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2 **Effects of spontaneous movement on alert distance and flight initiation distance in**3 **yellow-bellied marmots (*Marmota flaviventris*)**4 *Student:* Dana Williams5 *Mentor:* Dan Blumstein

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8

9 **Abstract**

10 When approached by a predator, prey make economic decisions between remaining
11 where they are and obtaining benefits from their current activity or leaving and enhancing
12 their safety. The 'flush early and avoid the rush' (FEAR) hypothesis suggests that animals
13 are likely to flee as soon as they alerted to an approaching predator, thus reducing any
14 costs that they may be incurred by monitoring predator behavior. While this hypothesis
15 has been supported by several studies, some argue the relationship may be entirely or in
16 part a consequence of spontaneous vigilance and/or spontaneous movement rather than
17 an effect of alert distance (predator-prey distance when the prey becomes aware of and
18 begins to monitor the predator, AD) on escape decisions. If this were true, spontaneous
19 vigilance might be inaccurately recorded as alert distance and spontaneous movement
20 might be incorrectly recorded as flight initiation distance (the predator-prey distance
21 when escape begins, FID). To evaluate these potential artifactual effects of AD on FID,
22 we studied individually marked yellow-bellied marmots (*Marmota flaviventris*). We used
23 focal animal samples to determine the natural interval between bouts of vigilance and

bouts of locomotion and factors that influenced them. We found that both intervals between vigilance and locomotion were influenced by general activity. Using coefficients estimated from a linear mixed effects model, we then estimated the distance a person could approach a marmot under a variety of conditions before it would naturally look or move without having noticed an approaching predator. We used these thresholds to then filter a large data set of FIDs to remove observations that could have occurred after these thresholds were reached. Any way we analyzed our FID data, the strong relationship between AD and FID remained. This suggesting that although spontaneous vigilance and spontaneous movement may lead to some increase in FID as AD increases, the relationship that remains when their effects have been removed supports the economic basis of the flush early hypothesis.

Introduction

Escape behavior in response to predators is of critical importance to animals because failure to escape results in death and termination any future contribution to fitness. However, escaping too early can also result in a loss of benefits such as finding food or a mate. Individuals behaving optimally will flee at the point where the benefits of staying are outweighed by the risks (Ydenberg and Dill 1986) or expected future fitness is maximized (Cooper and Frederick 2007).

Animals may behave differently as a function of their distance to the threat. Blumstein (2003) suggested that when a predator is far away, prey may not flee because either predators are not detected, or because the benefits of continuing current activity outweigh the risk of predation. By contrast, when a predator initiates its approach close to

the prey, prey will flee immediately because the risk of predation is extreme. Between these two distances is an interval in which the prey monitors the predators' approach and assesses the costs of not fleeing and of fleeing before making an economic decision between staying and leaving (Blumstein 2003). Flight initiation distance (FID = distance at which prey flees from an approaching predator) can be used to test risk perception and decision-making in escape behavior (Ydenberg and Dill 1986; Cooper and Frederick 2007; Stankowick and Blumstein 2005).

The finding that many avian species have longer FID when starting distance (predator-prey distance when the approach begins, SD) is longer (Blumstein 2003) was difficult to explain using existing economic escape theory and might have been a consequence of greater opportunity for spontaneous movements during longer approaches (Cooper 2005). Blumstein (2003, 2010), proposed the 'flush early and avoid the rush' (FEAR) hypothesis according to which prey flee from an approaching predator sooner after detection at longer SD or AD in order to minimize costs incurred by monitoring predator behavior. Ongoing monitoring is expected to increase costs by diverting attention away from beneficial activities, as well as incurring energetic costs (Dukas 2004; Blumstein 2010). The addition of monitoring costs to the economic model shifts the optimal flight distance to earlier in the sequence of the predator's approach. Samia et al. (2013) conducted a meta-analysis of the FEAR hypothesis and found strong support for it in birds and mammals. Nonetheless, there have been some challenges to it.

A recent study questioned the generality of the expected relationship in the FEAR hypothesis on statistical grounds (Dumont et al. 2012). The expected pattern in the FEAR hypothesis is a positive relationship between FID and AD or its proxy SD. However,

because FID is upper limited by AD-SD and down limited by values closer zero meters (envelope constraint), Dumont et al. 2012 argues that even randomly chosen SD, AD and FID values still exhibited a positive relationship, leading them to question whether the relationship is due to mathematical artifact or biological effect. In response to Dumont et al.'s analysis, Chamaillé-Jammes and Blumstein (2012) used quantile regression and found that the positive relationship remained in low quantiles for which spontaneous movements were improbable and concluded that the relationship was unlikely to generally be a statistical artifact. Still, Samia et al.'s null model showed that only a small fraction of the species tested to-date should have been product of spurious relationship.

