmental factors such as group size and habitat characteristics only explain variation in the time allocated to vigilance. Thus, our findings reveal not only the importance of considering effects of both internal and environmental factors in explaining behavioral trade-offs but also the value in evaluating the subtle ways in which factors explaining vigilance and foraging differ.

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Significance statement
Studies on foraging and vigilance typically focus either on internal or environmental factors that influence behavior. This paper makes contributions to the field by integrating both internal factors, such as parasite infection, body condition, and fecal glucocorticoid hormone levels, and external factors, such as group size and habitat characteristics, in evaluation of behavioral trade-offs. We find that foraging and vigilance are affected differently by internal and external factors. This highlights the fact that even though foraging and vigilance are closely related, they are unique behaviors and there are opportunities in understanding how the factors that influence them differ.

Keywords Foraging · Vigilance · Environmental drivers · Parasites · Glucocorticoids

Introduction

Predation is a major evolutionary force, and animals may be especially vulnerable to predation while foraging (Stephens et al. 2007). In response to this risk, animals can make a variety of behavioral adjustments including modulating what to eat, when to eat, and how quickly to resume foraging after a disturbance (Lima and Dill 1990) as well as allocating time to antipredator vigilance (Lima 1995; Beauchamp 2015). Vigilance, however, comes with a cost. Many vigilance behaviors are partially or completely incompatible with foraging. Therefore, the decision to forage or exhibit vigilance is often viewed as a trade-off between the dangers of energetic shortfall and predation (Lima et al. 1985), although recent theoretical work on herbivore-plant interactions suggests that the costs and benefits created by food quality (e.g., plant toxins) and food quantity should be integrated into this conceptual framework as well

(McArthur et al. 2014). These risks, created by energetic shortfall and predation, fluctuate according to a diverse array of internal and environmental factors, suggesting that time allocated to vigilance and foraging should vary accordingly.

Many environmental correlates of antipredator vigilance have been identified. For instance, peripheral visibility (Bednekoff and Blumstein 2009), group size (Holmes 1984; Carey and Moore 1986; Elgar 1989), distance to cover (Stankowich and Blumstein 2005), incline (Blumstein and Daniel 2004), and vegetation height (Carey and Moore 1986) have been shown to influence vigilance while foraging in a variety of mammals. By contrast, the effect of internal state on antipredator behavior is less well understood. Many studies on state-dependence and behavioral trade-offs while foraging have focused on how individual quality affects foraging site selection and giving up density of specific food resources. Studies looking at how internal state affects simple time allocation trade-offs between vigilance and foraging have focused on age and sex (Arenz and Leger 2000; Lea and Blumstein 2011b), body condition (Bachman 1993), stress levels (Mateo 2007), and illness (Lindstrom et al. 2003), with a few recent studies examining personality differences in risk taking while foraging (Dammhahn and Almeling 2012). While behavioral differences across age-sex classes have been well studied (Lea and Blumstein 2011b), investigations of illness or parasite infection on antipredator behavior are less common (Hedrick and Kortet 2006; Kortet et al. 2007).

Illness or parasite infection might affect foraging behavior and antipredator vigilance in two opposing ways. First, the energetic load caused by parasite infection might increase the risk of energetic shortfall causing an individual to spend more time foraging and less time on antipredator vigilance. A few studies suggest that when internal state is improved by food supplementation (Bachman 1993), individuals increase vigilance. This suggests that energy levels must achieve a minimum threshold for an animal to compromise foraging opportunities and exhibit vigilance (Beale and Monaghan 2004). However, if substandard individuals are more vulnerable to predators (Temple 1987; Genovart et al. 2010), they may instead allocate more time to antipredator vigilance (Lindstrom et al. 2003; Martin et al. 2006).

Yellow-bellied marmots (*Marmota flaviventris*) are large hibernating sciurid rodents found in western North America (Armitage 1991). Ninety-eight percent of marmot deaths during the active season can be attributed to predation (Van Vuren 2001). Marmots fall victim to a diverse array of predators including coyotes (*Canis latrans*), badgers (*Taxidea taxus*), American martens (*Martes americana*) and golden eagles (*Aquila chrysaetos*) (Van Vuren 2001). Additionally, marmots exhibit several antipredator behaviors including antipredator vigilance and alarm calling, which makes them an appropriate system in which to test hypotheses about individual decisions to exhibit foraging and antipredator vigilance. While a number of studies on marmot foraging and vigilance have been conducted, most have focused on the importance of environmental factors in shaping behavior (Blumstein et al. 2004a; Bednekoff and Blumstein 2009). Internal factors that have been examined to date include age-sex classes, body condition (Lea and Blumstein 2011a), and variation in running speed (Blumstein et al. 2004a; Blumstein et al. 2010).

