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Original Article

The flush early and avoid the rush hypothesis holds after accounting for spontaneous behavior

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When approached by a predator, prey make economic decisions between remaining where they are and obtaining benefits from their current activity or leaving and enhancing their safety. The "flush early and avoid the rush" hypothesis suggests that animals that flee to escape approaching threats flee soon after they become alert to an approaching predator so as to reduce any costs incurred by ongoing monitoring of the predator. This hypothesis has been supported by several studies, but some researchers argue the relationship may be partially or entirely a consequence of bouts of spontaneous vigilance and/or bouts of spontaneous locomotion (vigilance or locomotion that occur when the animal is unaffected by a predator), rather than an economic decision related to the approaching predator. If this were true, spontaneous vigilance might incorrectly be recorded as alert distance (predator–prey distance when the prey becomes aware of and begins to monitor the predator) and spontaneous locomotion might be incorrectly recorded as flight initiation distance (predator–prey distance when escape begins). To evaluate these potential effects, we recorded the intervals between bouts of spontaneous vigilance and locomotion by yellow-bellied marmots (*Marmota flaviventris*). We used these baseline rates to conduct a series of alert distance–flight initiation distance regressions after removing potentially spurious observations recorded as alert distance or flight initiation distance. Although spontaneous vigilance and spontaneous locomotion may lead to artifactual increases in flight initiation distance as alert distance increases, the fundamental relationship remains after effects of spontaneous movements have been removed, supporting the flush early and avoid the rush hypothesis. We tested a key challenge of the "flush early and avoid the rush" (FEAR) hypothesis; our results provide strong support for the hypothesis.

Key words: **alert distance, antipredator behavior, economics of escape, flight initiation distance, flush early and avoid the rush, starting distance, vigilance, yellow-bellied marmots.**

INTRODUCTION

Escape behavior in response to predatory threat is of critical importance to animals because failure to escape results in death and termination of any future contribution to fitness. However, escaping too early can also result in a loss of benefits from current activity (e.g., finding food or a mate). Individuals that behave optimally will flee at the point where the benefits of staying are outweighed by the risks of remaining (Ydenberg and Dill 1986) or at a distance where expected future fitness is maximized (Cooper and Frederick 2007). Flight initiation distance (FID), the predator–prey distance when escape begins, can be used to test risk perception and decision making in escape behavior (Ydenberg and Dill 1986; Stankowich and Blumstein 2005; Cooper and Frederick 2007). Animals may behave differently as a function of their distance from the threat, their escape strategy, and their ability to escape to a refuge. Cooper (2005) found that approach speed and behavior of predator affects FID in certain species of lizards. Cryptic prey are predicted to flee immediately when alerted to the presence of an approaching predator or to remain immobile and flee only when the predator has detected it (Broom and Ruxton 2005).

A crucial factor affecting the optimal decision to flee is the prey's distance from the predator. Blumstein (2003) suggested

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that prey must respond differently depending on which distance category (zones) the prey is located. These distances are divided into 3 response categories, large enough to be distinguished from one another, related to predator–prey distance. At long predator–prey distances (Zone III), the predator either has not been noticed or does not appear to pose a threat to the prey. By contrast, when a predator is detected or initiates its approach close to the prey within Zone I, the predator is "too close" and the prey will flee immediately because the risk of predation is very high. Between these 2 intervals is a Zone II, in which the prey monitors the predator's approach and is expected to make economic decisions about when to flee (Blumstein 2003). However, the monitoring of the predator behavior in Zone II may be costly to the prey because the prey's attention must be diverted from its current activity (e.g., foraging) to monitor the predator (Chan and Blumstein 2011).

In many bird species that flew to escape an approaching predator, the finding that FID was positively correlated with the predator's starting distance (predator distance from prey when the approach begins; commonly used as proxy to alert distance) was difficult to explain with the previously existing economic escape theory (Blumstein 2003). Therefore, Blumstein (2010) proposed the "flush early and avoid the rush" (FEAR) hypothesis that prey within Zone II will flee from an approaching predator sooner (at a longer FID) in order to minimize the monitoring costs. Cooper and Blumstein (2014) reevaluated the FEAR hypothesis and incorporated another factor that could explain the "flush early" response: as duration of monitoring increases, the assessed risk of predation dynamically increases. Thus, the proposed effects of monitoring during the predator–prey encounter were accommodated by optimal escape theory (Cooper and Blumstein 2014).

In a recent phylogenetic meta-analysis, Samia et al. (2013) found results consistent with the FEAR hypothesis in several species of birds, mammals, and lizards, corroborating the idea that prey generally flush early from predators. Nonetheless, despite the accumulated evidences, the FEAR hypothesis has been challenged on biological grounds.

Cooper (2005) hypothesized that the relationship between starting distance and FID may be due to a *biological* effect. As starting distance increases, the duration of the predator's approach increases. Thus, prey may be more likely to move spontaneously, in a manner unrelated to predator approach (Cooper et al. 2009). Vigilance (behaviors aimed to detect potential threats—e.g., looking around) and locomotion (behaviors related to dispersion—e.g., walking or running) are considered to be spontaneous when observers are unable to detect the presence of a predator (e.g., by directly seeing a predator or hearing its vocalizations or alarm calls). In a potentially artifactual way, spontaneous vigilance and locomotion could be recorded as alert distance and FID, creating noise in the analysis (Cooper 2005). The effect of these artifactual records was theoretically demonstrated by computational modeling (Chamaillé-Jammes and Blumstein 2012).

Despite these theoretical arguments, detailed empirical studies addressing the influence of spontaneous vigilance and locomotion on alert distance and FID and their implications for the FEAR hypothesis are lacking. The most effective way to account for these potentially confounded effects may be to record baseline rates of spontaneous vigilance and locomotion and use the baseline rates to adjust observed alert distance and FIDs (Cooper 2005; Chamaillé-Jammes and Blumstein 2012). The baseline data for spontaneous movements would aid in distinguishing between predator-related and spontaneous bouts of vigilance and locomotion and help determine whether alert distance and FID were potentially being falsely recorded and, in turn, spuriously supporting the FEAR hypothesis.