Cooper et al. (2008) hypothesized that the relationship may be due a biological effect. A longer SD or AD increases the duration of approach. In the meantime, prey may be more likely to move spontaneously in a manner unrelated to predator approach (Cooper et al. 2008). Spontaneous movements may include vigilance and the natural rate of movement, which can affect estimates of AD and FID respectively (Blumstein et al. 2010). When spontaneous movement was simulated with an exponential distribution, it was found to be a key factor in the relationship between SD and FID, suggesting that in mobile animals spontaneous movements may be falsely recorded as ADs and FIDs (Chamaillé-Jammes and Blumstein 2012). Spontaneous movement has also been accounted for in previous studies by adjusting for approach speed, for duration of approach and by using a Poisson distribution to account for natural rate of leaving (Cooper 2005; Chamaillé-Jammes and Blumstein 2012). SD is a proxy for AD used when AD cannot be ascertained, and is subject to effects of spontaneous movement when the prey has not detected the predator. Therefore, we focus on the relationship between AD

and FID in studies of economic escape decisions, but must account for effects of spontaneous vigilance and spontaneous translational movement.

At some level, however, escape from a predator is an obvious response to approach and most researchers do not record natural movements clearly unrelated to approach as “escapes” Review of literature showed that most experimenters use a standardized procedure for approaching animals (*sensu* Blumstein 2003) in which doubtful observations are discarded (Blumstein et al. 2005; Stankowick and Blumstein 2005; Weston et al. 2012; Samia et al. 2013)

Although the monitoring costs proposed by the FEAR hypothesis have been unclear, making it difficult to incorporate the FEAR hypothesis into economic escape theory, a recent theoretical paper describes several ways in which monitoring a predator may affect costs of not fleeing and costs of fleeing (Cooper and Blumstein, in press). To clarify the relative influences of spontaneous movements and economic factors on the positive correlation between AD and FID, future research must focus on the extent of spontaneous vigilance and translational movements and on determining the magnitudes of the proposed economic effects of monitoring on escape decisions.

Detailed studies of spontaneous movement are lacking and the most effective way to account for spontaneous movement may be to record a baseline of spontaneous movement and use it to adjust observed AD and FID values (Cooper 2008; Chamaillé-Jammes and Blumstein 2012). This baseline would aid in distinguishing between real alerting and spontaneous looks and between escape and spontaneous movements. After spontaneous movements have been removed from a data set, any remaining positive correlation between AD and FID must have an economic basis.

While no previous studies have been conducted on intervals between bouts of vigilance, Blumstein et al. (2004) found that group size and substrate explained variation in FID, allowing closer approaches. Li et al. (2011) found that the different marmot colonies experience different amounts of human traffic and thus react differently to human approach.

Here we determine whether and how spontaneous vigilance and movement affects our estimate of the relationship between AD and FID using a large set of individually-marked in yellow-bellied marmots (*Marmota flaviventris*). We calculated the natural intervals between bouts of vigilance and between bouts of spontaneous locomotion and used the predicted values, temporal intervals between bouts of vigilance or locomotion converted to spatial intervals, under a variety of conditions to filter a large set of FID experiments conducted on marmots so as to exclude those results that might be confounded by spontaneous vigilance or movement. With these “filtered” data sets we calculated the relationship between AD and FID to test the FEAR hypothesis.

Methods

Study area

We studied individually marked yellow-bellied marmots in and around the Rocky Mountain Biological Laboratory in Gothic, CO (38°77'N, 106°59'W), the site of a long-term study of marmot behavioral ecology and population biology (Armitage 2010; Blumstein 2013).

Focal samples

We used two-minute focal animal samples to study the natural intervals between bouts of vigilance and bouts of locomotion (Altmann 1974). Focal observations were conducted during peak hours of marmot activity (07:00i 10:30 h and 15:30i 18:30 h) on days when the wind was below Beauford Scale 3, and it was not raining or snowing. Marmots were observed through either binoculars or a 15-45x spotting scope at distances (over 100 m from animals) that did not obviously influence their behavior. Our ethogram included quadrupedal looking, rear (sitting on hind legs) looking, quadrupedal foraging, rear foraging, walking, running and other behaviors. Focal observations were dictated into a microcassette recorder (Blumstein et al. 2004, 2010). Our complete dataset was composed of 1759 focals, with three different types of beginning behaviors, hereafter named as focal types. The focal type "foraging" is composed of observations on foraging marmots (1608 focals collected between 2002-2012). Focal type "non-foraging" is composed of marmots exhibiting relaxed behavior, where animal was not rearing up or nervously looking around (102 focals collected in 2013). Finally, the focal type "prior FID" is composed of observations of "relaxed" animals immediately before initiating an experimental FID approach (48 focals also collected in 2013).

Animals sometimes moved out of sight during focal observations. We restricted our analysis to those observation in which the subject was in sight the entire time. We recorded three other factors that might influence patterns of vigilance or locomotion, the number of other marmots within 10 m, the incline category on which animals were observed (0-10°, 11-30°, >30°), and the substrate on which animals were observed (dirt/stone/low vegetation, high vegetation, and talus) (*sensu* Blumstein et al. 2010).

Focal animal samples were scored in JWatcher 0.9 or 1.0 (Blumstein and Daniel 2007). Observers were trained both in identifying the behaviors and in scoring them (criteria: 100% correct identification in the field; 100% correct behaviors consistently scored in JWatcher; scoring of behaviors was over 95% accurate for time allocation estimates when the same focal observations were scored more than once). Using JWatcher we calculated the “natural” interval between any bout of looking (i.e., we combined quadrupedal looking and rear looking), and any bout of locomotion (i.e., we combined walking and running). In JWatcher, natural intervals are estimated only when the entire interval (start and termination of the behavior) was observed within the two-minute focal period. Thus, if an individual was quadrupedally looking on a rock the entire duration of the focal observation (as many did when not foraging), the interval between bouts of vigilance and the interval between bouts of locomotion were not estimated. For these instances we defined the interval as the focal duration. By doing so, we recognize that this likely underestimates the true duration but it does permit us to develop a conservative estimate of it.

