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RESEARCH PAPER

Does Locomotor Ability Influence Flight Initiation Distance in Yellow-Bellied Marmots?

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Abstract

Flight initiation distance (FID) is the distance between a potential threat and the point at which a potential prey flees. Animals may modify their FID to compensate for increased risk generated by external/extrinsic factors such as habitat type, visibility, group size, time of year, predator-approach velocity, and distance to burrow, as well as internal/intrinsic factors such as physical condition, body temperature, crypsis, and morphological antipredator defenses. The intrinsic speed at which an animal can escape a predator is a factor that should influence FID. We studied the relationship between an individual's intrinsic escape speed and FID in yellow-bellied marmots (*Marmota flaviventris*) to determine whether marmots compensated for slower escape speeds by fleeing at greater distances. We found no evidence of risk compensation. Rather, we found that slower marmots tolerated closer approaches. This behavioral syndrome may be explained by a coevolution of FID and escape speed in determining an individual's antipredator behavior, an idea upon which we expand.

Introduction

When threatened by predators, most animals eventually flee (Edmunds 1974; Ydenberg & Dill 1986; Lima & Dill 1990). Flight initiation distance (FID) is the distance between a potential predator and the point at which a potential prey flees (Ydenberg & Dill 1986; Cooper & Blumstein 2015). While species may vary in their relative flightiness (Blumstein et al. 2003), a number of external/extrinsic factors may influence FID. For instance, previous studies have shown that habitat type (Frid 1997), visibility (Ebensperger & Hurtado 2005), group size (Beauchamp 2008), time of year (Metcalfe & Furness 1984), predator-approach velocity (Ydenberg & Dill 1986), distance to burrow (Dill & Houtman 1989), to name a few, all explain variation in FID.

Many antipredator decisions are also influenced by a variety of internal/intrinsic factors, such as stress hormone levels (Mateo 2007), body size (Caro 2005; Gotanda et al. 2009), lactational state (Holmes 1991), pregnancy (Braña 1993), reproductive opportunity (Cooper 1997, 1999), degree of habituation (Cooke 1980; Burger & Gochfeld 1983; Lord et al. 2001), prior experience with predators (Cooper 1997), and body condition (Bachman 1993). Importantly, FID has been reported to fluctuate based on a variety of internal/intrinsic factors such as physical condition (Kenward 1978), body temperature (Rand 1964; Rocha & Bergallo 1990), crypsis (Broom & Ruxton 2005), and morphological antipredator defenses (Abrahams 1995).

The maximum speed at which an animal can escape a predator may influence survival (Husak 2006) and is itself influenced by a variety of external/extrinsic factors, such as substrate (Djawdan & Garland 1988), incline (Taylor et al. 1972), and distance run (Blumstein 1992), as well as internal/intrinsic factors, such as body temperature (Hertz et al. 1982), body size (Schulte-Hostedde & Millar 2002), gravidity (Seigel et al. 1987; Shine 2003), and illness (Hertz et al.1982; Okafor 2010). We assume that the relative ability to escape a predator should influence antipredator behavior. For instance, previous studies of snakes reported that the success of antipredator defenses depended, in part, on an individual's inherent locomotor capacity (Garland 1988).

Importantly, antipredator behaviors do not evolve independently (Loughry & McDonough 1988; DeWitt et al. 1999; Blumstein 2006), and there is considerable evidence of risk compensation whereby individuals compensate for physical shortcomings. For instance, birds that have brighter colors, compensate for increased detectability to predators, associated with their color, by being more responsive to the sounds of their predators (Journey et al. 2013). Yellow-bellied marmots (*Marmota flaviventris*) that run relatively slowly, forage more intently and therefore likely reduce the amount of time they forage in exposed places (Blumstein et al. 2004). Importantly, there is a genetic correlation between running speed and time allocated to vigilance (Blumstein et al. 2010) demonstrating that selection has acted on risk compensation.