Here, we determine whether and how bouts of spontaneous vigilance and bouts of spontaneous locomotion affect the positive alert distance–FID relationship predicted by the FEAR hypothesis. To do so, we recorded the intervals between bouts of spontaneous vigilance and bouts of spontaneous locomotion for focal observations collected on individually marked yellow-bellied marmots (*Marmota flaviventris*) under natural conditions (i.e., in activities not related to predator avoidance) to create a baseline of the natural rates of these behaviors. We converted the intervals between bouts of spontaneous vigilance and locomotion from a temporal to a spatial scale based on the predator's approach speed. Movements that occurred within this predicted spatial interval between spontaneous vigilance and locomotion (i.e., between alert or approach distance and the distance at which a spontaneous movement was expected from the baseline data) were excluded as potentially spurious from analysis of a large data set. We subsequently conducted 28 alert distance–FID regressions with these filtered data, 1 regression with the entire data set and 27 more regressions based on filtered data that represent all possible combination of behaviors, focal types, and intervals to verify whether the alert distance–FID relationship remained positive.

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 2-min focal animal samples (Altmann 1974) to study the natural intervals between bouts of spontaneous vigilance and bouts of spontaneous locomotion. Focal observations were conducted during peak hours of marmot activity (07:00–10:30 and 15:30–18:30 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 to ×45 spotting scope at distances (more than 100 m from animals) that did not obviously influence their behavior. Our ethogram included quadrupedal looking, rear (standing on hind legs) looking, quadrupedal foraging, rear foraging (bipedal foraging while standing on hind legs), walking, running, and other behaviors. Thus, our ethogram would permit us to record all forms of spontaneous vigilance and spontaneous locomotion. Importantly, we did not analyze focals collected when a predator was detected or animals were heard alarm calling during or immediately prior to the focal. Focal observations were dictated into a microcassette recorder (Blumstein et al. 2004, 2010). Our complete data set included 1759 focal observations recorded from 2002 to 2013, observed under 3 different types of beginning behaviors (hereafter, focal types). The focal type "foraging" was composed of observations on foraging marmots exhibiting foraging and moving behaviors (1608 focals). The focal type "nonforaging" was composed of observations on marmots exhibiting relaxed behaviors, excluding rearing up or "nervous looking around" (102 focals). Finally, the focal type "prior FID" was composed of observations of "relaxed" animals exhibiting similar behaviors to "non-foraging" individuals immediately before initiating an experimental FID approach (48 focals).

Animals sometimes moved out of sight during focal observations. We restricted our analysis to those observations in which the subject was in sight the entire time. We recorded 3 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 (flat ground: 0–10°, shallow incline: 11–30°, and steep incline: >30°), and the substrate on which animals were observed (dirt/stone/low vegetation, high vegetation, and talus). Vegetation was considered to be low if it did not reach above the marmots' head (sensu Blumstein et al. 2010). These 3 factors have previously been found to affect running speed and thus escape behavior (Blumstein et al. 2004).

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; ≥95% accuracy 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 vigilance (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 2-min focal period. Thus, if an individual was quadrupedally looking on a rock for the entire duration of the focal observation (as many did when not foraging), the interval between bouts of spontaneous vigilance and the interval between bouts of spontaneous locomotion were not estimated (12 observations were excluded from analysis for this reason, 17 other observations were excluded for being too short, under 60 s out of a total 120 s). 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. Animals may perceive humans as predators and human approach was used as a proxy for natural predator approach (Frid and Dill 2002). Observers identified a relaxed marmot and sat quietly for 10 min to eliminate possible effects of observer arrival before initiating an approach. For "prior FID" focal observations, experimental approaches were preceded by an additional 2-min focal interval required to measure the spontaneous behaviors as explained above. Observers were trained to walk directly toward the subject at 0.5 m/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 of the approach. Subsequent flags were dropped when the animal first oriented itself toward the approaching human and when the animal began to flee. The distances between these markers were afterward measured to the nearest 0.1 m and used to estimate starting distance, alert distance, and FID, respectively. In each trial, we recorded the age and sex of individuals, distance to burrow, the incline of the slope, and the number of marmots within 10 m. Individual marmots were tested no more than once per day. These data were pooled together before analyses were run.

Statistical analyses

Our analytical approach is summarized in Figure 1. We asked 3 questions.

1) What factors influence intervals between bouts of spontaneous vigilance and bouts of spontaneous 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, age class, sex, colony, incline, substrate type, 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 and Bates 2000). We estimated the variation

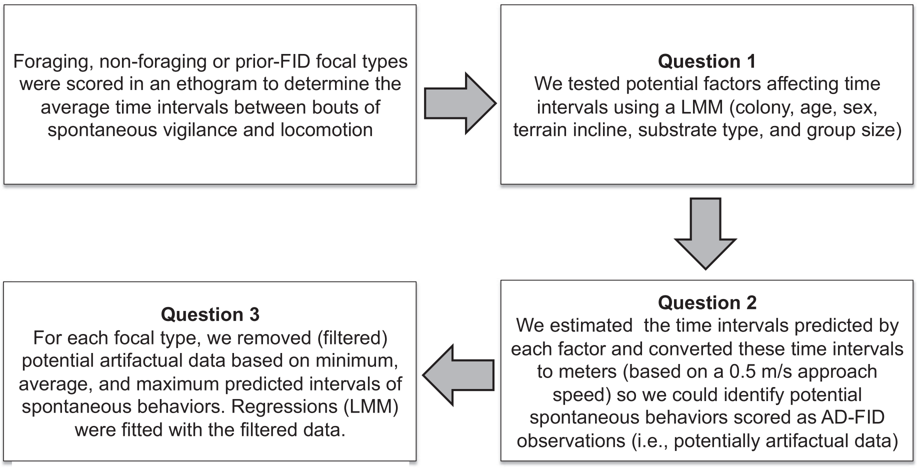

Figure 1
Flow chart illustrating our multistep analysis procedure to identify (and remove) observations of alert distance and FID that might be potentially spurious because they could have reflected spontaneous vigilance or spontaneous locomotion.

explained by the model with the Extract Fixed Effects function, fixef(), which extracted coefficients of fixed effects (Pinheiro and Bates 2000).