Flight initiation distance

We estimated FID of individually-marked marmots in a standardized way. Observers identified a relaxed marmot and sat quietly for 10 min to eliminate possible effects of observer arrival before initiating an approach. Observers were trained to walk directly towards the subject at 0.5m/s, while minimizing excessive vertical movement across a variety of terrains (Blumstein et al. 2004; Runyan and Blumstein 2004). A marker was dropped at the starting point (SD) of the approach. Subsequent flags were dropped when

the animal first oriented itself towards the approaching human (AD), when the animal began to flee (FID), until the original position of the animal was reached. The distance between these markers were afterwards measured to the nearest 0.1 m and used to estimate SD, AD, initial FID and any subsequent FID. Observers measured the incline of the slope at the marmot's initial location with a clinometer (Li et al. 2011). In addition, we recorded the age, sex, distance to burrow and number of marmots within 10 m. Individual marmots were tested no more than once per day. In 2013, in addition to waiting for 10 minutes, we conducted a 2-min focal animal sample on 48 subjects using the same ethogram as the other focals prior to standing and walking towards them. All other approaches for FID data were not preceded by a 2 min focal observation. Two minutes was considered an optimal time in order to ensure that animals would be in sight for the greatest amount of time.

Statistical analyses

We asked three questions.

1) What factors influence intervals between bouts of vigilance and bouts of locomotion?

We fitted linear mixed effects models (LMM) using the function lmer from the package lme4 from the software package R, version 2.14.0 (R Development Core Team 2011). Our fixed effects were focal type (non-foraging, foraging, pre-FID), age class (we focused on yearlings and adults), sex, colony, incline, substrate, and the number of conspecifics within 10 m. We used marmot identity as a random effect. We $\log_{10}(x+1)$

transformed calculated natural intervals to ensure normality. We used a log-likelihood ratio test (LRT) to determine significance of models with and without the fixed effect of focal type (Pinheiro & Bates 2000). We estimated the variation explained by the model with the Extract Fixed Effects function, `fixef()`, which extracted coefficients of fixed effects (Pinheiro & Bates 2000).

2) What are the expected intervals between vigilance and locomotion?

Because the sample sizes of the different types of focal observations were disproportionally unbalanced, we elected to estimate coefficients for each effect focal type separately by fitting three different models; one for each focal type. We estimated the significance of model parameters by comparisons to a probability distribution obtained by 10,000 Markov Chain Monte Carlo simulations with the function `pvals.fnc` in "languageR" (details in Baayen et al. 2008). We used a log-likelihood ratio test (LRT) to determine significance of fixed effects between a model with and without a given fixed effect (Pinheiro & Bates 2000). Using the coefficient estimates, we calculated the predicted intervals between bouts of vigilance and locomotion for adults and yearlings of both sexes at each of the 10 colonies, over all three substrates, and in group sizes that ranged from 1-4 marmots. We back-transformed these estimated intervals and then multiplied these temporal intervals by 0.5 m/s to create a spatial interval. These predicted spatial thresholds served as a null model of the effects of spontaneous vigilance and locomotion in different situations.

230 3) Does the relationship between AD and FID hold after removing observations that
231 could be accounted for by spontaneous vigilance and locomotion?

232
233 We compiled all FID observations collected between 2003 and 2013 (N = 896). First,
234 using the entire data set, we fitted a LMM to estimate the relationship between AD and
235 FID after controlling for the random effect of individual identity. We then conducted a
236 series of LMM analyses with all possible combinations with filtered data. By filtering, we
237 mean to remove the paired FID-AD observations with distance equal to or below a given
238 parameter describing spontaneous vigilance or locomotion. The three parameters used
239 were the minimum, maximum, and mean spatial intervals between vigilance and
240 locomotion. The parameters were calculated independently for each focal type (foraging
241 focals, non-foraging focals, and focals that immediately preceded an experimental
242 approach). Thus, for example, to filter data based on average bouts of vigilance observed
243 in foraging marmots, we excluded from the complete data set all FID-AD observation
244 coming from AD equal to or lower than 2.44 m (see Table 3), and then conducted the
245 FID-AD correlations with the remaining data.

246 The relationship between FID and AD is a constrained envelope pattern. By
247 definition, FID can only assume values equal to or lower than its actual AD; a prey
248 cannot run away from a predator before it has detected it. This constraint can potentially
249 (1) violate the homoscedasticity assumption of regression analysis (because variance in
250 FID can increase as AD increase), and (2) artificially inflate the correlation coefficient of
251 regression. Because of these drawbacks, we are unable to use the traditional null
252 hypothesis testing to infer significance of FID-AD relationship. Thus, we ran a null

model test (*sensu* Samia et al. 2013) by comparing each observed r -values from the expected by random numbers distributed according to the constrained relationship FID-AD (details in supplementary material). All p-values from FID-AD relationship showed in the results were yielded by this latter null model, adopting an alpha of 0.05.