The current study sought to simultaneously examine the effects of internal and environmental factors on foraging and vigilance. This extends previous work (Lea and Blumstein 2011a) by examining baseline foraging decisions at periods of low predation risk and by focusing on new internal state variables (parasite infection and fecal glucocorticoid metabolites) in addition to measures such as age and sex. Recent studies demonstrate that yellow-bellied marmots are infected by a variety of parasites (Lopez et al. 2013) including *Typanosoma lewisi* (a blood parasite transmitted by fleas and lice) and *Ascaris* spp. (an intestinal nematode). In addition to the direct effects of parasite infection on animal health, parasite infection may have secondary effects by affecting predation risk and antipredator vigilance (Crane et al. 2011). Glucocorticoids, which could fluctuate in response to parasite infection, as well as numerous other factors reflecting an individual's energetic balance, are known to promote foraging behavior (Landys et al. 2006). Additionally, one study found an association between antipredator alarm calling and fecal glucocorticoid levels in marmots (Blumstein et al. 2006).

We test the expectation that both internal state and the external environmental simultaneously influence the amount of time that marmots allocate to vigilance during foraging bouts. For the purposes of this analysis, internal factors are defined as properties of an organism's status (e.g., disease status, age, and sex) that influence metabolic demands of the organism. External factors are defined as biotic and geophysical properties of the habitat in which an organism lives (e.g., vegetation, slope, and number of conspecifics). Since our observations were conducted at periods of low predation risk when no predators were observed at the research site, we hypothesized that factors associated with higher energetic demand, such as parasite infection or higher glucocorticoid levels, would be associated with less vigilance and more foraging during behavioral samples. Additionally, we compare the relative importance of internal factors and external factors already known to influence marmot vigilance. While we acknowledge that internal factors and external factors can interact, this was not the primary focus of this analysis.

Methods

Study subjects, trapping, and sample collection

Marmots have been studied extensively at Rocky Mountain Biological Laboratory (RMBL) in Gunnison County, Colorado since 1962 (Armitage 1991, 2014; Schwartz et al. 1998; Blumstein 2013). Marmot behavior at this site is characterized by winter hibernation, emergence in late April– early May, and birth of young a few weeks later with weaning at age 25 days (Armitage 1991,2003). The long history of research in this system and an extensive record of foraging behavior with corresponding individual level and habitat data make it a powerful system in which to test hypotheses about the relative importance of internal and external factors affecting behavior. Data for this study were collected from 2005 to 2008 at six colonies. Marmots live in colony sites, which were trapped biweekly over 2–4 consecutive days. Tomahawk live traps (Tomahawk Live Trap, Hazlehurst, WI) were baited with horse feed (Omalene 100) in the early morning (0600–1000 h) and late afternoon (1500–1900 h) from late May until early September. When captured, marmots were permanently marked with metal ear tags with unique number combinations and temporarily marked for identification from afar with black Nyanzol® cattle-dye markings. Marmots were weighed in a canvas bag with a spring-loaded scale to the nearest 50 g, and sex, age (yearling or adult), and reproductive status of each individual was noted. When trapped, all males were visually assessed as scrotal or non-scrotal, and females were assessed as having small, medium, large, or lactating nipples. Females with small or medium nipples were considered as not actively reproductive, and females with large or lactating nipples were considered to be reproductively active. Blood samples of 0.5 to 2.5 ml were taken from the femoral vein and immediately placed into heparinized tubes on ice for transport to the lab where blood smears were made. When available, fresh fecal samples were collected in a self-sealing plastic bag on ice for fecal glucocorticoid metabolite and intestinal parasite assays (Blumstein et al. 2006; Lopez et al. 2013). Marmots were in traps for a maximum of 3 h (often substantially less time) before they were processed, and all subjects were released immediately after processing at the site of capture.

Behavioral observations

Two-minute foraging focal samples were collected in the early morning (0600–1100 h) and late afternoon (1600–2000 h), when marmots are most active, from late April to late August from a distance of up to 250 m to minimize disruption to the colony. Observers continuously recorded the following mutually exclusive focal marmot behavioral transitions: standing (all four legs on ground) and foraging, standing and looking, rearing (on hind legs) and foraging, rearing and looking, walking, running, out of sight, and others. Focal observations were dictated into a microcassette recorder and later scored using JWatcher 1.0 software (Blumstein and Daniel 2007). Given that data were collected on focal animals in the field, it was not possible for observers to be blind to marmot identity. Samples were not collected or were discarded when predators were present or when individuals had been alarm calling in the previous ≤15 min (most were not associated with calls heard that day). Therefore, they are best thought of as "baseline" foraging observations (Lea and Blumstein 2011a) and reflect an animal's vigilance or foraging decisions without immediate predation risk or other acute stressors. Since animals sometimes disappeared into their burrows or behind vegetation, focal observations <60 s were discarded. Overall, the mean (±SD) duration of focals analyzed was 115.3 ± 11.887 s. Dominant substrate (high vegetation above the marmots shoulders or low vegetation below marmot shoulders) dirt, rock, and incline (low (0–10°), medium (10–30°), high (>30°)) of the local environment as well group size, defined as the number of conspecifics within 10 m of the focal subject, were also recorded because these factors can influence marmot vigilance.