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

Because the sample sizes of focal types were unbalanced, we elected to estimate each effect coefficients separately 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" package (details in Baayen et al. 2008). We used the LRT to determine significance of fixed effects between a model with and without a given fixed effect (Pinheiro and Bates 2000). Using the coefficient estimates, we calculated the predicted intervals between bouts of spontaneous vigilance and locomotion for adults and yearlings of both sexes at each of the 10 colonies, over all 3 substrates, and in group sizes that ranged from 1 to 4 marmots. We back-transformed these estimated intervals and then multiplied these temporal intervals by 0.5 m/s (the approach speed) 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.

3) Does the relationship between alert distance and FID hold after removing observations that could be accounted for by bouts of spontaneous vigilance and bouts of spontaneous locomotion?

We compiled all FID observations collected between 2003 and 2013 ($N = 893$). First, using the entire data set, we fitted a LMM to estimate the relationship between alert distance and FID. We controlled for repeated observations and possible acclimation in some individuals by setting individual identity as a random effect. In sequence, we conducted a series of LMM analyses with data filtered (see below) according to the predicted spatial intervals between spontaneous vigilance and locomotion of yellow-bellied marmots.

Our algorithm to filter data based on spontaneous vigilance was to remove from the analysis the paired alert distance–FID observations in which the difference between starting distance and alert distance was less than or equal to a given predicted interval between bouts of vigilance. Similarly, to filter the data based on spontaneous locomotion, we removed from the analysis the paired alert distance–FID observations in which the differences between alert distance and FID were less than or equal to a given predicted interval between bouts of locomotion. In addition, one could imagine an extreme situation in which an individual's spontaneous vigilance was erroneously recorded as alert distance, and spontaneous locomotion was erroneously recorded as FID. To account for this latter situation, we also filtered data by removing from analysis the paired alert distance–FID observations in which both the difference between starting distance and alert distance was less than or equal to a given predicted interval between bouts of vigilance, and the difference between alert distance and FID was less than or equal to a given predicted interval between bouts of locomotion.

Testing the significance of the alert distance–FID relationship

The relationship between alert distance and FID is a constrained envelope. By definition, FID can only assume values equal to or lower than the actual alert distance; a prey cannot run away from a predator before it has detected it. This constraint can potentially 1) violate the homoscedasticity assumption of regression analysis (because variance of FID can increase as alert distance increases) and 2) artificially inflate the strength of the relationship between the variables. These considerations precluded simply using traditional null hypothesis testing to infer significance of the alert distance–FID relationship.

Therefore, we fitted a null model in which we compared the observed slope of a LMM model to slopes expected from a set of FIDs simulated given that FID must be less than or equal to alert distance (Gotelli and Graves 1996). To simulate FIDs, the null model algorithm extracted N (= the observed sample size) random values from a truncated normal distribution that had an upper limit of observed alert distance and a lower limit of 0 m. To be consistent with the analyses of observed data, we fitted a LMM to model the simulated FIDs as a function of observed alert distances and likewise set individual identity as a random effect to account for multiple observations per individual. We stored the simulated slope in a temporary vector and replicated this analysis 10 000 times. The P value of the observed slope was calculated by dividing the number of simulated slopes greater than or equal to the observed slope by 10 000 (i.e., the number of iterations). We forced these models through the origin (i.e., we eliminated the intercept) because a marmot that first became alerted to an approaching threat at 0 m could only flee at 0 m. Forcing the slope through the origins allows the slopes to be meaningfully comparable. For example, a slope of 0.6 and intercept of 0 describes a different relationship than a slope of 0.6 with an intercept of −20. However, P values of models in which intercepts were kept (both in observed and simulated models) were exactly the same as those without intercept (see Supplementary Material). Although adjusting the significance level due to multiple tests is generally not indicated in behavioral studies (Nakagawa 2004; Garamszegi 2006), we conservatively interpreted as significant P values ≤ 0.002 (i.e., 0.05/28). The R code used to run the null model is provided in Supplementary Material.

Effect size of the alert distance–FID relationship

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 on magnitude of the effect (Nakagawa 2004; Garamszegi 2006; Nakagawa and Cuthill 2007; Borenstein et al. 2009). We used the marginal coefficient of determination (R^2 for LMM) to estimate the amount of variance in FID accounted for by alert distance (Nakagawa and Schielzeth 2013). Møller and Jennions (2002) reviewed the predictive power of published meta-analyses in biology, allowing evaluation of the magnitude of biological effects in a consistent fashion. Average effect sizes found in most biological studies are small to intermediate, explaining on average 7% of the variance (Møller and Jennions 2002).

RESULTS

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

Although some of the factors that influenced intervals between bouts of spontaneous vigilance and bouts of spontaneous locomotion were found to be significant, the model explained little of the variation of 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 spontaneous vigilance (1.1%) and locomotion (7.1%). Models fitted to explain variation in nonforaging marmots explained a substantial amount of the variation in intervals between vigilance (17.6%) and locomotion (35.0%). Models fitted to explain variation in marmot behavior immediately preceding our approaches to measure FID (prior FID) also explained considerable variation in the intervals between vigilance (37.2%) and locomotion (11.4%).