Statistical significance is not synonymous with biological significance (Cohen 1992; Nakagawa and Cuthill 2007; Borenstein et al. 2009). As suggested by recent studies, our inferences about biological effects were based in magnitude of the effect (Nakagawa 2004; Garamszegi, 2006; Nakagawa and Cuthill 2007; Borenstein et al. 2009). The correlation coefficient (r) is a standardized metric of effect size (frequently used in meta-analytic studies), what permits us to compare our results with those of previously published studies (Borenstein et al. 2009). Despite Cohen's (1992) thresholds to be widely used to classify magnitude of effect, his criteria were based in explanation power of previous studies from the psychology field. More recently, Møller and Jennions (2002) reviewed the predictive power of all published meta-analysis in biology so that we are now able to evaluate the magnitude of biological effects in a fairer fashion. Second these latter, r effect size of 0.10, 0.30, and 0.50, are respectively considered low, medium, and high.

Results

1) What factors influence intervals between bouts of vigilance and locomotion?

Although significant, this model explained little of the variation in either vigilance (1.7%), or locomotion (3.4%). The amount of variation explained by focal type varied among models. Models fitted to explain variation in foraging marmots explained very little variation of the intervals between bouts of vigilance (1.1%), and locomotion (7.1%). Models fitted to explain variation in non-foraging marmots explained a substantial amount of the variation in intervals between vigilance (17.6%) and locomotion (35.0%). Models fitted to explain variation in marmots immediately preceding our approaches to measure FID also explained considerable variation in the intervals between vigilance (37.2%), and locomotion (11.4%). However, as the three parameters (mean, minimum and maximum intervals) differed considerably in terms of data that must be filtered to analysis (Table 3), we conservatively modeled it separately in the subsequent AD-FID analyzes.

Predicted intervals between bouts of vigilance ($G^2 = 36.73$, $P = 0.0002$; $N = 1759$ observations) and locomotion ($G^2 = 87.36$, $P < 0.001$, $N = 1759$ observations) differed significantly among the three types of focal observations. The interval between vigilance varied among marmot colonies. For foraging marmots, intervals between bouts of vigilance were longer when marmots foraged in high vegetation, and longer as group size increased (Table 1). Foraging animals had longer intervals between locomotion when they foraged in high vegetation, when they were on talus, and longer as group size increased (Table 2). Intervals between bouts of locomotion while foraging varied significantly among colonies, and foraging animals had shorter intervals between bouts of locomotion in different colonies and on slopes $>11^\circ$ than on flat ground or shallower slopes (Table 2). Intervals between either locomotion or vigilance were not significantly

affected by model parameters for non-foraging animals (Table 1 -2) although the effect of group size was marginal for locomotion (Table 2) For animals observed immediately preceding approaches to measure FID, intervals between bouts of vigilance differed significantly among colonies, and increased significantly as group size increased (Table 1). Intervals between bouts of locomotion for animals observed immediately before measurement of FIDs differed significantly among colonies (Table 2).

2) What are the expected intervals between bouts of vigilance and locomotion?

Based on these estimates of coefficients, our predicted spatial thresholds for vigilance and locomotion varied considerably (Table 3). We used the minimum, mean, and maximum values in subsequent analyses.

3) Does the relationship between AD and FID hold after eliminating observations that could be accounted for by spontaneous vigilance and locomotion?

In all ways that we examined the data, the relationship between AD and FID was large and significant even after removing observations that might have been influenced by natural bouts of vigilance or locomotion (Figure 1). All r values were above 0.70 (Table 4).

Discussion

Factors related to rates of spontaneous vigilance and locomotion

Flight initiation distance measurements used to assess the economic escape decisions of animals do not typically take into account the possible confounding effects of spontaneous movements of prey animals. These spontaneous movements that indicated vigilance or movement from place to place may be falsely recorded as AD or FID, respectively causing inaccuracies in data. We examined how baseline rates of spontaneous movements of both types affect the relationship between AD and FID. We found that what animals were initially doing (quantified by comparing focal animal samples) affected both intervals between bouts of vigilance and intervals between bouts of locomotion. Specifically, animals have different intervals when they are foraging and when they are not foraging.

Foraging animals

Of several factors in our models that often explain variation in the average duration between bouts of vigilance (e.g., Blumstein et al. 2004), some explained substantial proportions of the variation in mean duration of the intervals between bouts of vigilance. Other factors did not affect these intervals. Both intervals between bouts of vigilance and between bouts of locomotion differed among colonies. This is likely because colonies have different predation pressures, different amounts of interaction with human beings, and other underlying differences that could effect how animals perceive risk (Li et al. 2011). Differences in availability of food among colonies might also affect movement rates (Stephens and Krebs 1986). Foraging animals had longer intervals between bouts of vigilance and between bouts of locomotion when they were in high vegetation. Blumstein et al. (2004) found that marmots were more wary in high vegetation than when foraging on other substrates. Longer intervals between bouts of vigilance may occur because they

wanted to forage more efficiently so as to spend less time in a risky habitat. Furthermore, since they were foraging, high vegetation potentially provided more food in a single area. In such area where food is concentrated, marmots could spend more time feeding and less time moving to find food.