The purpose of this study was to determine whether individuals compensated for the increased risk associated with being relatively slow by fleeing approaching threats at greater distances. We focused on a well-studied population of yellow-bellied marmots, in which the velocity that individuals can run after release, after controlling for a variety of other factors that influence running speed, was previously reported to be heritable (Blumstein et al. 2010), and there was some degree of repeatability in FID (Petelle et al. 2013). We predicted that relatively slow animals might be relatively more flighty while relatively fast animals would tolerate closer approach.

Methods

Study Site and Organism

We observed yellow-bellied marmots located in the upper East River Valley in and around the Rocky Mountain Biological Laboratory (RMBL; 38°57′N, 106°59′W) in Gothic, Colorado (see Langenheim (1962) for a description of the topography, geology, and vegetation of the area). Marmots live in discrete locations called colonies (Armitage 1991); we focused on Avalanche, Bench, Boulder, Horse Mound, Gothic Townsite, Marmot Meadow, Picnic, and River colony sites. While marmots are active between mid-Apr. and October at our subalpine study site, experiments were conducted between May and Sep. We aimed to live trap individuals every other week. We set Tomahawk live traps (Tomahawk Co., Hazelhurst, WI) in burrow entrances and baited them with horse feed (Omalene 100; Ralston Purina, St. Louis, MO, USA). Upon reaching a trap, we transferred individuals into a canvas handling bag, checked their uniquely numbered ear tags (No. 3, fingerling fish tags; National Band and Tag, Newport, KY, USA), checked their reproductive status, weighed them with a digital spring scale to the nearest 10 g, checked their fur mark and re-marked them, if required, with Nyanzol dye (Greenville Colorants, Greenville, SC; detailed methods in Armitage 1991). Processing was routine and typically took between 5 and 15 min per subject depending upon what data needed to be collected and procedures that needed to be carried out.

Quantifying Running Speed and Calculating Run-Time-BLUPs

Between 2002 and 2013, we measured marmot running speed when we released marmots from their handling bag. Starting in late Jul., individual marmots were encouraged (by yelling and arm waving) to run to its burrow (details in Blumstein et al. 2004). Briefly, we measured the time it took to cross a homogeneous substrate (run-time in s) and angle (in degrees), and the distance interval over which it was timed (distance in m). Substrate was defined as: stones/talus, dirt/low vegetation—below a foraging marmots ears, and tall vegetation—above a foraging marmots ears). We also recorded the distance to the burrow (in m). Observations were excluded if the animal did not run in a straight line or ran across a different substrate or incline. Individuals had various numbers of measurements within and across years (Table 1).

We calculated the best linear unbiased predictors (BLUPs) of run-time (run-time-BLUPs; hereafter, rt-BLUP). Using BLUPs, we were able to capitalize on the repeated measures of each individual's run-time (in a given year) and generate an expected value that controlled for a variety of factors that are known to influence running speed (Blumstein 1992; Blumstein et al. 2004), some of which we included as fixed factors in our calculation. We used an individual's ID in a given year (ID-year) as our unit of replication to account for potential changes in running speed with age. rt-BLUP captures running speed because, after controlling for distance run, rt-BLUP is represents the time an animal took to run a given distance. A larger rt-BLUP means that it took longer for an individual in a given year to run a given distance, which corresponds to a slower animal. We examined run-time to avoid a ratio correlation problem that emerges if one were to model velocity as a function of distance

Table 1: Summary statistics of variables used in calculation of rt-BLUPs and in flight initiation distance (FID) analysis

	rt-BLUP					FID			
	Distance run (m)	Burrow distance (m)	Trial number	Run-time (s)	Alert distance (m)	Burrow distance (m)	Alert distance (m)	Trial number	FID (m)
$\bar{x}$	9.46	12.59	1.55	2.65	47.78	4.67	47.78	3.26	31.64
$\tilde{x}$	8.30	10.60	1	2.31	44.50	1.50	44.50	3	28.50
SD	5.44	7.72	0.92	1.51	20.87	6.68	20.87	2.12	18.78
Min	1.10	0.00	1	0.41	9.00	0.00	9.00	1	5.00
Max	40.70	50.00	7	18.34	102.00	38.00	102.00	9	88.00
N	235	235	235	235	235	44	44	44	44