Analysis of blood and fecal samples

Following collection, one drop of fresh blood was used to make thin film smears. Slides were stained and fixed using a Fisher Scientific Hema 3 stain kit and scored for the presence or absence of *Trypanosoma lewisi* under a microscope at 40×. If no *Trypanosoma lewisi* were observed in 30 min, the sample was scored as parasite free.

To test for intestinal parasites, a portion of each fecal sample was preserved shortly after collection in 10 % buffered neutral formalin at collection. These samples were later tested for parasites with fecal flotation using zinc sulfate heptahydrate (Ovafloat®, Butler Company, Columbus, OH), which is optimized for isolating helminth eggs, coccidian oocysts, and other protozoan cysts. Samples were tested for presence/absence of *Ascaris* spp.; if no oocysts were found in 30 min, slides were scored as parasite free.

To measure fecal glucocorticoid metabolites, the remainder of each fecal sample was frozen at −20 °C within 2 h of collection. The radioimmunoassay for metabolites was conducted as described in (Smith et al. 2012). Hormone metabolite values were initially published in Smith et al. (2012), and they report an inter-assay coefficient of variation of 8.3 % and an intra-assay variation of 1.4 %. Because gut passage time is slow in marmots and response to ACTH challenge takes up to 35 h to affect fecal cortisol concentrations, reported fecal glucocorticoid metabolites are considered baseline measures (Blumstein et al. 2006; Smith et al. 2012).

Data analysis

Out of >1000 focal observations collected over the study period, 221 (84 of males and 137 of females) were included in the analysis, representing 93 individuals (35 males and 58 females). Focal samples were selected based on availability of corresponding records for fecal glucocorticoid metabolites and parasites that were collected within 2 weeks of the observation date. Given that fecal glucocorticoid metabolites may fluctuate over a few days, we ran a complementary analysis restricted to samples collected within 1 week of observation date. Since results indicate that the importance of fecal glucocorticoid metabolite levels were the same with one-week and two-week sampling intervals, and a one-week sampling interval precluded including parasites in the model, we only present two-week sample results here. In a few cases, multiple observations from the same individual were included in the final data set. To account for potential effects of pseudoreplication, a random intercept for individual identity was included in our final statistical model (see below). Additionally, only observations of marmots on high or low vegetation were included because there were very few instances of foraging bouts on dirt- or rock-dominated areas. Observations on medium and low inclines were combined into one category of "low slope" to contrast with "high slope" because initial analyses indicated that overall behavior was very similar on low and medium inclines. We initially considered potential effects of social dominance following methods reported in Huang et al. (2011). However, initial analyses suggested that dominance rank never significantly explained time allocation to foraging or vigilance and indeed are largely determined by age, sex, and condition, consistent with previous findings (Huang et al. 2011). For these reasons, we eliminated dominance rank as a predictor in all further analysis.

We fitted linear mixed-effects models with restricted maximum likelihood estimation using R version 2.14.2 and package 'lme4' (Bates et al., 2004). Dependent variables were the proportion of time in sight allocated to foraging (stand forage and rear forage behaviors) and vigilance (stand look and rear look behaviors square root transformed). Group (colony within year), year, and individual ID were included as random factors. Fixed effects included in each model were as follows: slope, vegetation height, Julian date, number of marmots within 10 m, body condition, log-transformed fecal glucocorticoid metabolites, *Ascaris* spp. (presence/ absence), and *Trypanosoma lewisi* (presence/absence). Since marmot mass varies with age class, sex, colony location, year, and time of year (Armitage et al. 1976), marmot condition was calculated by taking the residuals of a linear model of mass against these variables. All continuous predictor variables were centered to mean of 0 and divided by their standard deviation to create standardized coefficients.

Full models with main effects for all variables and two-way interactions for age and sex, slope and substrate, and age and sex by all internal variables were fit initially. If interactions were not significant, they were dropped from the final model. Multi-collinearity between predictors and normality of model residuals were checked. Results from the final simplified models are reported with standard error and p values calculated using the Satterthwaite approximation implemented in R package 'lmerTest' (Kuznetsova et al., 2014).