Predicted intervals between bouts of spontaneous vigilance (χ^2 = 36.73, P = 0.0002, N = 1759 observations) and locomotion (χ^2 = 87.36, P < 0.001, N = 1759 observations) differed significantly among the 3 types of focal observations. For foraging marmots, intervals between bouts of spontaneous vigilance differed significantly among colonies and were longer when marmots foraged in high vegetation and as group size increased (Table 1). Foraging animals had longer intervals between bouts of spontaneous locomotion when they foraged in high vegetation, when they were on talus, and longer as group size increased (Table 2). Intervals between bouts of spontaneous locomotion while foraging varied significantly among colonies, and foraging animals had shorter intervals between bouts of spontaneous locomotion in different colonies and on inclines >10° than on flat ground (<10°) (Table 2). Intervals between either bouts of spontaneous locomotion or bouts of spontaneous vigilance were not significantly affected by model parameters for nonforaging animals (Tables 1 and 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 spontaneous vigilance differed significantly among colonies and increased significantly as group size increased (Table 1). Intervals between bouts of spontaneous locomotion for animals observed immediately before measurement of FIDs differed significantly among colonies (Table 2).

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

Based on these estimates of coefficients, our predicted spatial interval for spontaneous bouts of vigilance and locomotion varied considerably (Table 3). Thus, we used the minimum, mean, and maximum predicted intervals of each focal type to filter data in order to account for this variation.

3) Does the relationship between alert distance and FID hold after removing observations that could be accounted for by bouts of spontaneous vigilance and bouts of spontaneous locomotion?

Anyway examined, the relationship between alert distance and FID was large and highly significant, both in the entire data set and in every analysis of filtered data (Figure 2). The slopes of regressions ranged from 0.61 to 1.0 (Table 4). The explanatory power of all regressions was large, with R^2 values ranging from 0.73 to 1 (Table 4). All slopes obtained were highly significant (P < 0.0001), which makes it highly unlikely that alert distance–FID relationship was spurious (Table 4).

DISCUSSION

FID measurements used to assess the economic escape decisions of animals do not typically take into account the possible confounding effects of spontaneous vigilance and locomotion of prey animals. These spontaneous behaviors may lead to inaccurate or spurious estimates of alert distance and/or FID. Our explicit test of how both types of spontaneous behavior affect the alert distance–FID relationship showed that alert distance remains strongly correlated with FID after removing the effects of spontaneous vigilance and locomotion. This finding offers strong support for the FEAR hypothesis. Other

Table 1

Coefficient estimates, standard errors (SE), *t* values and *P* values for estimates, and *P* values for possible factors influencing the interval between bouts of spontaneous vigilance in yellow-bellied marmots

Focal type	Category	Estimate	SE	*t*	*P*
Foraging	Intercept	3.42	0.088	39.2	<0.001*
	Colony				<0.001*
	Avalanche	0			
	Bench	0.163	0.088	1.8	0.058
	Boulder	0.144	0.091	0.9	0.306
	Gothic Town	−0.003	0.160	−0.03	0.952
	Horse Mound	−0.011	0.099	−0.11	0.823
	Marmot Meadow	0.201	0.088	2.28	0.006*
	North Picnic	0.269	0.104	2.60	0.003*
	Picnic	0.313	0.088	3.55	<0.001*
	River	0.191	0.089	2.16	0.014*
	Stonefield	0.174	0.105	1.66	0.072
	Age class				1
	Adult	0			
	Yearling	0.015	0.018	0.86	0.504
	Sex				1
	Female	0			
	Male	0.038	0.022	1.74	0.099
	Incline				1
	0–10°	0			
	10–30°	0.006	0.016	0.38	0.996
	>30°	0.016	0.028	0.57	0.45
	Substrate				0.019*
	DSLV	0			
	HV	0.080	0.019	4.26	<0.001*
	T	−0.048	0.063	−0.75	0.282
	Group size			0	<0.001*
	Number in 10 m	0.033	0.007	4.90	<0.001*

Table 1
Continued

Focal type	Category	Estimate	SE	*t*	*P*
Nonforaging	Intercept	3.84	0.427	8.98	<0.001*
	Colony				0.121
	Avalanche	0			
	Bench	0.013	0.681	0.02	0.989
	Boulder	1.15	1.02	1.13	0.246
	Gothic Town	0.566	0.669	0.85	0.421
	Marmot Meadow	0.228	0.439	0.52	0.693
	Picnic	−0.924	0.876	−1.05	0.282
	River	0.469	0.466	1.01	0.31
	Age class				1
	Adult	0			
	Yearling	0.016	0.327	0.05	0.922
	Sex				1
	Female	0			
	Male	−0.030	0.279	−0.11	0.974
	Incline				0.281
	0–10°	0			
	10–30°	−0.427	0.425	−1	0.266
	>30°	0.558	0.81	0.69	0.507
	Substrate				0.635
	DSLV	0			
	HV	0.187	0.374	0.5	0.64
	T	0.462	0.331	1.4	0.174
	Group size				0.75
	Number in 10 m	−0.255	0.197	−1.3	0.214
Prior FID	Intercept	5.2	0.631	8.25	<0.001*
	Colony				0.006*
	Avalanche	0			
	Bench	−3.27	1.81	−1.81	0.08
	Boulder	−2.88	1.24	−2.32	0.028*
	Marmot Meadow	−0.572	0.556	−1.03	0.312
	Picnic	−1.13	0.488	−2.31	0.03
	River	−0.57	0.793	−0.72	0.482
	Age class				0.763
	Adult	0			
	Yearling	−0.072	0.444	−0.16	0.897
	Sex				1
	Female	0			
	Male	−0.039	0.372	−0.11	0.921
	Incline				0.592
	0–10°	0			
	10–30°	−0.329	0.398	−0.83	0.414
	>30°	0.073	0.573	0.127	0.908
	Substrate				0.05
	DSLV	0			
	HV	1.575	1.349	1.17	0.245
	T	0.804	0.51	1.58	0.124
	Group size				0.117
	Number in 10 m	−0.354	0.147	−2.41	0.02*

DSLV, dirt, stones, low vegetation; HV, high vegetation; T, talus.
*$P < 0.05$.

novel findings are that ecological factors and prey behavior while being approached affect rates of spontaneous vigilance and locomotion that in turn affect the alert distance–FID relationship.