(Blumstein 1992). To calculate rt-BLUP, we fit a linear mixed effect model using maximum likelihood. Our dependent variable, run-time, was transformed (log10 $(x + 1)$) to meet the assumption of normality. We controlled for age and sex by including a fixed effect concatenating age class (pup, yearling, or adult) with sex (age-sex), which had six levels (adult male, adult female, pup male, pup female, yearling male, and yearling female). In addition, we included distance to burrow to control for the effect that marmots farther from the burrow will tend to run more slowly than marmots that are experimentally chased when they are closer to the burrow (Ydenberg & Dill 1986; Sih 1987). To control for habituation, we included trial number as a fixed effect. Finally, we included distance run to account for the fact that run-times were measured for marmots running different distances. Continuous fixed effects, distance to burrow and distance ran, were transformed (log10 $(x + 1)$) to meet the assumptions of normality. Our random effect was ID-year. We used the estimated intercept for each ID-year as the rt-BLUP.

Flight Initiation Distance

Between 2003 and 2013, we measured FID (details in Blumstein et al. 2004 and Li et al. 2011) of relaxed marmots (i.e., one not engaged in heightened vigilance or having just responded to an alarm call or predator visit) by walking at a constant pace of 0.5 m/s toward a focal animal (Runyan & Blumstein 2004). We recorded starting distance (the distance between animal and the observer's starting point), alert distance (the distance between observer and animal at which the animal oriented toward the observer), and the distance the marmot was to the nearest burrow when the marmot fled. By marking the observer's starting location with a flag and noting landmarks at the animal's location, these distances were measured using a tape measure. Distances were measured to the nearest 0.5 m. We waited at least 3 d before re-testing subjects. Because wind may influence flightiness and more general antipredator behavior (Blumstein & Daniel 2003), marmots were only experimentally approached if the wind was <3 on the Beaufort scale.

Statistical Analysis

We constructed 16 linear mixed effects models. All models were estimated using reduced maximum likelihood with FID as the dependent variable and ID-year as a random variable. To aid in the interpretation of effect sizes, we standardized continuous independent and dependent variables by subtracting an observation from the mean of the variable, and dividing by the standard deviation of that variable. By standardizing continuous variables, the coefficients of these parameters are comparable to one another. We did not standardize non-continuous parameters as we were not interested in their effects and they were entered into the model simply as a statistical control. As with the calculation of rt-BLUP, we concatenated ID-year to account for changes in running speed with age, and fit this as a random effect. Due to the known correlation of alert distance with FID (Blumstein 2010), and to control for habituation, we included alert distance and trial number in all models. These two fixed effects were combined with every subset of the following fixed effects, which are known to influence FID: distance to burrow (Dill & Houtman 1989), age-sex (Frid & Dill 2002), and colony (Mainini et al. 1993; Li et al. 2011), which yielded eight models. To test for the effect of running speed on FID, our set of models also contained these eight models with rt-BLUP. Thus, our final set of models contained a total of 16 models (Table 2).

We used AIC multimodel inference on a subset of these 16 models with the expectation that if the time that it took a marmot to run a certain distance, reflected in rt-BLUP, strongly influenced FID, then rt-BLUP should appear in our top-AIC models. For each model, we calculated ΔAIC, which conveys the

Table 2: Number of parameters (*K*), ΔAIC, and likelihood ratios (l_i) of our set of initial hypotheses, and the Akaike weights (w_i) of our top-ranking ΔAIC models