Because adult reproductive status can influence fecal glucocorticoid metabolite levels (Smith et al. 2012), we also checked for effect of reproductive status on time allocated to foraging and vigilance by conducting separate analyses for adult females and adult males. Adult females were scored as not actively reproductive if they had small or medium-sized nipples, and they were scored as actively reproductive if they had large or lactating nipples. Adult males were considered actively reproductive if they were scrotal and not actively reproductive if they were non-scrotal. Because sample sizes were lower ($n = 111$ on adult females, $n = 38$ adult males), we included fewer predictors in these models. For adult females, we included reproductive status (1/0 actively reproductive/ not), fecal glucocorticoid metabolite levels, number of conspecifics nearby, and the interaction between reproductive status and the other covariates. For adult males, we included reproductive status, fecal glucocorticoid metabolites, and the interaction between them. We removed non-significant interactions from the final models.

Results

Overall, there was a strong negative correlation between time spent foraging and time spent vigilant ($r = -0.89$, $n = 221$, $p < 0.001$). Internal factors significantly explained variance in both the time allocated to foraging (Table 1) and vigilance (Table 2). Marmots spent more time foraging as levels of fecal glucocorticoid metabolites increased ($t = 2.282$, $df = 153$, $p = 0.024$; Fig. 1). Similarly, marmots infected with *Trypanosoma lewisi* spent more time foraging than uninfected individuals ($t = 2.390$, $df = 141$, $p = 0.018$; Fig. 2) In contrast, animals infected with *Ascaris* spp. spent less time foraging ($t = -2.041$, $df = 202$, $p = 0.043$; Fig. 3) than uninfected individuals. Increasing levels of fecal glucocorticoid metabolites ($t = -3.136$, $df = 124$, $p = 0.002$) were associated with decreasing vigilance and individuals infected with *Trypanosoma lewisi* spent less time vigilant ($t = -2.606$, $df = 157$, $p = 0.010$) than parasite free marmots. Adult marmots spent less time vigilant as condition increased ($t = -2.346$, $df = 134$, $p = 0.020$), but yearling marmots showed the opposite pattern increasing vigilance with increases in condition (yearling by condition interaction as follows: $t = 2.280$, $df = 160$, $p = 0.024$; Fig. 4). Age, condition, and sex did not explain variance in proportion of time spent foraging. Sex and *Ascaris* spp. infection did not explain variation in proportion of time spent vigilant.

By contrast, no environmental variables significantly predicted variation in proportion of time foraging (Table 1), but some factors explained variance in proportion of time allocated to vigilance (Table 2). Substrate ($t = -2.536$, $df = 201$, $p = 0.019$), slope ($t = -2.479$, $df = 198$, $p = 0.014$), and an interaction between these two factors ($t = 2.24$, $df = 204$,

Table 1 Results for linear mixed effects model of the proportion of time foraging. For each fixed effect, model estimates, standard error (*SE*), degrees of freedom (*df*), *t* value, and *p* value are presented. FGM stands for fecal glucocorticoid metabolites and the factor labels in parentheses indicate the factor level for which estimates are provided. For each random effect, variance and standard deviation (*SD*) are presented

		Variable	Estimate	*SE*	*df*	*t*	*P* value
Fixed effects							
	Internal-state variables	Intercept	0.496	0.062	31	8.055	<0.001
		log-transformed FGM	0.031	0.015	153	2.282	0.024
		Trypanosoma lewisi infection	0.127	0.053	140	2.390	0.018
		Ascaris spp. infection	−0.089	0.044	202	−2.041	0.041
		Age	0.0004	0.028	115	−0.015	0.988
		Condition	0.011	0.012	133	0.921	0.359
		Sex (male)	−0.040	0.027	52	−1.513	0.136
		Julian date	−0.027	0.016	98	−1.688	0.094
	Environmental variables	Marmots within 10 m	0.008	0.011	205	0.751	0.454
		Slope (low)	0.080	0.049	149	1.627	0.106
		Substrate (low vegetation)	0.023	0.029	201	0.777	0.438
		Variable	Variance	*SD*			
Random effects							
		Individual id	0.003	0.053			
		Colony-year	0.003	0.05			
		Year	0.003	0.053			

$p = 0.027$) all explained variation in proportion of time spent vigilant. Marmots spent similar amounts of time vigilant regardless of vegetation height when on low slopes, while marmots on high slopes spent more time vigilant in high vegetation than in low vegetation. There was also a trend for marmots to spend less time vigilant when there were more marmots within 10 m ($t = -1.772$, $df = 208$, $p = 0.078$) of small effect size ($\beta = 0.016$). Day of the year did not explain variation in proportion of time spent vigilant.

