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Marmots do not consistently use their left eye to respond to an approaching threat but those that did fled sooner

Daniel T. Blumstein[a,b,*], Alexis Diaz[b], and Lijie Yin[c]

[a]Department of Ecology and Evolutionary Biology, University of California, 621 Young Drive South, Los Angeles, CA 90095-1606, USA, [b]Rocky Mountain Biological Laboratory, Crested Butte, CO 81224, USA, and [c]School of Life Sciences, Peking University, Beijing 100871, China

*Address correspondence to Daniel T. Blumstein. E-mail: marmots@ucla.edu.

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Abstract

In many vertebrates, the brain's right hemisphere which is connected to the left visual field specializes in the processing of information about threats while the left hemisphere which is connected to the right visual field specializes in the processing of information about conspecifics. This is referred to as hemispheric lateralization. But individuals that are too predictable in their response to predators could have reduced survival and we may expect selection for somewhat unpredictable responses. We studied hemispheric lateralization in yellow-bellied marmots *Marmota flaviventer*, a social rodent that falls prey to a variety of terrestrial and aerial predators. We first asked if they have lateralized responses to a predatory threat. We then asked if the eye that they used to assess risk influenced their perceptions of risk. We recorded the direction marmots were initially looking and then walked toward them until they fled. We recorded the distance that they responded to our experimental approach by looking, the eye with which they looked at us, and the distance at which they fled (i.e., flight initiation distance; FID). We found that marmots had no eye preference with which they looked at an approaching threat. Furthermore, the population was not comprised of individuals that responded in consistent ways. However, we found that marmots that looked at the approaching person with their left eye had larger FIDs suggesting that risk assessment was influenced by the eye used to monitor the threat. These findings are consistent with selection to make prey less predictable for their predators, despite underlying lateralization.

Key words: antipredator behavior, behavioral lateralization, flight initiation distance, yellow-bellied marmots.

The left and right hemispheres of many vertebrate brains are specialized to carry out specific activities (Bisazza et al. 1998; Andrew 2002). In humans, much research has shown that the left hemisphere is generally responsible for interpreting language and the right hemisphere is generally responsible for alert responses (Andrew 2002). Hemispheric lateralization controlling the response to threats has been shown to be an ancestral trait found in a variety of mammals including primates and rodents (Kim et al. 2012). For instance, Japanese monkeys *Macaca fuscata*, upon hearing an alarm call, looked longer at a picture of a snake with their left eye, a finding that suggests right hemispheric dominance during visual processing of threatening stimuli (Shibasaki et al. 2014). Mice *Mus musculus* use their right hemisphere to control observational fear learning (Kim et al. 2012). But not all studies of lateralization find support for it. For instance, about half the tested population of inbred mice *Mus molossinus* and *Mecyclothorax castaneus* retrieved food with their left hand while the other half retrieved food with their right hand (Collins 1985) and several environmental/ecological factors (CO_2 levels—Domenici et al. 2012; predation risk—Brown et al. 2004) may modify or eliminate lateralized responses in fishes.

The advantage of a lateralized brain is that it helps individuals perform tasks simultaneously (Rogers et al. 2004). For example, lateralized eye use in chickens *Gallus gallus* permits them to forage with 1 eye and be alert to predators with the other eye (Rogers et al. 2004). However, the benefits of lateralization may not come without costs (Chivers et al. 2017). For instance, if individuals respond in consistent and predictable ways by looking at their predators, predators can learn how they escape and capitalize on this predictability (Vallortigara 2000). Hence, it is possible that eye preference varies across individuals within a population (Vallortigara 2000; Chivers et al. 2017) and, that at a population level, there may be no evidence for lateralization in how a species responds to threats.

Animals perceive approaching humans as predators (Frid and Dill 2002) and by walking directly toward an animal, it is possible to elicit an antipredator response. Flight initiation distance (FID), the distance between a predator and its prey at which the prey initiates flight, is a widely used method to quantify risk assessment (Cooper and Blumstein 2015). When approached by a potential predator, the prey may change their posture and look toward the approaching threat to monitor it. This alert response can be used to study eye preference and hence hemispheric lateralization.

Although evidence for hemispheric lateralization has been studied in many species, there are relatively few studies of rodents (Kim et al. 2012), especially in the field. However, we know that rodents have lateralized brain function (Glick et al. 1977). Thus, our aim was to study hemispheric lateralization in a free-living rodent. We focused on yellow-bellied marmots *Marmota flaviventer* that are prey to a variety of terrestrial and aerial predators (Van Vuren 2001) and asked 2 related questions. First, when approached by a human, did marmots respond by looking at us with their left eye. Second, did the eye with which they looked at us influence the distance at which they fled.