Fixed factors	K	ΔAIC	l_i	w_i
Alert distance + rt-BLUP + burrow distance + trial	14	0.00	1.00	0.41
Alert distance + burrow distance + trial	13	0.80	1.49	0.27
Alert distance + rt-BLUP + burrow distance + age-sex + trial	17	1.34	1.95	0.21
Alert distance + burrow distance + age-sex + trial	16	2.53	3.54	0.11
Alert distance + rt-BLUP + burrow distance + colony + trial	20	7.10	34.89	
Alert distance + burrow distance + age-sex + colony + trial	22	7.43	41.07	
Alert distance + burrow distance + colony + trial	19	7.88	51.45	
Alert distance + rt-BLUP + burrow distance + age-sex + colony + trial	23	8.04	55.69	
Alert distance + rt-BLUP + trial	13	11.94	392.07	
Alert distance + trial	12	13.90	1045.19	
Alert distance + rt-BLUP + age-sex + trial	16	13.99	1093.04	
Alert distance + rt-BLUP + colony + trial	19	15.73	2601.97	
Alert distance + age-sex + trial	15	17.02	4951.91	
Alert distance + colony + trial	18	17.11	5193.58	
Alert distance + age-sex + colony + trial	21	17.25	5560.25	
Alert distance + rt-BLUP + age-sex + colony + trial	22	17.30	5713.75	

All models contained ID-year as a random effect. We calculated *w* with respect to only those models falling below the first natural break in ΔAIC values (i.e., $l_i \leq 3.54$).

information loss relative to the AIC-best model, and the evidence ratio, l_i, which indicates the number of times that the evidence of the AIC-top model is stronger compared to model *i* (Burnham & Anderson 2002). As models with smaller evidence ratios are better supported by the data, we defined our top-AIC models as those with evidence ratios less than the value of the lowest natural break in evidence ratios values of the whole set of models. We then calculated Akaike weights, *w*, for this set of top models. To calculate an average model, we weighted the estimates of our top-AIC models according to *w* (Burnham & Anderson 2002). We calculated the unconditional standard error (SE) of each parameter, which is a model-averaged SE. If a parameter did not appear in a model, then we specified its estimate for that model as 0 (Burnham & Anderson 2002).

Results

Because the nature of taking running speed and FID measurements does not allow measuring both in a single trial, some ID-years that had rt-BLUP measurements did not have FID measurements, and vice versa. To calculate rt-BLUPs with the most accuracy, we calculated rt-BLUP using our entire dataset (n = 235). We modeled FID only for those ID-years that had rt-BLUP measurements (n = 44). The number of times that running speed was measured for a given animal in a given year ranged between 1 and 7. The number of times that FID was measured for a given animal in a given year ranged between 1 and 9 (Table 1).

The first natural break in l_i in our set of hypotheses occurred between models ranked the 4th and 5th AIC-best models, where $l_4 = 3.54$ and $l_5 = 34.89$ (Table 2). Therefore, our subset of models that we averaged consisted of the four models with $l_i \leq 3.54$. Two of these models contained rt-BLUP indicating relatively strong evidence for a link between running speed and FID.

Our averaged model (Table 3) indicates that marmots with larger rt-BLUPs have smaller FIDs, which means that slower marmots tolerated closer approaches compared to faster marmots (est. = −1.80, SE = 1.10). Individuals (in a given year) that alerted at a greater distance from the observer tended to have a greater FID (est. = 11.95, SE = 1.13). Marmots farther from the burrow had greater FIDs (est. = 4.01, SE = 1.06). Our model averaged from the top-ranking models also contained the variables trial number and age-sex, the effects of which are shown in Table 3.

Discussion

We expected to find evidence of risk compensation whereby intrinsically faster individuals tolerated closer approaches because they would be capable of returning to the safety of their burrow in less time compared to intrinsically slower individuals. We based this logic on studies such as one that found that

Table 3: Model average estimates (Est.) and unconditional standard errors (SE) of variables in our model average

Fixed factors	Est.	SE
(intercept)	29.88	2.05
Alert distance	11.95	1.13
rt-BLUP	−1.80	1.10
Burrow distance	4.01	1.06
Age-sex (adult male)	1.43	3.59
Age-sex (yearling female)	5.56	2.85
Age-sex (yearling male)	1.20	3.12
Trial number (1)	−4.10	5.43
Trial number (2)	4.89	5.18
Trial number (3)	−2.37	4.79
Trial number (4)	1.64	4.32
Trial number (5)	2.89	4.00
Trial number (6)	−2.89	3.65
Trial number (7)	0.00	3.48
Trial number (8)	−3.86	3.25