Factors related to intervals between bouts of spontaneous vigilance and bouts of spontaneous locomotion

We found that what animals were initially doing (quantified by comparing focal animal samples) affected intervals between bouts of both spontaneous vigilance and locomotion. Specifically, animals have different interbout intervals when they are foraging and when they are not foraging.

Foraging animals

Of several factors included in our models that often explain variation in marmot vigilance behavior (e.g., Blumstein et al. 2004), colony, substrate, and group size explained substantial proportions of the variation in mean duration of the intervals between bouts of spontaneous vigilance. Age, incline, and sex did not affect these intervals. Both intervals between bouts of spontaneous vigilance and between bouts of spontaneous 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 affect 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 spontaneous vigilance and between bouts of spontaneous 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 spontaneous vigilance may occur because marmots forage more efficiently so as to spend less time in a risky habitat (a form of risk reduction). Furthermore, because they were foraging, high vegetation potentially provided more food in a single area. In areas 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 spontaneous vigilance and locomotion when in larger groups. This group size effect on vigilance 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

Table 2

Coefficient estimates, standard errors (SE), *t* values and *P* values for coefficient estimates, and *P* values for possible factors influencing the interval between bouts of spontaneous locomotion in yellow-bellied marmots

Focal type	Category	Estimate	SE	*t*	*P*
Foraging	Intercept	4.12	0.088	46.8	<0.001*
	Colony				1
	Avalanche	0			
	Bench	−0.247	0.092	−2.69	0.002*
	Boulder	0.093	0.163	0.57	0.573
	Gothic Town	−0.17	0.092	−1.86	0.037*
	Horse Mound	−0.193	0.099	−1.94	0.051
	Marmot Meadow	−0.262	0.088	−2.98	0.001*
	North Picnic	−0.172	0.106	−1.63	0.082
	Picnic	−0.156	0.088	−1.79	0.058
	River	−0.266	0.088	−3.01	0.002*
	Stonefield	−0.311	0.109	−2.86	0.003*
	Age class				1
	Adult	0			
	Yearling	0.007	0.02	0.34	0.522
	Sex				1
	Female	0			
	Male	−0.004	0.022	−0.2	0.803
	Incline				1
	0–10°	0			
	10–30°	−0.041	0.195	−2.09	0.016*
	>30°	−0.09	0.034	−2.67	0.004*
	Substrate				<0.001*
	DSLV	0			
	HV	0.119	0.023	5.18	<0.001*
	T	0.307	0.077	3.98	<0.001*
	Group size				0.106
	Number in 10 m	0.025	0.008	3.08	0.005*
Nonforaging	Intercept	4.58	0.513	8.93	<0.001*
	Colony				0.134
	Avalanche	0			
	Bench	−0.351	0.829	−0.42	0.662
	Boulder	0.504	1.23	0.41	0.687
	Gothic Town	−0.254	0.838	−0.30	0.763
	Marmot Meadow	−0.504	0.516	−0.98	0.347
	Picnic	−0.336	1.12	−0.30	0.757
	River	0.373	0.564	0.66	0.508
	Age class				0.43
	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
	Incline				0.22
	0–10°	0			
	10–30°	−0.531	0.542	−0.98	0.339
	>30°	0.369	1.05	0.35	0.727
	Substrate				0.795
	DSLV	0			
	HV	−0.019	0.489	−0.04	0.99
	T	0.218	0.431	0.51	0.616
	Group size				0.182
	Number in 10 m	−0.473	0.246	−1.92	0.053

Table 2
Continued

Focal type	Category	Estimate	SE	*t*	*P*
Prior FID	Intercept	5.27	0.307	17.2	<0.001*
	Colony				0.044*
	Avalanche	0			
	Bench	−1.651	0.881	−1.87	0.069
	Boulder	−1.47	0.603	−2.43	0.02*
	Marmot Meadow	−0.843	0.271	−3.12	0.004*
	Picnic	−0.265	0.237	−1.12	0.272
	River	−0.486	0.386	−1.26	0.216*
	Age class				1
	Adult	0			
	Yearling	−0.052	0.216	−0.24	0.81
	Sex				1
	Female	0			
	Male	0.101	0.181	0.56	0.579
	Incline				1
	0–10°	0			
	10–30°	−0.108	0.194	−0.56	0.582
	>30°	−0.298	0.279	−1.07	0.292
	Substrate				0.981
	DSLV	0			
	HV	0.177	0.656	0.27	0.789
	T	0.015	0.248	0.06	0.951
	Group size				1
	Number in 10 m	−0.015	0.071	−0.21	0.839

DSLV, dirt, stones, low vegetation; HV, high vegetation; T, talus.
*$P < 0.05$.

Table 3
Predicted minimum, average, and maximum spatial intervals (in meters) between bouts of spontaneous vigilance and locomotion in yellow-bellied marmots measured under 3 different beginning behaviors (focal types; see text for details)

Behavior	Focal type	Minimum	Average	Maximum
Vigilance	Foraging	1.26	2.44	5.25
	Nonforaging	0.62	8.35	74.4
	Prior FID	0.11	16	85.8
Locomotion	Foraging	2.84	4.12	11.6
	Nonforaging	0.23	20	196
	Prior FID	3.16	37.2	80.5

each individual when a predator attacks the group (i.e., risk dilution hypothesis—Hamilton 1971) and because the vigilance of an individual can be lessened by reliance on vigilance of other group members to detect predators (i.e., many eyes hypothesis—Pulliam 1973; Lima and Dill 1990; Roberts 1996).