For adult females, reproductive status did not have any effect on proportion time foraging ($t = 0.141$, $df = 98$, $p = 0.888$), and consistent with results from the model for all

Table 2 Results for linear mixed effects model of the square root transformed proportion of time vigilant. For each fixed effect, model estimates, standard error (*SE*), degrees of freedom (*df*), *t* value, and *p* value are presented. FGM stands for fecal glucocorticoid metabolites and the factor labels in parentheses indicate the factor level for which estimates are provided. For each random effect, variance and standard deviation (*SD*) are presented

		Variable	Estimate	*SE*	*df*	*t*	*P* value
Fixed effects							
	Internal state variables	Intercept	0.899	0.130	200	6.891	<0.001
		Log-transformed FGM	−0.341	0.011	124	−3.136	0.002
		Trypanosoma lewisi infection	−0.110	0.042	157	−2.606	0.010
		Ascaris spp. infection	0.046	0.034	162	1.336	0.183
		Age (yearling)	0.002	0.023	116	0.089	0.930
		Condition	−0.027	0.011	134	−2.346	0.020
		Sex (Male)	0.015	0.022	65	0.697	0.488
		Condition × age (yearling)	0.047	0.020	160	2.280	0.024
		Julian date	0.009	0.011	65	0.840	0.404
	Environmental variables	Marmots within 10 m	−0.017	0.009	208	−1.772	0.078
		Slope (low)	−0.325	0.131	198	−2.479	0.014
		Substrate (low vegetation)	−0.320	0.135	201	−2.356	0.019
		Slope (low) × substrate (low vegetation)	0.305	0.137	204	2.224	0.027
		Variable	Variance	*SD*			
Random effects							
		Individual id	2.20×10^{-3}	4.70×10^{-2}			
		Colony-year	$6.4*10^{-4}$	$2.54*10^{-2}$			
		Year	0	0			

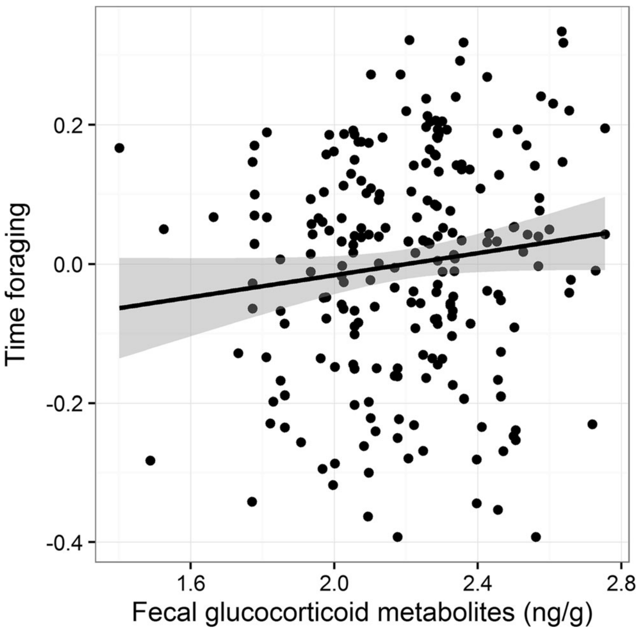

Fig. 1 Marmots with higher levels of fecal glucocorticoid metabolites spent more time foraging. Values shown for fecal glucocorticoid metabolites are log10-transformed, and values shown for time foraging represent residual variance after controlling for other predictor variables in the model. Gray shaded regions =95 % confidence intervals

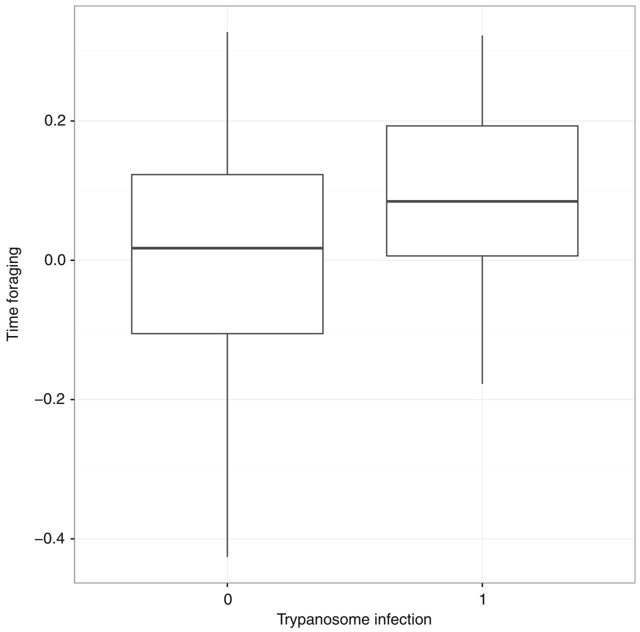

Fig. 2 Marmots infected with *Trypanosoma lewisi* spent more time foraging. Box plots represent median values and interquartile ranges, with minimal and maximal values shown as vertical lines. Values shown for time foraging represent normal (unstandardized) residuals from a model of proportion time foraging, after controlling for all other predictor variables described in Table 2