Estimates of age-sex and trial number are with respect to adult female and the 9th trial, respectively.

gravid females, which had compromised locomotor ability and a greater cost of not escaping due to potential death of self and offspring, fled at greater distances than non-gravid females (Braña 1993). However, we found the opposite. Marmots that tolerated closer approaches (i.e., those with smaller FIDs) have slower intrinsic running speeds that we measured by chasing them after releasing them from livetraps. This result was unexpected because yellow-bellied marmots engage in risk compensation in a variety of other ways. Marmots only emit alarm calls when relatively close to their burrows (Collier et al. 2010), they forage more intently if they run slowly (Blumstein et al. 2004, 2010), they forage less when the visibility of their surroundings is reduced (Bednekoff & Blumstein 2009), and they forage less after hearing (Blumstein et al. 2008b), smelling (Blumstein et al. 2008a), or seeing (Blumstein et al. 2009) predators.

Our results may be understood by examining the costs and benefits associated with a given pairing of FID and running speed. Animals must often trade-off the risk of predation with the benefits of other activities such as foraging, reproduction, or socializing (Lima & Dill 1990). In our study, we simulated a threat by approaching marmots and measuring their FID. By retreating inside their burrow, marmots paid several costs. First, there was a locomotor cost associated with fleeing, which may be particularly high if an animal's energy reserves are low. Second, individuals had to make a subsequent decision to emerge; itself an economic decision influenced by both costs and benefits (Sih 1992; Martín & López 1999; Blumstein & Pelletier 2005; Rhoades & Blumstein 2007). For instance, while in the burrow marmots were unable to assess the true risk of subsequent predation and they lost opportunities to engage in other activities while hiding.

Marmots that run more slowly may be able to assess if a threat has dissipated before expending more energy than is needed to escape a predator. For example, consider two marmots foraging 15 m from their burrow. Assume one is slow and the other relatively fast. Our results suggest that the fast animal would flee before the slow animal. Because the slow marmot delays its flight, it will permit the predator to approach more closely, during which time the marmot may obtain more energy while foraging and may acquire more information about the approaching predator by increasing its vigilance. In some cases, predators might abort their hunt if the prey focuses its attention on them. In this case, the faster marmot that fled early would suffer all the costs (energetic, opportunity, re-emergence) associated with flight while the slower marmot would not suffer those costs.

Speed, however, may be useful when being pursed. Thus, it is possible that slower marmots are more likely to be killed when being pursued while faster marmots are more likely to pay the costs associated with swift and early escape. Thus, the FID and running speed syndrome may be maintained by this tradeoff. A meta-analysis of the fitness consequences of personality traits found that bold animals (boldness is often measured by FID) may have increased reproductive success but also suffer an increased risk of predation (Smith & Blumstein 2008). Thus, the positive relationship between FID and running speed that we found may reflect a spectrum of antipredator strategies defined by paired FID and running speed.

Explaining the relationship between FID and running speed as an antipredator strategy dovetails with the Pace of Life Syndrome (POLS) hypothesis (Ricklefs & Wikelski 2002; Réale et al. 2010). Individuals in a population can possess a diversity of life-history strategies (Roff & Fairbairn 2007). The POLS hypothesis suggests that correlated behaviors coevolved with an individual's life-history strategy (Réale et al. 2010). In our study, the facet of life-history strategy we examined was antipredator behavior. A slower running marmot may make up for higher predation risk by increasing its foraging gains through tolerating a closer approach and reducing energy expenditure by being able to more accurately assess the level of risk posed by a threat.

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Literature Cited

Abrahams, M. V. 1995: The interaction between antipredator behaviour and antipredator morphology: experiments with fathead minnows and brook sticklebacks. Can. J. Zool. **73**, 2209—2215.