Marmots also had longer intervals between bouts of vigilance and locomotion when in larger groups. This group size effect occurs in many prey taxa (Childress and Lung 2003, Beauchamp 2008) and was expected for yellow-bellied marmots because the presence of conspecifics dilutes the risk for each individual when a predator attacks the group and because the vigilance of an individual can be lessened by reliance on vigilance of other group members to detect predators (Roberts 1996).

Marmots foraging on talus also had longer intervals between bouts of locomotion than marmots on other substrates. We suspect that it may be more difficult for marmots to move across slippery talus than in low vegetation or on soil. Marmots moved after shorter intervals on slopes steeper than $>11^\circ$. Because this effect is independent of substrate type, the shorter inter-movement intervals on steeper slopes might indicate that food was sparser on steeper slopes, requiring more frequent foraging movements. (Steeper slopes may be more exposed, this contradicts earlier statement). Intervals between bouts of vigilance were not affected by slope, suggesting that perceived risk of predation is not influenced by steepness of the terrain.

Age category (adult or yearling) showed no effect on either vigilance or locomotion for any of the focal types. This reflects the results found by Blumstein et al. 2004, who found that juveniles differed significantly in behavior time allocation from

other age categories but yearlings and adults did not differ from each other. Sex has also been found to have no effect on time allocation (Blumstein et al. 2004).

Non-foraging marmots and marmots approached to measure FID

We found no effects of any factor on intervals between bouts of vigilance or locomotion among non-foraging marmots. The interval between bouts of locomotion increased as group size increased, but this effect was marginal. If predation risk is lower for non-foraging than foraging marmots because foraging individuals must relax vigilance to find food and eat, individual vigilance may suffice while not foraging risk may be relatively unaffected by variation in factors such as group size and colony. Less frequent movement may be needed when not foraging, reducing any potential effects of factors such as slope and substrate type on intervals between bouts of locomotion.

For marmots observed immediately before being approached to measure FID, both intervals between bouts of locomotion and between bouts of vigilance varied among colonies, which may indicate different amounts of interaction with human beings (Li et al 2011). Age category, sex, slope and substrate all had no effect on intervals between bouts of locomotion or vigilance. These lack of effects could be artifact of the small sample size of the pre-FID focals (N=48). Intervals between bouts of vigilance increased as group size increased, as predicted by the many eyes and risk dilution hypotheses. Intervals between bouts of locomotion were not related to group size. This could indicate that the behavior of these “relaxed” marmots was not primarily foraging and/or that the smaller sample size did not permit detection of a significant relationship. Because the P value for group size is so large, the latter possibility is remote.

390

391 *Relationship between AD and FID*

392 Our main conclusion is that even after removing FID data that could have been
393 influenced by spontaneous bouts of vigilance or locomotion, the relationship between AD
394 and FID remained large. This empirical result adds to a number of simulation and
395 modeling approaches which often (Chamaillé-Jammes and Blumstein 2012) but not
396 always (Dumont et al. 2012) have supported the large relationship between AD and FID.
397 Importantly, we empirically studied the AD-FID relationship in a was on a close relative
398 of the marmot species studied by Dumont et al. (2012). Although, some variables that
399 have large effects in comparative studies do not have similarly large effects in single-
400 species studies (e.g., body mass's effect on explaining in FID's Blumstein 2006), AD
401 seems to have a general and important effect both within and between species. The AD-
402 FID relationship is not entirely a consequence of spontaneous vigilance, spontaneous
403 movement or any artifactual relationship as proposed by Dumont et al. (2012). The
404 FEAR hypothesis suggests that monitoring the predator during its approach affects
405 assessment of costs of fleeing and not fleeing.

406

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Table 1. Coefficient estimates, standard error of estimate (SEM), t-value and p-value for estimates, and p-values for the possible factors that explain the fixed effects influencing the interval between bouts of vigilance in yellow-bellied marmots.

Focal Type	Category	Estimate	SEM	t-value	p-value
Foraging	Intercept	3.42	0.0875	39.2*	0.0001*
	Colony				<0.001*
	Avalanche	0			
	Bench	0.163	0.0875	1.80	0.0582*
	Boulder	0.144	0.0912	0.900	0.306
	Gothic Town	-0.003194	0.160436	-0.03	0.9518
	Horse Mound	-0.0111	0.099	-0.110	0.8230
	Marmot	0.201	0.0881	2.28*	0.0056*
	Meadow				
	North Picnic	0.269	0.104	2.60*	0.0032*
	Picnic	0.313	0.0879	3.55*	0.0001*
	River	0.191	0.0886	2.16*	0.0142*
	Stonefield	0.174	0.105	1.66	0.0718
	Age Class				1.00
	Adult	0			
	Yearling	0.0153	0.0178	0.86	0.504
	Sex				1.00
	Female	0			
	Male	0.0384	0.0221	1.74	0.0988
	Slope				1.00
	0-10°	0			
	10-30°	0.00617	0.0161	0.38	0.996
	>30°	0.0159	0.0279	0.57	0.4500
	Substrate				0.0193*
	DSL V	0			