Materials and Methods

Study site and subjects

Between 5 June 2017 and 23 July 2017, we measured responses of adult yellow-bellied marmots (≥2 years old) to an approaching human. We studied marmots in the upper East River Valley in and around the Rocky Mountain Biological Laboratory (RMBL; 38°77’N, 106°50’W) in Gothic, Colorado, the site of a long-term study (Blumstein 2013; Armitage 2014). All marmots are regularly live-trapped and individually marked with ear tags, for permanent identification, and we use fur dye to mark each individual with a unique dorsal mark that permits identification from afar (Armitage 1982).

Quantifying lateralization using FID

We assumed that marmots treated humans as predators (Frid and Dill 2002) and studied lateralization while measuring FID (Blumstein et al. 2015). Observers were trained to approach marmots at a standardized velocity of 0.5 m/s (Blumstein et al. 2004; Runyan and Blumstein 2004; Petelle et al. 2013). If more than 1 marmot was at a location, we focused on a single subject.

Once a subject was identified, we waited at least 10 min to ensure it was in a relaxed state, which we defined as foraging, looking, standing and looking, or lying down and looking, before we approached it. We dropped flags at the location we started the experimental approach, the location where the marmot moved its head and looked toward the approaching person, and the location where it fled by either walking or running to their burrow. We then walked to the location where the animal was when we began the experimental approach and measured the following distances (in meter): starting distance (first flag to initial position); alert distance (second flag to initial position); and FID (third flag to initial position). In addition, we recorded the number of other marmots within 10 m of the focal subject, the escape substrate (dirt, stone, talus, low, or high vegetation), slope of the terrain over which the marmot fled, and the distance to its escape burrow.

To quantify lateralization, we first noted the closest eye to the observer at the start of the experimental approach and quantified this as straight (looking with both eyes directly at observer), right (right eye toward observer), left (left eye toward observer), or away (both eyes facing away from the observer). We recorded the eye direction when the marmot alerted to us in the same way (straight, right, left, or away).

Statistical analyses

To explain variation in looking direction when alerted, we fitted generalized linear mixed-effect models (GLMER) with a binomial error structure, using the following R packages lme4 (Bates et al. 2017), lmerTest (Kuznetsova et al. 2016), and optimx (Nash and Varadhan 2011). We used gplot2 (Wickham and Chang 2016) to plot residuals and predicted values. We focused on those marmots that either responded by looking left or right (5 adults for which we were not certain of the eye directed at us were not analyzed). We then modeled the direction they looked in response to our approach (looking direction when alerted) as a function of their initial looking direction (left, right, straight, or away) and sex (male or female). We included a random effect of individual marmot because most marmots were approached more than once. We tested for individual consistency by comparing a model with and without the random effect of individual with a likelihood ratio test and by fitting a model with only individual marmot as a fixed effect. We plotted residuals versus predicted values and generated qq-plots to evaluate distributional assumptions.

To study variation in FID, we fitted linear mixed-effects models and modeled FID as a function of alert distance, the eye with which they looked at us during the experimental approach, sex, and the 2-way interactions between alert distance and sex and alert distance and looking direction. Again, marmot identity was included as a random effect, and we re-plotted residuals versus predicted values and generated qq-plots to evaluate distributional assumptions.

Because risk perception may be influenced by other factors, but because our sample size was somewhat limited and we did not wish to over-fit the model by including them all at once, we systematically added distance to burrow, escape substrate (stone, dirt, talus, low vegetation, or high vegetation), and escape incline, along with their 2-way interaction with alert distance, to our basic linear model.

Results

We conducted 104 flushes on 39 unique adults (mean 2.8; range 1–9 flushes) that either looked left or right in response to our approach (58 of these approaches generated a look with their left eye, 46 approaches generated a look with their right eye). The random effect of identity explained no variation in looking direction when alerted (Table 1; likelihood ratio test comparing a general linear model with the mixed effects model containing initial head position to a mixed effects model with only head position, $P = 0.666$; the models with sex and initial position were also not significantly different, $P = 0.424$). We also found no effect of prior looking direction, or of the marmot’s sex on looking direction when alerted (Table 2).