Armitage, K. B. 1982: Yellow-bellied marmot. In: CRC Handbook of Census Methods for Terrestrial Vertebrates. (Davis, D. E., ed). CRC Press Inc, Boca Raton, Florida, pp. 148—149.

Armitage, K. B. 1991: Social and population dynamics of yellow-bellied marmots: results from long-term research. Annu. Rev. Ecol. Syst. **22**, 379—407.

Bachman, G. C. 1993: The effect of body condition on the trade-off between vigilance and foraging in Belding's ground squirrels. Anim. Behav. **46**, 233—244.

Beauchamp, G. 2008: What is the magnitude of the group-size effect on vigilance? Behav. Ecol. **19**, 1361—1368.

Bednekoff, P. A. & Blumstein, D. T. 2009: Peripheral obstructions influence marmot vigilance: integrating observational and experimental results. Behav. Ecol. **20**, 1111—1117.

Blumstein, D. T. 1992: Multivariate analysis of golden marmot maximum running speed: a new method to study MRS in the field. Ecology **73**, 1757—1767.

Blumstein, D. T. 2006: The multi-predator hypothesis and the evolutionary persistence of antipredator behavior. Ethology **112**, 209—217.

Blumstein, D. T. 2010: Flush early and avoid the rush: a general rule of antipredator behavior? Behav. Ecol. **21**, 440—442.

Blumstein, D. T. & Daniel, J. C. 2003: Foraging behavior of three Tasmanian macropodid marsupials in response to present and historical predation threat. Ecography **26**, 585—594.

Blumstein, D. T. & Pelletier, D. 2005: Yellow-bellied marmot hiding time is sensitive to variation in costs. Can. J. Zool. **83**, 363—367.

Blumstein, D. T., Anthony, L. L., Harcourt, R. & Ross, G. 2003: Testing a key assumption of wildlife buffer zones: is flight initiation distance a species-specific trait? Biol. Conserv. **110**, 97—100.

Blumstein, D. T., Runyan, A., Seymour, M., Nicodemus, A., Ozgul, A., Ransler, F., Im, S., Stark, T., Zugmeyer, C. & Daniel, J. C. 2004: Locomotor ability and wariness in yellow-bellied marmots. Ethology **110**, 615—634.

Blumstein, D. T., Barrow, L. & Luterra, M. 2008a: Olfactory predator discrimination in yellow-bellied marmots. Ethology **114**, 1135—1143.

Blumstein, D. T., Cooley, L., Winternitz, J. & Daniel, J. C. 2008b: Do yellow-bellied marmots respond to predator vocalizations? Behav. Ecol. Sociobiol. **62**, 457—468.

Blumstein, D. T., Ferando, E. & Stankowich, T. 2009: A test of the multipredator hypothesis: yellow-bellied marmots respond fearfully to the sight of novel and extinct predators. Anim. Behav. **78**, 873—878.

Blumstein, D. T., Lea, A. J., Olson, L. E. & Martin, J. G. A. 2010: Heritability of anti-predatory traits: vigilance and locomotor performance in marmots. J. Evol. Biol. **23**, 879—887.

Braña, F. 1993: Shifts in body temperature and escape behaviour of female *Podarcis muralis* during pregnancy. Oikos **66**, 216—222.

Broom, M. & Ruxton, G. D. 2005: You can run—or you can hide: optimal strategies for cryptic prey against pursuit predators. Behav. Ecol. **16**, 534—540.

Burger, J. & Gochfeld, M. 1983: Behavioural responses to human intruders of herring gulls (*Larus argentatus*) and great black-backed gulls (*L. marinus*) with varying exposure to human disturbance. Behav. Processes **8**, 327—344.

Burnham, K. P. & Anderson, D. R. 2002: Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd edn. Springer, New York.

Caro, T. M. 2005: Antipredator Defenses in Birds and Mammals. Univ. of Chicago Press, Chicago.

Collier, T. C., Blumstein, D. T., Girod, L. & Taylor, C. E. 2010: Is alarm calling risk? Marmots avoid calling from risky places. Ethology **116**, 1171—1178.