Flight Initiation Distance	HV	0.0802	0.0188	4.26*	0.0001*
	T	-0.0476	0.0632	-0.75	0.282
	Group Size	0			0.000166*
	Number in 10 m	0.0329	0.00673	4.90*	0.0001*
	Intercept	5.20	0.631	8.25*	0.0001*
	Colony				0.0058*
	Avalanche	0			
	Bench	-3.27	1.81	-1.81	0.0796
	Boulder	-2.88	1.24	-2.32*	0.0282*
	Marmot Meadow	-0.572	0.556	-1.03	0.312
Non- foraging	Picnic	-1.13	0.488	-2.31*	0.0296
	River	-0.570	0.793	-0.718	0.482
	Age Class				0.763
	Adult	0			
	Yearling	-0.0721	0.444	-0.162	0.897
	Sex				1.00
	Female	0			
	Male	-0.0389	0.372	-0.105	0.921
	Slope				0.592
	0-10°	0			
	10-30°	-0.329	0.398	-0.828	0.414
	>30°	0.0729	0.573	0.127	0.908
	Substrate				0.050
	DSL V	0			
	HV	1.575	1.349	1.17	0.245
	T	0.804	0.510	1.58	0.124
	Group size				0.117
	Number in 10 m	-0.354	0.147	-2.41*	0.0196*
	Intercept	3.84	0.427	8.98*	0.0001*
	Colony				0.121

Avalanche	0				
Bench	0.0132	0.681	0.019	0.989	
Boulder	1.15	1.02	1.13	0.246	
Gothic Town	0.566	0.669	0.846	0.421	
Marmot	0.228	0.439	0.520	0.693	
Meadow					
Picnic	-0.924	0.876	-1.05	0.282	
River	0.469	0.466	1.01	0.310	
Stonefield					
Age class				1.00	
Adult	0				
Yearling	0.0163	0.327	0.050	0.922	
Sex				1.00	
Female	0				
Male	-0.0296	0.279	-0.106	0.974	
Slope				0.281	
0-10°	0				
10-30°	-0.427	0.425	-1.00	0.266	
>30°	0.558	0.810	0.689	0.507	
Substrate				0.635	
DSL V	0				
HV	0.187	0.374	0.499	0.640	
T	0.462	0.331	1.40	0.174	
Group size				0.750	
Number in 10 m	-0.255	0.197	-1.30	0.214	

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Table 2. Coefficient estimates, standard error of estimate (SEM), t-value and p-value for coefficient estimates, and p-values for the possible factors that explain the fixed effects influencing the interval between bouts of locomotion in yellow-bellied marmots.

Focal Type	Category	Coefficient	SEM	t-value	p-value
Foraging	Intercept	4.12	0.0879	46.8	0.0001*
	Colony				1.00
	Avalanche	0			
	Bench	-0.247	0.0917	-2.69*	0.002*
	Boulder	0.0934	0.163	0.57	0.573
	Gothic Town	-0.170	0.0917	-1.86	0.0366*
	Horse Mound	-0.193	0.0998	-1.94	0.0514
	Marmot Meadow	-0.262	0.0879	-2.98*	0.0014*
	North	-0.172	0.106	-1.63	0.0820
	Picnic	-0.156	0.0875	-1.79	0.0580
	Picnic	-0.156	0.0875	-1.79	0.0580
	River	-0.266	0.0884	-3.01*	0.0016*
	Stonefield	-0.3107	0.109	-2.86*	0.0034*
	Age class				1.00
	Adult	0			
	Yearling	0.00680	0.0198	0.34	0.522
	Sex				1.00
	Female	0			
	Male	-0.00430	0.0217	-0.2	0.803
	Slope				1.00
	0-10°	0			
	10-30°	-0.0406	0.195	-2.09*	0.0162*

	>30°	-0.0901	0.0337	-2.67*	0.0044*
	Substrate				<0.001*
	DSL V	0			
	HV	0.119	0.0230	5.18*	0.0001*
	T	0.307	0.0770	3.98*	0.0001*
	Group size				0.106
	Number in 10 m	0.0252	0.00818	3.08*	0.0046*
Flight Initiation Distance	Intercept	5.27	0.307	17.2*	<0.001*
	Colony				0.044*
	Avalanche	0			
	Bench	-1.651	0.881	-1.87	0.0694
	Boulder	-1.47	0.603	-2.43*	0.0204*
	Marmot Meadow	-0.843	0.271	-3.12*	0.0037*
	Picnic	-0.265	0.237	-1.12	0.272
	River	-0.486	0.386	-1.26	0.216*
	Age class				1.00
	Adult	0			
	Yearling	-0.0523	0.216	-0.242	0.810
	Sex				1.00
	Female	0			
	Male	0.101	0.181	0.560	0.579
	Slope				1.00
	0-10°	0			
	10-30°	-0.108	0.194	-0.556	0.582
	>30°	-0.298	0.279	-1.07	0.292
	Substrate				0.981
	DSL V	0			
	HV	0.177	0.656	0.270	0.789