Marmots foraging on talus also had longer intervals between bouts of spontaneous 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 both shallow and steep inclines >11°. Because this effect is independent of substrate type, there are at least 2 possible reasons that might account for more frequent movements. First, shorter intermovement intervals on steeper inclines might indicate that food was sparser on steeper inclines. Second, marmots may have been foraging more intensively to minimize their time in an exposed area and this resulted in more movements. Intervals between bouts of spontaneous vigilance were not affected by incline, suggesting that perceived risk of predation was not influenced by terrain steepness.

Neither vigilance nor locomotion varied between age categories (adults and yearlings) for any of the focal types. This finding is consistent with a previous report that juveniles differed significantly in behavioral 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 to these behaviors (Blumstein et al. 2004).

Nonforaging marmots and marmots immediately prior to an FID experiment

No measured variables explained variation in the intervals between bouts of spontaneous vigilance or locomotion among nonforaging marmots. The interval between bouts of spontaneous locomotion increased as group size increased, but this effect was marginal. Predation risk may be lower for nonforaging than for foraging marmots because foraging individuals reduce vigilance to find food and eat. Individual vigilance may suffice for foraging marmots, whereas risk for nonforaging marmots 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 incline and substrate type on intervals between bouts of spontaneous locomotion.

For marmots observed immediately before being approached to measure FID, both intervals between bouts of spontaneous