Cooke, A. S. 1980: Observations on how close certain passerine species will tolerate an approaching human in rural and suburban areas. Biol. Conserv. **18**, 85—88.

Cooper, W. E. 1997: Factors affecting risk and cost of escape by the broad-headed skink (*Eumeces laticeps*): predator speed, directness of approach, and female presence. Herpetologica **53**, 464—474.

Cooper, W. E. 1999: Tradeoffs between courtship, fighting, and antipredatory behavior by a lizard, *Eumeces laticeps*. Behav. Ecol. Sociobiol. **47**, 54—59.

Cooper, W. E. & Blumstein, D. T. 2015: Escape behavior: importance, scope, and variables. In: Escaping from Predators: An Integrative View of Escape Decisions (Cooper, W. E. & Blumstein, D. T., eds). Cambridge Univ. Press, Cambridge, in Press.

DeWitt, T. J., Sih, A. & Hucko, J. A. 1999: Trait compensation and cospecialization in a freshwater snail: size, shape and antipredator behavior. Anim. Behav. **58**, 397—407.

Dill, L. M. & Houtman, R. 1989: The influence of distance to refuge on flight initiation distance in the gray squirrel (*Sciurus carolinensis*). Can. J. Zool. **67**, 233—235.

Djawdan, M. & Garland, T. Jr 1988: Maximal running speeds of bipedal and quadrupedal rodents. J. Mammal. **69**, 765—772.

Ebensperger, L. A. & Hurtado, M. J. 2005: On the relationship between herbaceous cover and vigilance activity of degus (*Octodon degus*). Ethology **111**, 593—608.

Edmunds, M. 1974: Defense in Animals: A Survey of Antipredator Defenses. Longman, Harlow, UK.

Frid, A. 1997: Vigilance by female Dall's sheep: interactions between predation risk factors. Anim. Behav. **53**, 799—808.

Frid, A. & Dill, L. M. 2002: Human-caused disturbance stimuli as a form of predation risk. Conserv. Ecol. **6**, 11.

Garland, T. 1988: Genetic basis of activity metabolism. I. Inheritance of speed, stamina and antipredator displays in the garter snake *Thamnophis sirtalis*. Evolution **42**, 335—350.

Gotanda, K. M., Turgeon, K. & Kramer, D. L. 2009: Body size and reserve protection affect flight initiation distance in parrotfishes. Behav. Ecol. Sociobiol. **63**, 1563—1572.

Hertz, P. E., Huey, R. B. & Nevo, E. 1982: Fight versus flight: body temperature influences defensive responses of lizards. Anim. Behav. **30**, 676—679.

Holmes, W. G. 1991: Predator risk affects foraging behaviour of pikas: observational and experimental evidence. Anim. Behav. **42**, 111—119.

Husak, J. F. 2006: Does survival depend on how fast you can run or how fast you do run? Funct. Ecol. **20**, 1080—1086.

Journey, L., Drury, J. P., Haymer, M., Rose, K. & Blumstein, D. T. 2013: Vivid birds respond more to acoustic signals of predators. Behav. Ecol. Sociobiol. **67**, 1285—1293.

Kenward, R. E. 1978: Hawks and doves: factors affecting success and selection in goshawk attacks on woodpigeons. J. Anim. Ecol. **47**, 449—460.

Langenheim, J. H. 1962: Vegetation and environmental patterns in the Crested Butte area, Gunnison County, Colorado. Ecol. Monogr. **32**, 249—285.

Li, C., Monclús, R., Maul, T. L., Jiang, Z. & Blumstein, D. T. 2011: Quantifying human disturbance on antipredator behavior and flush initiation distance in yellow-bellied marmots. Appl. Anim. Behav. Sci. **129**, 146—152.

Lima, S. L. & Dill, L. M. 1990: Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. **68**, 619—640.

Lord, A., Waas, J. R., Innes, J. & Whittingham, M. J. 2001: Effects of human approaches to nests of northern New Zealand dotterels. Biol. Conserv. **98**, 233—240.