Table 1. Generalized linear mixed-effect models fitted in R to explain variation in looking direction and to test for random effects of individual marmot on lateralized eye use

Description	Model	AIC
Model with only random effect	Looking direction ∼ (1|uid)	146.4
Mixed-effect model	Looking direction ∼ Initial head position + sex + (1|uid)	149.7
Fixed-effect only model	Looking direction ∼ Initial head position	146.5
Fixed-effect only model	Looking direction ∼ Initial head position + sex	148.3

Table 2. Results from linear mixed-effects model explaining variation in looking direction

Variable	Estimate (SE)	*z*	*P*-value
A) Intercept	0.0004 (0.517)	0.001	0.999
Initial head (L)	−1.065 (0.650)	−1.638	0.101
Initial head (R)	−0.039 (0.575)	−0.067	0.947
Initial head (S)	0.021 (0.850)	0.024	0.981
Sex (M)	0.104 (0.533)	0.195	0.845
B) Intercept	0.035 (0.487)	0.072	0.942
Initial head (L)	−1.080 (0.647)	−1.669	0.095
Initial head (R)	−0.039 (0.577)	−0.067	0.947
Initial head (S)	0.002 (0.848)	0.002	0.998

Initial direction includes: left (L), right (R), straight (S) or away (the reference category). The first mixed-effects model (A) included sex and initial head position. The second model (B) included only initial head position ($N = 104$ on 39 unique individuals for both models)

Table 3. Results of linear mixed-effects model explaining variation in flight initiation distance as a function of eye use

Variable	Estimate (SE)	df	*P*-value
Intercept	3.812 (3.197)	38.48	0.240
Looking head (R)	3.997 (3.706)	78.56	0.284
Sex (M)	−7.629 (5.434)	28.19	0.171
Alert distance	0.668 (0.057)	65.62	<2e−16
Looking head (R) × Alert distance	−0.158 (0.072)	94.16	0.030
Sex (M) × Alert distance	0.199 (0.097)	57.53	0.045

Main effects only are presented ($N = 104$ on 39 unique individuals).

However, we found that for a given alert distance, marmots that responded to an approaching person by looking at them with their left eye, fled at greater distances (Table 3, Figure 1), and we found that for a given alert distance, males fled at a greater distance than females (Table 3, Figure 2). The 3 covariates tested had significant interactions between alert distance and distance to burrow ($P = 0.029$), escape substrate ($P = 0.008$), and escape incline ($P = 0.021$), but all models retained the significant interaction between look direction and alert distance ($P = 0.004$, 0.004, and 0.046, respectively). Furthermore, when added one at a time to our basic model, there was an effect of social group size ($P = 0.045$), vegetation height ($P = 0.032$), and the day of data collection on FID ($P = 0.020$) on FID. Thus, while other variables explain some variation in FID, we can conclude that the eye with which marmots looked at the approaching human was always a significant factor.

Discussion

Male marmots fled at greater distances once alerted than did females, but we found no support that marmots overall preferentially used their left eye to monitor approaching humans. Although it is possible that with a substantially larger data set we would have detected individual consistency in the eye marmots used to monitor an approaching threat, we did not detect it in our data set that included an average of 3 (and up to 9) repeated approaches on individuals. It is also possible that our predator manipulation was insufficiently risky to generate the expected lateralized response. Levels of predator exposure influence lateralization in fishes, where individuals with the greatest risk of predation exhibited the most lateralized behavior (Heuts 1999; Ferrari et al. 2015; Chivers et al. 2017; Lucon-Xiccato et al. 2017) and populations with very low predation risk may lose lateralized eye use (Brown et al. 2004). Thus, lateralization is not fixed but can change based on environmental pressures over development (e.g., Andrew 2002) and with changes in the environment (Chiandetti et al. 2005). Nonetheless, this lack of a visual bias is striking because many studies (Hook-Costigan and Rogers 1998; Santi et al. 2002) have reported hemispheric lateralization of antipredator responses, even if it was for a subset of antipredator behaviors (Lippolis et al. 2002).

Although we found no lateralization in the eye used, we found a consequence of the eye marmots used to monitor the approaching human. Marmots that used their left eye to monitor an approaching threat presumably assessed a higher risk and fled sooner. And this second finding suggests that marmots have lateralized antipredator behavior. Taken together these results are striking because while we might expect selection against animals being too predictable in their escape behavior (Briffa 2013), we might expect that there is relatively less cost to predictably looking at a predator and relatively more cost to predictably escaping from it. Given that predators may learn any bias in how individual prey respond to their attacks and use this to their advantage, we expect strong selection on prey to respond to predators in an unpredictable manner, which is consistent with the nonsignificant repeatability. In marmots, it may be that the costs of predictably using 1 specific eye outweigh the benefits and perhaps variation in the relative costs and benefits explains some of the variation in lateralization seen across species (Chivers et al. 2016, 2017).