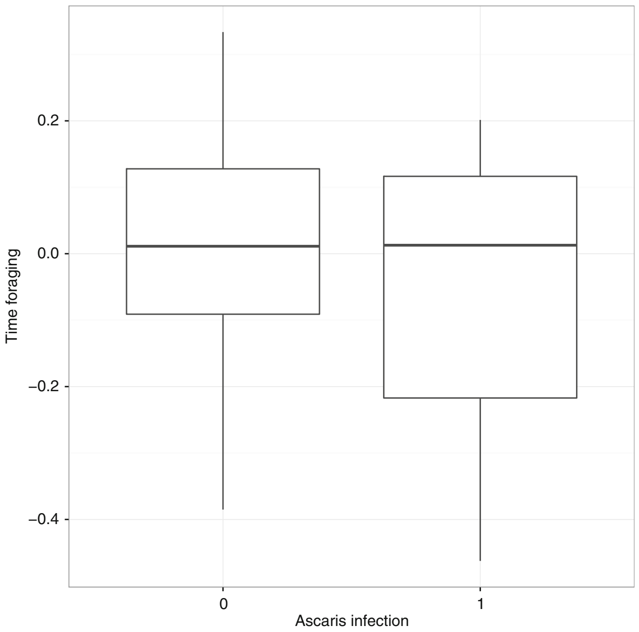

Fig. 3 Marmots infected with *Ascaris* spp. *s*pent less time foraging. Box plots represent median values and interquartile ranges, with minimal and maximal values shown as vertical lines. Values shown for time foraging represent normal (unstandardized) residuals from a model of proportion time foraging, after controlling for all other predictor variables described in Table 2

individuals, adult females with higher FGM levels spent more time foraging ($t = 3.007$, $df = 78$ $p = 0.004$), while number of other marmots within 10 m had no effect ($t = 1.253$, $df = 104$, $p = 0.213$). There were no significant interactions between reproductive status and other predictors. Reproductive status did not have a significant main effect on proportion time spent vigilant ($t = 0.480$, $df = 92$, $p = 0.633$) and did not interact with FGM levels. However, there was a significant interaction between reproductive status and number of other marmots within 10 m, such that actively reproductive females did not reduce vigilance in the presence of more conspecifics ($t = 2.798$,

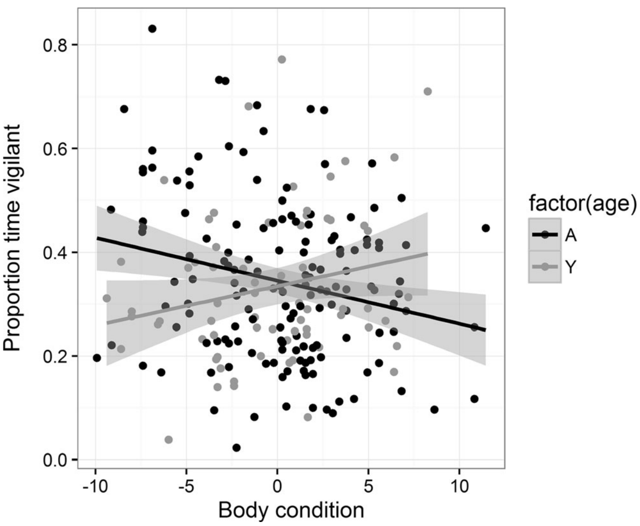

Fig. 4 Age and body condition interacted to influence proportion time vigilant. Proportions shown are raw values. Body condition values are standardized residuals from a regression of body mass against age, sex, year, Julian day, and colony elevation. Gray shaded regions =95 % confidence intervals, *A* adult, *Y* yearling

df = 106, $p = 0.006$), though there was a main effect of reducing vigilance in the presence of more conspecifics ($t = -2.625$, *df* = 99, $p = 0.010$). Consistent with the results from the model for all individuals, individuals with higher FGM levels spent less time vigilant ($t = -3.728$, *df* = 46, $p < 0.001$).

For adult males, actively reproductive males spent a higher proportion of time foraging ($t = 2.696$, *df* = 29, $p = 0.012$) than non-reproductive males, and there was no significant interaction with FGM levels. FGM levels had no main effect on adult male foraging behavior ($t = -1.478$, *df* = 34, $p = 0.149$). Reproductive status did not have any effect on proportion of time vigilant in adult males ($t = -1.100$, df = 35, $p = 0.279$), and there was no significant interaction with FGM levels. Contrary to results from the model with all individuals, there was no main effect of FGM levels on adult male vigilance behavior ($t = 0.732$, *df* = 32, $p = 0.470$).