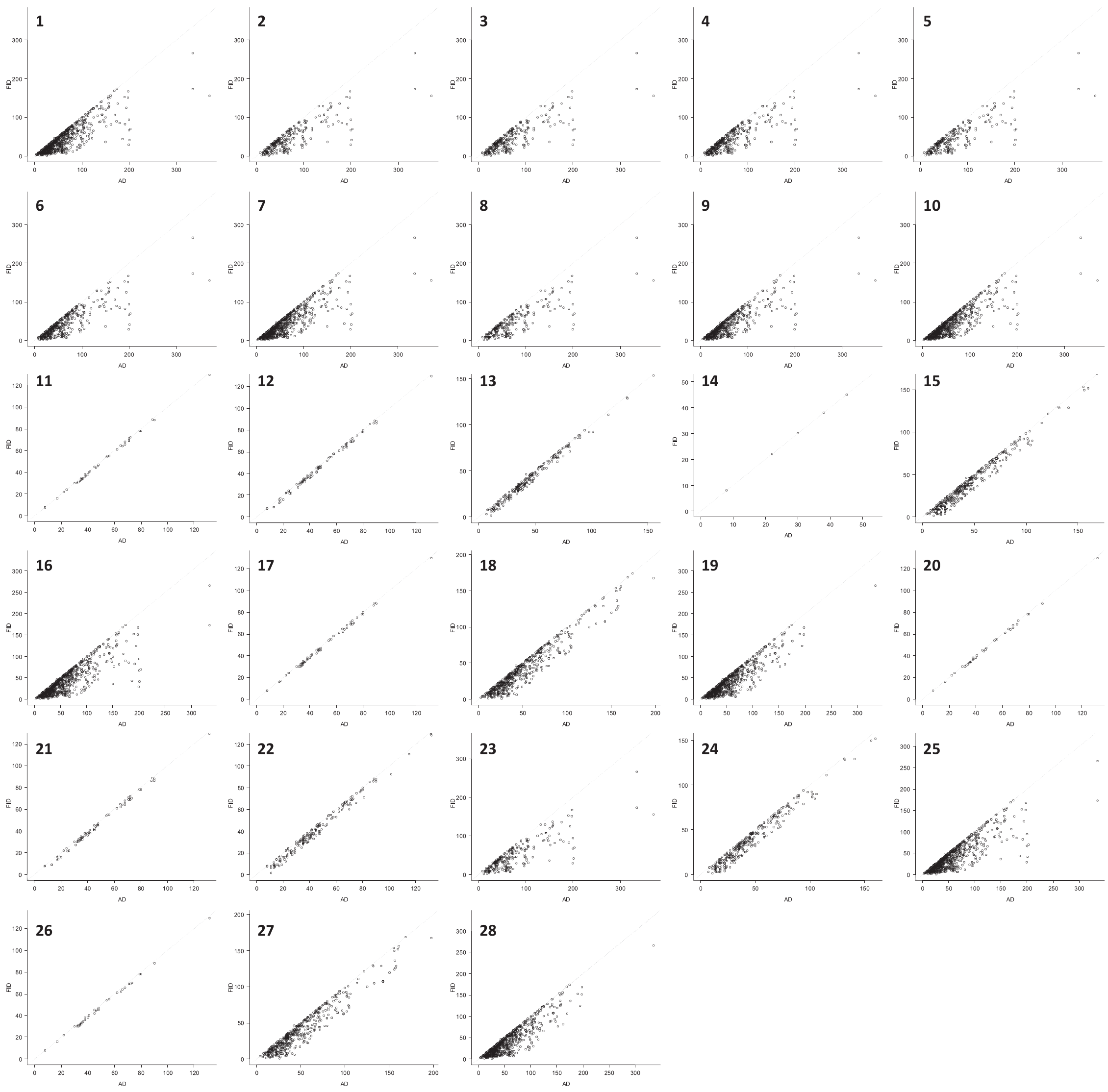

Figure 2

The relationship between alert distance (AD) and FID after removing potentially artifactual data (line illustrates 1:1 relationship). We systematically excluded from subsequent analysis prey's natural vigilance and locomotion that potentially might be recorded as alerting or fleeing responses, respectively (see text for details). 1) Analysis of the complete data set ($N = 893$). Analysis after removing data based on 2) minimum vigilance of foraging marmots ($N = 291$), 3) average vigilance of foraging marmots ($N = 321$), 4) maximum vigilance of foraging marmots ($N = 407$), 5) minimum vigilance of nonforaging marmots ($N = 262$), 6) average vigilance of nonforaging marmots ($N = 479$), 7) maximum vigilance of nonforaging marmots ($N = 871$), 8) minimum vigilance of prior FID marmots ($N = 262$), 9) average vigilance of prior FID marmots ($N = 621$), 10) maximum vigilance of prior FID marmots ($N = 882$), 11) minimum locomotion of foraging marmots ($N = 41$), 12) average locomotion of foraging marmots ($N = 88$), 13) maximum locomotion of foraging marmots ($N = 236$), 14) minimum locomotion of nonforaging marmots ($N = 6$), 15) average locomotion of nonforaging marmots ($N = 404$), 16) maximum locomotion of nonforaging marmots ($N = 892$), 17) minimum locomotion of prior FID marmots ($N = 60$), 18) average locomotion of prior FID marmots ($N = 637$), 19) maximum locomotion of prior FID marmots ($N = 843$), 20) minimum vigilance and locomotion of foraging marmots ($N = 36$), 21) average vigilance and locomotion of foraging marmots ($N = 72$), 22) maximum vigilance and locomotion of foraging marmots ($N = 188$), 23) minimum vigilance and locomotion of nonforaging marmots ($N = 262$), 24) average vigilance and locomotion of nonforaging marmots ($N = 321$), 25) maximum vigilance and locomotion of nonforaging marmots ($N = 870$), 26) minimum vigilance and locomotion of prior FID marmots ($N = 38$), 27) average vigilance and locomotion of prior FID marmots ($N = 527$), and 28) maximum vigilance and locomotion of prior FID marmots ($N = 843$).

locomotion and between bouts of spontaneous vigilance varied among colonies, which may indicate different amounts of interaction with human beings (Li et al. 2011). Age category, sex, incline, and substrate all had no effect on intervals between bouts of spontaneous locomotion or vigilance. The lack of significant effects could be an artifact of the small sample size of prior FID focal type ($N = 48$). Intervals between bouts of spontaneous vigilance increased as group size increased, a finding that could be predicted by the many eyes and risk dilution hypotheses (Hamilton 1971; Pulliam 1973). Intervals between bouts of spontaneous locomotion were not related to group size. This could indicate that the smaller sample size did not permit detection of

Table 4

Sample size (*N*), slope, confidence interval (CI), *P* values, and explanation power (R^2) of relationship between alert distance (AD) and FID in yellow-bellied marmots using both complete data set ("All") and a number of filtered data

Behavior	Focal_type	Interval	*N*	Slope	CI	*P*	R^2
All			893	0.70	0.68–0.72	<0.0001	0.74
Vigilance	Foraging	Minimum	291	0.62	0.59–0.65	<0.0001	0.73
		Average	321	0.62	0.59–0.65	<0.0001	0.73
		Maximum	407	0.64	0.61–0.67	<0.0001	0.73
	Nonforaging	Minimum	262	0.61	0.58–0.64	<0.0001	0.73
		Average	479	0.66	0.63–0.68	<0.0001	0.74
		Maximum	871	0.70	0.68–0.72	<0.0001	0.74
	Prior FID	Minimum	262	0.61	0.58–0.64	<0.0001	0.73
		Average	621	0.68	0.66–0.7	<0.0001	0.74
		Maximum	882	0.70	0.68–0.72	<0.0001	0.74
Locomotion	Foraging	Minimum	41	0.98	0.98–0.99	<0.0001	0.99
		Average	88	0.97	0.97–0.98	<0.0001	0.99
		Maximum	236	0.95	0.94–0.96	<0.0001	0.98
	Nonforaging	Minimum	6	1.00	1–1	<0.0001	1.00
		Average	404	0.91	0.9–0.93	<0.0001	0.95
		Maximum	892	0.71	0.69–0.73	<0.0001	0.74
	Prior FID	Minimum	60	0.98	0.97–0.98	<0.0001	0.99
		Average	637	0.86	0.84–0.87	<0.0001	0.90
		Maximum	843	0.77	0.75–0.78	<0.0001	0.81
Both	Foraging	Minimum	36	0.98	0.97–0.98	<0.0001	0.99
		Average	72	0.97	0.96–0.98	<0.0001	0.99
		Maximum	188	0.94	0.93–0.96	<0.0001	0.97
	Nonforaging	Minimum	262	0.61	0.58–0.64	<0.0001	0.73
		Average	321	0.90	0.88–0.91	<0.0001	0.93
		Maximum	870	0.71	0.69–0.73	<0.0001	0.74
	Prior FID	Minimum	38	0.97	0.96–0.98	<0.0001	0.99
		Average	527	0.84	0.83–0.86	<0.0001	0.89
		Maximum	843	0.77	0.75–0.78	<0.0001	0.81

"Both" category indicates data filtering assuming that both AD and FID were simultaneously inaccurately recorded (see text for details).

a significant relationship. Because the *P* value for group size is so large, the latter possibility is remote.

Relationship between alert distance and FID

One of the criticisms of the FEAR hypothesis is that bouts of spontaneous vigilance and locomotion may bias the estimates of the alert distance–FID relationship (Cooper et al. 2009). Here, we explicitly tested this potential confound by removing from analysis potentially spurious observations. Our main conclusion is that even after removing alert distance and FID estimates that could have been the result of spontaneous movements, the alert distance–FID relationship remained large and highly significant. This empirical result supports the findings of a number of previous empirical studies (reviewed by Samia et al. 2013) and by modeling (Chamaillé-Jammes and Blumstein 2012) that found a strong relationship between alert distance and FID.

Our results are consistent with the hypothesis that monitoring costs influence the decision to flee because prey cannot gain full benefit from their current activity if their attention is distracted by an approaching predator. This reduces the benefits of staying in the location versus fleeing. Because monitoring may increase with increased approach duration, this leads to the declining benefits and increasing costs that cause the prey to make economic decisions. Cooper and Blumstein (2014) suggested that this may lead to increased FID. The results are also with the dynamic increase in assessed risk as the duration and distance of approach increased, the other major effect of monitoring identified by Cooper and Blumstein (2014).