Loughry, W. J. & McDonough, C. M. 1988: Calling and vigilance in California ground squirrels: a test of the tonic communication hypothesis. Anim. Behav. **36**, 1533—1540.

Mainini, B., Neuhaus, P. & Ingold, P. 1993: Behaviour of marmots (*Marmota marmota*) under the influence of different hiking activities. Biol. Conserv. **64**, 161—164.

Martín, J. & López, P. 1999: When to come out from a refuge: risk-sensitive and state-dependent decisions in an alpine lizard. Behav. Ecol. **10**, 487—492.

Mateo, J. M. 2007: Ecological and hormonal correlates of antipredator behavior in adult Belding's ground squirrels (*Spermophilus beldingi*). Behav. Ecol. Sociobiol. **62**, 37—49.

Metcalfe, N. B. & Furness, R. W. 1984: Changing priorities: the effect of pre-migratory fattening on the trade-off between foraging and vigilance. Behav. Ecol. Sociobiol. **15**, 203—206.

Okafor, A. I. 2010: The influence of body temperature on sprint speed and anti-predatory defensive responses of the North African monitor lizard, *Varanus griseus*. Afr. J. Biotechnol. **9**, 778—781.

Petelle, M. B., McCoy, D. E., Alejandro, V., Martin, J. G. A. & Blumstein, D. T. 2013: Development of boldness and docility in yellow-bellied marmots. Anim. Behav. **86**, 1147—1154.

Rand, A. S. 1964: Inverse relationship between temperature and shyness in the lizard *Anolis lineatopus*. Ecology **45**, 863—864.

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V. & Montiglio, P. O. 2010: Personality and the emergence of the pace-of-life syndrome concept at the population level. Philos. Trans. R. Soc. B **365**, 4051—4063.

Rhoades, E. & Blumstein, D. T. 2007: Predicted fitness consequences of threat-sensitive hiding behavior. Behav. Ecol. **18**, 937—943.

Ricklefs, R. E. & Wikelski, M. 2002: The physiology/life-history nexus. Trends Ecol. Evol. **17**, 462—468.

Rocha, C. F. D. & Bergallo, H. G. 1990: Thermal biology and flight distance of *Tropidurus oreadicus* (Sauria Iguanidae) in an area of Amazonian Brazil. Ethol. Ecol. Evol. **2**, 263—268.

Roff, D. A. & Fairbairn, D. J. 2007: The evolution and genetics of migration in insects. Bioscience **57**, 155—164.

Runyan, A. M. & Blumstein, D. T. 2004: Do individual differences influence flight initiation distance? J. Wildl. Manage. **68**, 1124—1129.

Schulte-Hostedde, A. I. & Millar, J. S. 2002: Effects of body size and mass on running speed of male yellow-pine chipmunks (*Tamias amoenus*). Can. J. Zool. **80**, 1584—1587.

Seigel, R. A., Huggins, M. M. & Ford, N. B. 1987: Reduction in locomotor ability as a cost of reproduction in gravid snakes. Oecologia **73**, 481—485.

Shine, R. 2003: Effects of pregnancy on locomotor performance: an experimental study on lizards. Oecologia **136**, 450—456.

Sih, A. 1987: Predator and prey lifestyles: an evolutionary and ecological overview. In: Predation: Direct and Indirect Impacts on Aquatic Communities (Kerfoot, W. C. & Sih, A., eds). Univ. Press of New England, Hanover, pp. 203—224.

Sih, A. 1992: Prey uncertainty and the balancing of antipredator and feeding needs. Am. Nat. **139**, 1052—1069.

Smith, B. R. & Blumstein, D. L. 2008: Fitness consequences of personality: a meta-analysis. Behav. Ecol. **19**, 448—455.

Taylor, C. R., Caldwell, S. L. & Rowntree, V. J. 1972: Running up and down hills: some consequences of size. Science **178**, 1096—1097.

Ydenberg, R. C. & Dill, L. M. 1986: The economics of fleeing from predators. Adv. Stud. Behav. **16**, 229—249.