Non-foraging	T	0.0152	0.248	0.061	0.951
	Group size				1.00
	Number in 10 m	-0.0147	0.0714	-0.205	0.839
	Intercept	4.58	0.513	8.93*	0.0001*
	Colony				0.134
	Avalanche	0			
	Bench	-0.351	0.829	-0.423	0.662
	Boulder	0.504	1.23	0.409	0.687
	Gothic Town	-0.254	0.838	-0.303	0.763
	Marmot Meadow	-0.504	0.516	-0.975	0.347
	Picnic	-0.336	1.12	-0.302	0.757
	River	0.373	0.564	0.662	0.508
	Age class				0.430
	Adult	0			
	Yearling	-0.423	0.398	-1.06	0.303
	Sex				0.414
	Female	0			
	Male	0.417	0.339	1.23	0.227
	Slope				0.220
	0-10°	0			
	10-30°	-0.531	0.542	-0.981	0.339
	>30°	0.369	1.05	0.350	0.727
	Substrate				0.795
	DSL V	0			
	HV	-0.0190	0.489	-0.039	0.990
	T	0.218	0.431	0.506	0.616
	Group size				0.182
	Number in 10 m	-0.473	0.246	-1.92	0.0534

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 500 **Table 3.** Predicted average, minimum and maximum intervals between bouts of vigilance
 501 and locomotion in yellow-bellied marmots measured on three different situations (focal
 502 type).

Behavior	Model	503	
		Predicted Temporal Distance (s)	Predicted Spatial Distance (m)
Vigilance	Non-Foraging		
		?	16.7
		Min	0.616
		Max	74.4
	FID		
		?	32.0
		Min	0.210
		Max	85.8
	Foraging		
		?	4.88
		Min	1.26
		Max	5.25
Locomotion	Non-Foraging		
		?	40.0
		Min	0.227
		Max	196
	FID		
		?	74.4
		Min	3.16
		Max	80.5
	Foraging		

		8.24	504
	?		504
	Min	5.68	2.84 505
	Max	23.2	506
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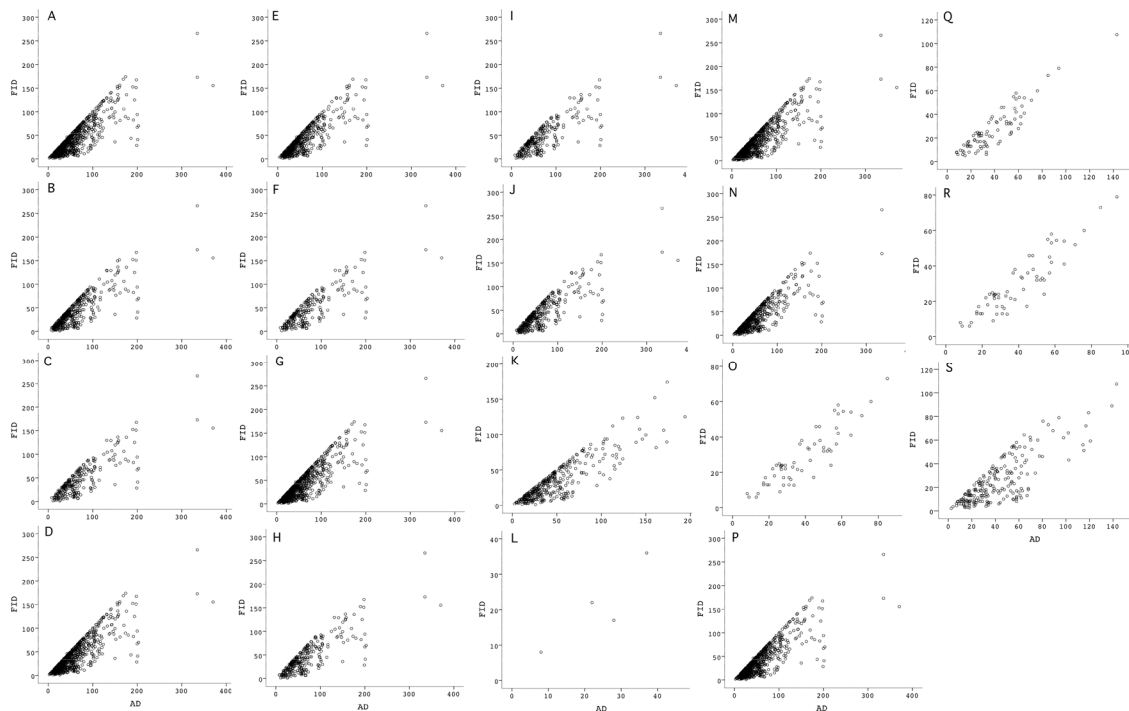
Table 4. Sample size (N), linear regression coefficient (r), and p-values calculated from a linear mixed effect model to account for repeated observations of individuals (p-values calculated using MCMC) for models explaining the relationship between AD and FID after removing observations that could have occurred because of bouts of intermittent vigilance or locomotion.