Our results reject alternative hypotheses about the relationship between alert distance and FID. For instance, if FID were to decrease as alert distance increases, we might infer that monitoring is associated with decreased assessed risk and/or increased ability to gain benefits during approach. Alternatively, alert distance and FID might not be related at all, a finding that would suggest there was no effect of monitoring on assessed risk or ability to gain benefits. Both alternatives are contradicted by numerous empirical studies.

Additionally, our study reinforces the conclusion that the alert distance–FID correlation is *not* simply a mathematical artifact. Dumont et al. (2012) suggested that because FID has an upper limit at alert distance and a lower limit at 0 m (a constraint envelope), even randomly selected numbers respecting such constraints could exhibit a significant positive relationship. To overcome potential spurious relationships, Chamaillé-Jammes and Blumstein (2012) used quantile regression and found that the positive relationship between alert distance and FID was still present in low quantiles, concluding that the relationship was unlikely to be a statistical artifact. Additionally, null model of Samia et al. (2013) that tested for no effect between alert distance and FID showed that only a small fraction of the significant relationships in species tested to date could have been the result of a spurious relationship. Here, our null model adds evidence against the spurious relationship hypothesis by showing that none of the 28 observed slopes were equal to those expected by chance. Importantly, we investigated the alert distance–FID relationship in yellow-bellied marmots, a close relative of the Alpine marmot (*Marmota marmota*) studied by Dumont et al. (2012).

We used a series of regressions in which, for each of them, we excluded potentially spurious data. However, the slope estimated for each regression did not depend on the slope estimated for a previous regression. This independence among regressions excludes problems that might be caused by propagation of the error (Wu

2006). On the other hand, the multiple tests could theoretically inflate Type I error. To avoid this problem, we applied the most conservative approach by using a Bonferroni correction. A potential concern with our approach is that some future studies might not have sufficient statistical power to employ it and would therefore be subject to Type II error (Nakagawa 2004; Garamszegi 2006). Hence, we suggest that authors either use a less rigorous alpha correction or plan data collection based on the expected effect size and the number of regressions that will be carried out (Cohen 1992).

Although modeling and a few empirical studies have pointed out that spontaneous vigilance and locomotion could potentially bias the alert distance–FID relationship (Cooper et al. 2009; Chamaillé-Jammes and Blumstein 2012), it is unlikely that such noise is present in real FID data. First, in taxa such as birds and mammals, escape from predators is an obvious response. Both birds and mammals obviously acknowledge an approaching threat (through orientation toward oncoming threat or by ceasing previous activities in order to engage in monitoring) and often engage in obvious escape. By contrast, in lizards, alert responses may not be as obvious, but flight responses remain obvious. Thus, it is conceivable that there may be more inaccuracies associated with observations of alert distance in studies of lizards, but in typical studies of escape by lizards, no attempt is made to recognize an alert distance and experimental approaches are conducted only after lizards have detected the simulated predator (Cooper 2008a, 2008b). Even using starting distance as a proxy for alert distance, lizards are presumed to have detected the predator before approach has begun. Our filtering approach (Figure 1) will be especially helpful to eliminate possible artifacts when testing the FEAR hypothesis in lizards and other taxa for which it is equally difficult to discriminate alert distance, but starting distance is readily measured, such as snakes and frogs.

Our experience shows that, with some training, it is typically easy for observers of many species to discriminate between spontaneous vigilance and locomotion and those triggered by predator presence. Moreover, the standardized protocol to measure FID also prevents spontaneous vigilance and locomotion that is not related to an approaching predator from being recorded as FID and/or alert distance. Reviews of literature showed that most experimenters use a standardized procedure (sensu Blumstein 2003) in which doubtful observations are discarded from records (Blumstein et al. 2005; Stankowich and Blumstein 2005; Weston et al. 2012; Samia et al. 2013).

The large amount of variance in FID that was explained by alert distance is striking. Alert distance alone explained between 73% and 100% of variation of FID of yellow-bellied marmots. Møller and Jennions (2002) showed that the explanatory power of any single factor in ecological and evolutionary studies is relatively small when compared with other natural sciences, such as physics and chemistry. This is likely because biological organisms are affected simultaneously by a number of biotic, abiotic, and historic factors (Møller and Jennions 2002). Given that an average of only 7% of the variance is explained in biological studies, evidence provided by the present and previous studies (Samia et al. 2013) indicates that alert distance has an unusually large influence on FID. This large average effect size enhances the plausibility of the FEAR hypothesis and its widespread influence in predator–prey interactions.

Although this study provides evidence that spontaneous behaviors are unlikely to seriously bias the expected relationship in the FEAR hypothesis, there are other potential biological effects that need to be tested in order to evaluate the generality of the FEAR hypothesis. Previous studies have raised a number of questions for potential future analysis. Even among species that flee soon after in response to predator approach, there is some variability in behavioral responses. In the meta-analysis by Samia et al. (2013), most species, but not all, showed a large correlation between starting distance (or alert distance) and FID. Yet, in contrast with birds and mammals, some lizards flushed early only when predators approached them rapidly. Importantly, this finding was not accounted for by the shared phylogenetic history among taxa (Samia et al. 2013). These findings lead to questions such as what differences between lizards, birds, and mammals account for the influence of speed of predator's approach in one but not all groups? Which biotic or abiotic factors make a species flush early, while others do not? Did tested lizards have low monitoring costs (ambush foragers) and flush early only when predation risk was high? If so, this fact would reinforce the idea that flushing early is caused by assessments associated with monitoring. Can the FEAR hypothesis be modified to explain the behavior of species that do not flee to escape predators (e.g., cryptic species)? Future studies that clarify such questions will help to better understand the mechanisms underlying the flushing early phenomenon.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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