Discussion

While both internal and environmental variables significantly predicted time spent vigilant, only internal state factors predicted time spent foraging. This suggests that while there is indeed a close (negative) relationship between vigilance and foraging, there are important differences in how these behaviors are modulated by environmental and state-dependent variation. Additionally, while foraging is mostly driven by internal state factors that might influence energetic demands, vigilance is determined by a combination of internal state and external cues that are likely informative about predation risk. Two of the same internal state factors (fecal glucocorticoid metabolites and *Trypanosome lewisi* infection) significantly predicted both proportion of time foraging and time vigilant, while no other variables were significant in both models. Unsurprisingly, the effects of fecal glucocorticoid metabolites and trypanosomes on vigilance and foraging largely opposed each other as animals spent the majority of time during focal observations either foraging or vigilant. While our data are correlative, which constrains the conclusions that may be drawn, they provide a powerful suggestion that foraging and vigilance should be treated as related but nonetheless distinct behaviors.

Marmots with high levels of fecal glucocorticoid metabolites spent less time vigilant and more time foraging. This result held across age-sex classes and did not change with reproductive status. Additionally, this result was consistent when our dataset was restricted to both one and two-week windows between behavioral observation and fecal sampling, leading us to be confident in findings despite the fact that glucocorticoids were likely modulated on a fine scale during that time. Glucocorticoids are metabolic hormones that promote food intake (Landys et al. 2006). At a proximate level, animals experiencing greater metabolic demand (or allostatic load) will have increased baseline glucocorticoid levels (Wingfield 2005). This is seen in changes in hormone values across the reproductive season: fecal glucocorticoid metabolites are high among pregnant female marmots, which must support developing offspring as well as themselves (Smith et al. 2012). Therefore, our finding that marmots with higher fecal glucocorticoid metabolite levels spend more time foraging is consistent with this body of theory. Studies in rats suggest that increases in glucocorticoids, even within the range normally expected across the day, may increase motivation to ingest calories (la Fleur et al. 2004). Importantly, the effect of glucocorticoids on feeding behavior is thought to vary depending upon whether hormone levels exceed "normal" levels and may be seasonally dependent (Landys et al. 2006). However, as noted by McArthur et al. (2014), responses to predator exposure as well as energetic shortfall may influence glucocorticoid levels. Animals that are exposed to risk (e.g., predators) may increase glucocorticoids and seek to reduce predator exposure while foraging by allocating more time to foraging when they forage. In line with this functional hypothesis are the observations that marmots forage more after hearing alarm calls from individuals that accurately detect predator presence (Blumstein et al. 2004b) as well as from older (and presumably more reliable) individuals (Blumstein and Daniel 2004).

The relationship between glucocorticoid levels and vigilance behavior in this and other systems is less well studied. Blumstein et al. (2006) found that the individual marmots had higher levels of fecal glucocorticoid metabolites when they alarm called compared to when they did not, suggesting a proximate relationship between stress hormones and response to predation risk. One previous study found a positive relationship between fecal glucocorticoid metabolite levels and vigilance rates in meerkats (*Suricata suricatta*) and also showed that meerkats treated with cortisol took longer to resume foraging after exposure to alarm call recordings (Voellmy et al. 2014). Of course, in nature, vigilance rates and glucocorticoid levels may be driven by a common cause: predator exposure. Predator cues increase tonic immobility in Fijian ground frogs (*Platymantis vitianus)* (Narayan et al. 2013), and tonic immobility increased in chickens implanted with CORT osmotic pumps (Jones et al. 1988). Additionally, environmental variation in predation may alter the glucocorticoid response (Sheriff et al. 2009) but see also (Anson et al. 2013).

While the long-term effects of *Trypanosoma lewisi* infection are unknown in marmots, if parasite infection increases the energetic needs of marmots, it is not surprising that infected marmots spend more time foraging. *Trypanosoma lewisi* infection may increase energetic demand by provoking costly immune defenses, thus increasing the importance of foraging opportunities. Direct effects of *Trypanosoma lewisi* infection on vigilance behavior are unreported in the literature. It seems likely that any effect of infection on vigilance is indirectly mediated through changes in foraging.

In contrast, marmots infected with *Ascaris* spp. (nematode worms) spent less time foraging. The literature suggests that intestinal parasites can cause a reduction in food intake or even anorexia (Jones et al. 2006; Laurenson et al. 2011). This relationship has been demonstrated across vertebrate taxa, though is particularly well studied in livestock (Jones et al. 2006). Infection with *Ascaris* spp. may have a similar suppressive effect on food intake in marmots. Interestingly, parasite infection can have effects on diet beyond reduced food intake. A study in lambs treated or left untreated for gastroparasite infection showed that infected lambs altered diet selection to make up for the energetic demands created by parasite infection (Cosgrove and Niezen 2000). Thus, it is possible that intestinal parasite infection could affect food choice in marmots though it was not possible to examine this relationship in the current study. Importantly, the contrasting effects of trypanosomes and nematodes emphasize that different types of parasites can have very different effects on behavior (Gilman et al. 2007).