Behavior	Model	N	R	p-value
All	All Focals	896	0.726	<0.001
Vigilance	Non-Foraging			
	?	481	0.713	<0.001
	Min	292	0.703	<0.001
	Max	874	0.730	<0.001
	FID			
	?	624	0.723	<0.001
	Min	263	0.705	<0.001
	Max	885	0.727	<0.001
	Foraging			
	?	322	0.704	<0.001
	Min	292	0.703	<0.001
	Max	408	0.707	<0.001
Locomotion	Non-Foraging			
	?	404	0.769	<0.001
	Min	6	0.792	<0.001
	Max	895	0.726	<0.001
	FID			
	?	638	0.724	<0.001

Foraging	Min	60	0.828	<0.001
				558
	Max	847	0.728	<0.001
				559
				560
				561
	?	88	0.974	<0.001
				562
	Min	60	0.979	<0.001
				563
	Max	236	0.936	<0.001
				564

Figure Legend

Figure 1. Relationship between FID and AD. FID data were systematically filtered based on the minimum, maximum, and mean intervals between bouts of vigilance and locomotion so as to remove observations that could have been potentially influenced by natural vigilance or locomotion (see text for details). In A, no data were removed; in B-S, the variable used to filter the data and the type of focal observation are specified: A) All FIDs used, N=896, B) Average predicted value from non-foraging vigilance focals used, N=481, C) Minimum predicted value from non-foraging vigilance focals used, N=292, D) Maximum predicted value from non-foraging vigilance focals used, N=874, E) Average predicted value from pre-FID vigilance focals used, N=624, F) Minimum predicted value from pre-FID vigilance focals used, N=263, G) Maximum predicted value from pre-FID vigilance focals used, N=885, H) Average predicted value from foraging vigilance focals used, N=322, I) Minimum predicted value from foraging vigilance focals used, N=292, J) Maximum predicted value from foraging vigilance focals used, N=408, K) Average predicted value from non-foraging locomotion focals used, N=404, L) Minimum predicted value from minimums from non-foraging locomotion focals used, N=6, M) Maximum predicted value from non-foraging locomotion focals used, N=895, N) Average predicted value from pre-FID locomotion focals used, N=638, O) Minimum predicted value from pre-FID locomotion focals used, N=60, P) Maximum predicted value from pre-FID locomotion focals used, N=847, Q) Average predicted value from foraging locomotion focals used, N=88, R) Minimum predicted value from foraging locomotion focals used, N=60, S) Maximum predicted value from foraging locomotion focals used, N=236.



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Supplemental Data

Table 5. Coefficient estimates, SEM, t-value and p-value for coefficient estimates, and p-values for the factors (estimated by MCMC details in text) that explain the fixed effects influencing the interval between bouts of locomotion and vigilance. Model contained 25 randomly selected foraging focals from categories: Adult Male, Adult Female, Yearling Male and Yearling Female combined with all non-foraging and pre-FID focals.

Behavior	Category	Estimated	SEM	t-value	p-value
Locomotion	Intercept	4.06	0.292	13.9*	0.0001*
	Focal Type				0.0172*
	Foraging	0			
	Flight	0.837	0.221	3.78*	0.0004*
	Initiation				
	Distance				
	Non-Foraging	0.235	0.200	1.18	0.250
	Colony				0.936
	Avalanche	0			
	Bench	-0.165	0.339	-0.486	0.626
	Boulder	0.145	0.672	0.215	0.824
	Gothic Town	0.0430	0.338	0.127	0.884
	Horse Mound	-0.162	0.676	-0.240	0.823
	Marmot	-0.208	0.248	-0.840	0.395
	Meadow				
	North Picnic	-0.450	1.15	-0.393	0.705
	Picnic	0.0191	0.269	0.071	0.943
	River	0.108	0.264	0.408	0.678
	Stonefield	-0.303	1.14	-0.267	0.791
	Age Class				0.802
	Adult	0			

	Yearling	-0.224	0.156	-1.43	0.153
	Sex				1
	Female	0			
	Male	0.0792	0.143	0.555	0.587
	Slope				1
	0-10°	0			
	10-30°	0.0419	0.18	0.238	0.823
	>30°	0.159	0.249	0.639	0.527
	Substrate				1
	DSL	0			
	HV	0.0517	0.205	0.253	0.791
	T	0.209	0.221	0.944	0.332
	Group Size				1
	Number in 10 m	-0.0595	0.0713	-0.834	0.398
Vigilance	Intercept	3.74	0.254	14.7*	0.0001*
	Focal Type				0.471
	Foraging	0			
	Flight Initiation Distance	0.550	0.192	2.86*	0.005*
	Non-Foraging	0.147	0.174	0.843	0.394
	Colony				0.974
	Avalanche	0			
	Bench	-0.149	0.295	-0.506	0.619
	Boulder	0.118	0.585	0.202	0.868
	Gothic Town	0.0111	0.294	0.038	0.957
	Horse Mound	-0.146	0.589	-0.247	0.809
	Marmot Meadow	0.0290	0.216	0.134	0.875
	North Picnic	-0.0664	0.997	-0.067	0.938
	Picnic	-0.291	0.234	-1.24	0.225

River	0.132	0.230	0.573	0.547
Stonefield	-0.406	0.988	-0.411	0.693
Age Class				1
Adult	0			
Yearling	0.00949	0.136	0.070	0.954
Sex				1
Female	0			
Male	-0.00784	0.124	-0.063	0.953
Slope				1
0-10°	0			
10-30°	-0.136	0.153	-0.890	0.377
>30°	0.167	0.217	0.771	0.438
Substrate		0.738		
DSL	0			
HV	0.0522	0.178	0.293	0.767
T	0.386	0.192	1.29*	0.0458*
Group Size				1
Number in 10 m	-0.0747	0.0621	-1.20	0.226

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