Yellow-bellied marmots at our study site are preyed upon by a variety of predators, a finding that given the Brown et al. (2004) results, made us expect that marmots should have lateralized eye use. Marmots are preyed upon by a variety of terrestrial predators (coyotes *Canis latrans*, badgers *Taxidea taxus*, American martens *Martes americana*, black bears *Ursus americanus*, and long-tailed weasels *Mustela frenata*, Van Vuren 2001), as well as aerial predators (golden eagles *Aguila chrysaetos*, red-tailed hawks *Buteo jamaicensis*, Swainson's hawks *Buteo swainsoni*, and goshawks *Accipiter gentilis*, Van Vuren 2001). It is possible that vulnerability to a variety of different and presumably cognitively sophisticated predators has increased the cost of marmots responding predictably with 1 eye and hence has selected for unpredictable eye use.

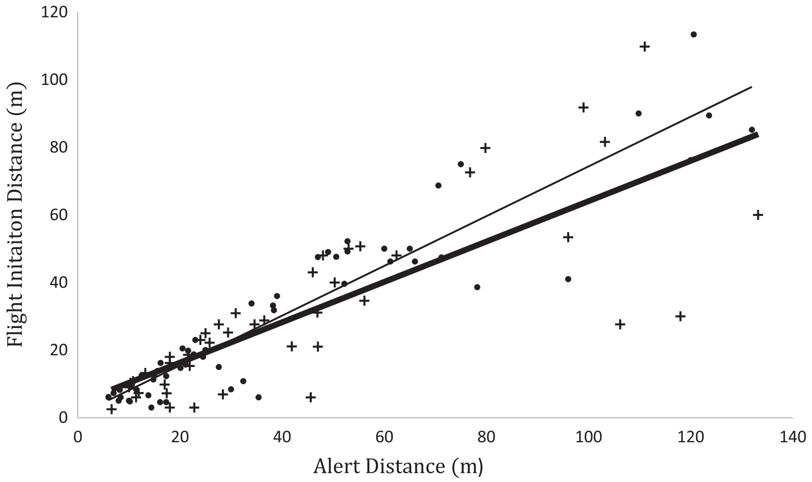

Figure 1. Relationship between alert distance and FID as a function of eye used when looking at approaching human. The plus sign indicates the right eye and dots the left eye. For any given distance, individuals monitoring approach with their right eye (thick line) had a shorter FID than those who monitored approach with their left eye (thin line).

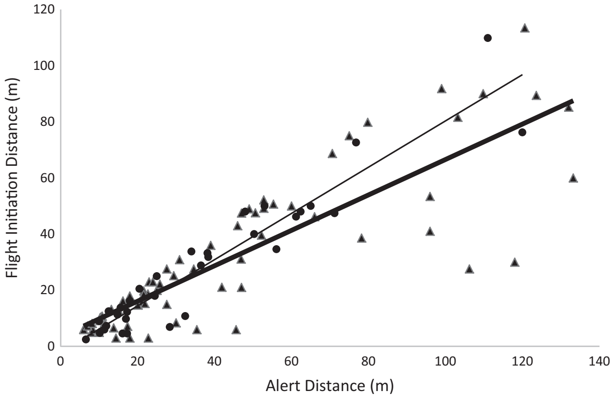

Figure 2. Relationship between alert distance and FID as a function of sex. Triangles indicate females and dots indicate males. For any given alert distance, females (thick line) tolerated closer approach compared with males (thin line).

Studies in other taxa have reported that predictable prey may be more vulnerable to predation. For instance, proactive jumping spiders *Portia labiate* captured more prey that responded predictably than unpredictable prey while docile spiders captured more unpredictable prey (Chang et al. 2017). Furthermore, hermit crabs *Paguroidea bernhardus* that fled in response to a predator *Carcinus maenas* had unpredictable re-emergence times, a finding consistent with this random response being an antipredator adaptation (Briffa 2013). Such unpredictable behavior may be the best method against predators that are able to learn sequential patterns in their prey (Bednekoff and Lima 2002).

Despite marmots responding unpredictably to an approaching predator, our results are also consistent with hemispheric lateralization of marmots' escape behavior. The eye marmots used to monitor an approaching predator was associated with the distance at which they fled the approaching predator. Because lateralized eye use seems to be an ancestral and wide spread trait for risk perception in vertebrates (fishes—Bisazza et al. 1998; birds—Andrew 2002; rodents—Kim et al. 2012; and primates—Shibasaki et al. 2014), we expected to see a greater FID when the left eye monitored approach because this was the eye that was associated with right hemispheric processing of risk-related stimuli. Therefore, when the right eye was used for risk assessment we expected that marmots would tolerate closer approaches.

Our results suggest that more information on the relative costs of the looking with each eye is warranted. Do marmots respond the same way to humans as they do their more "natural" predators? Are occasions when marmots look with their right eye and tolerate closer approaches more likely to end in a costly escape? And, the broader question of whether individuals are less likely to have lateralized antipredator responses when they deal with cognitively sophisticated predators remains to be determined.

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