Age class affected vigilance, but this effect varied with body condition. In adult marmots, vigilance decreased as body condition increased; however, in juvenile marmots vigilance increased with body condition. It is possible that this result may be influenced by social dominance because animals in better condition tended to be more socially dominant. However, because dominance did not have a direct effect on time allocated to foraging or vigilance, an alternative explanation is more likely. The literature on the relationship between age class and condition has yielded mixed results with some authors calling attention to the difference in risk levels under which individuals were tested (Lea and Blumstein 2011a). Interestingly, unlike previous work in marmots (Lea and Blumstein 2011a), this (much larger) study of natural foraging behavior found differences across age classes under baseline foraging conditions. Beyond this, few studies have tested the interaction between age class and condition. One study found that heavily food-supplemented juveniles increase time allocated to vigilance, exhibiting vigilance behavior comparable to that of adults, while moderately food-supplemented individuals decrease time allocated to vigilance (Arenz and Leger 2000). Condition-dependent responses to alarm calls have been documented in Belding's ground squirrels (Bachman 1993), with animals decreasing responsiveness to alarm calling after food supplementation, but this study was conducted only in juvenile females. Our finding that adults and juveniles have different condition-dependent changes in vigilance behavior suggests that thresholds in state-dependent behaviors may differ across age-sex classes.

Our results also suggest that environmental factors that influenced how well marmots could see explained variation in vigilance: in low vegetation, marmots were less vigilant than marmots in high vegetation, though this was modulated based on the angle of the slope on which marmots were observed foraging. On low-angle slopes, marmot behavior was relatively insensitive to vegetation height while on steeper slopes marmots increased vigilance markedly with vegetation height. This is consistent with previous work in marmots, which has shown flight initiation distance increases in high vegetation (Blumstein et al. 2004a) and also consistent with the previously identified importance of peripheral visibility (Bednekoff and Blumstein 2009). Findings with respect to the effect of incline and substrate on proportion of time allocated to foraging and vigilance differ slightly compared to results in one previous study (Blumstein et al. 2004a); however, this is likely due to the inclusion of substrate-slope interactions in the present study as well as a substantial increase in sample size. It is possible that more detailed observations of spatial habitat use by marmots would provide greater insight into the role of environmental factors shaping foraging-vigilance trade-offs and potential interactions between internal and external factors. For example, it is possible that marmots of different internal states may elect to forage in habitats of different quality, which in turn affects behavior. While an interesting avenue for future research, we have no way of testing the effect of variation in habitat quality in the current paper and aimed to minimize such effects by only observing marmots that had already made the decision to forage in a restricted geographic area (100 m) close to their burrows.

Unsurprisingly, there was a trend for marmots to decrease vigilance as the number of marmots within 10 m increased. This is consistent with a large body of literature on the group size effect within marmots (Carey and Moore 1986; Blumstein et al. 2004a) and in many taxa broadly (Roberts 1996). Interestingly, our supplementary analysis suggests that reproductive females do not alter their vigilance based on conspecifics, however, given the small sample size available for the present analysis these results should be interpreted with caution.

Conclusions

Foraging and vigilance are often treated as behaviors that are traded off against each other (Houston et al. 1993). While results from this study show a strong negative correlation between foraging and vigilance, they also indicate that the factors influencing vigilance are not the same as the set of factors influencing foraging. Only internal state-based factors influenced time spent foraging, while both state-based factors and environmental factors influenced vigilance. This suggests that vigilance involves more complex integration of signals than foraging. While focal samples were restricted to marmots that were already foraging, and the power of this study to detect environmental effects that decrease the probability of foraging may be low, the analysis highlights the value of analyzing factors that influence foraging and vigilance separately because they are unique behaviors that can be influenced subtly by different factors.

Additionally, our findings are consistent with an exciting new body of research that suggests that parasites can have indirect effects on behavior by influencing the trade-off between foraging, antipredator vigilance, and other behaviors. Of note, these changes were observed in periods of normal risk when predators were not actively present. While it is not particularly surprising that parasitism and other measures of internal state, such as fecal glucocorticoid metabolite levels, can influence behavioral trade-offs, this study suggests that attention should be paid to expanding the diversity of internal factors typically considered in foraging and vigilance research. Importantly, as our understanding of internal factors shaping behavior continues to improve, the way that internal and external factors interact to shape behavior will be a promising area for future research.

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Compliance with ethical standards

Ethical standards Marmots were studied under research protocol ARC 2001–191-01 as well as permits issued by the Colorado Division of Wildlife. The research protocol was approved by the UCLA Animal Care Committee on 13 May 2002 and renewed annually.

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