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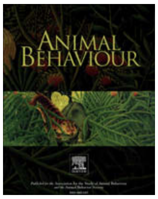

A test of the multipredator hypothesis: yellow-bellied marmots respond fearfully to the sight of novel and extinct predators

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Should prey retain an ability to respond to the sight of their extinct predators? The multipredator hypothesis (Blumstein 2006, *Ethology*, **112,** 209–217) assumes that antipredator adaptations evolve together and thus prey may respond to extinct predators as long as they have experience with other predators. We tested this prediction in yellow-bellied marmots, *Marmota flaviventris*, a species with both extant and extinct predators. Marmots were baited to a predetermined location and then shown one of five life-size photographic stimuli: a medium-size sub-Saharan antelope, the gray duiker, *Silvicapra grimmia*, as a control stimulus; a red fox, *Vulpes vulpes*, a low-risk predator; a coyote, *Canis latrans*, a higher risk predator; a mountain lion, *Felis concolor*, an extant predator, but one with which our population had no ontogenetic experience; and a wolf, *Canis lupus*, an extinct predator. Marmots responded differently to each stimulus: they stopped foraging after seeing the duiker, engaged in low vigilance after seeing the fox, seemed to monitor the coyote, fled the wolf, and engaged in high vigilance (and on one occasion alarm-called) in response to the mountain lion. This pattern of responses was consistent with the different risks associated with each species: foxes required monitoring but marmots could generally escape them, coyotes routinely kill adult marmots, solitary hunting mountain lions might be dissuaded from attack once detected, and socially hunting wolves were a very high risk predator, which would be best hidden from. The pattern of responses was not explained simply by stimulus size, stimulus detectability, or stimulus similarity. These results are consistent with the multipredator hypothesis: visual predator discrimination for ontogenetically and evolutionarily novel predators may be maintained in yellow-bellied marmots by extant predation risk.

Understanding the consequences of the loss of predators is of both theoretical and practical importance (Berger et al. 2001; Blumstein 2002; Stankowich & Coss 2007). Antipredator behaviour may be lost after the loss of a key predator (i.e. it is an example of trait loss after relaxed selection; Lathi et al., in press), or it may persist for many generations (Byers 1997). If an un-needed antipredator behaviour has substantial costs when expressed, then the loss of predators should lead to a rapid trait loss. For instance, cryptic coloration in male guppies, *Pocelia reticulata*, is quickly lost after the loss of predators because females prefer brightly coloured males in the absence of predators (Endler 1980). However, sometimes we see a persistence of traits after predator extinction (e.g. Coss 1999).

The multipredator hypothesis attempts to explain the persistence of antipredator behaviour under relaxed selection (Blumstein 2006): it assumes that selection will generate a suite of antipredator traits that will not evolve independently (i.e. there may be linkage; Curio 1973). Once such a suite of traits is created, the loss of one specific predator, but the persistence of others, should have a limited effect on the expression of antipredator behaviour for that now-missing species. Thus, we should expect vestigial, antipredator behaviour to be maintained by the benefit of possessing the syndrome. Provisional support for the multipredator hypothesis has been found in some kangaroos and wallabies, in which the loss of all predators seemingly led to a rapid loss of antipredator behaviours, whereas the loss of only one or two predators had a limited effect on the expression of antipredator behaviour for those missing species (Blumstein & Daniel 2002; Blumstein et al. 2004).

Species' ranges change both naturally and via anthropogenic action. Both the extinction and the reintroduction of predators can have profound ecological effects on their prey. Thus, it is essential to develop theoretical models to explain the conditions under which

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antipredator behaviour for recently extinct predators will persist in the absence of selection.

Wolves, *Canis lupus*, were eliminated from Colorado in the 1930s. This anthropogenic extinction created the opportunity to study its effect on the predator discrimination abilities of their prey. We focused on the yellow-bellied marmot, *Marmota flaviventris*, living in and around the Rocky Mountain Biological Laboratory, near Crested Butte, Colorado, U.S.A. Marmots are a common alpine and subalpine resident that, in other places, is preyed upon by wolves (e.g. Murie 1944). Marmots at the Rocky Mountain Biological Laboratory, however, have not experienced a complete loss of their predators: they are preyed on by a variety of predators including red foxes, *Vulpes vulpes*; coyotes, *Canis latrans*; badgers, *Taxidea taxus*; American martens, *Martes americana*; and raptors such as the golden eagle, *Aquila chrysaetos* (Van Vuren, 2001; Armitage 2004; D. T. Blumstein, personal observation).

Free-living marmots respond differently to the sight of their predators. Adult marmots naturally increase their vigilance when red foxes or martens are around, and they may alarm-call. However, these predators pose a limited threat to alert adults, and we have seen adult female marmots chase both foxes and martens. Coyotes, by contrast, are major predators on adult marmots. Interestingly, marmots do not respond to playbacks of coyote yips, but they do flee coyotes and may alarm-call after detecting them (Blumstein et al. 2008a). Although mountain lions, *Felis concolor*, have not been seen at our field site, they are not extinct in Colorado and live in Gunnison County. Thus, we expected that marmots at our site had recent/current ‘evolutionary experience’ with mountain lions but little to no ontogenetic experience. By contrast, marmots at our study site had no recent evolutionary experience with wolves. Mountain lions are stalking predators and typically have to approach within 5–10 m undetected to capture prey successfully (Smallwood 1993; Beier et al. 1995). Therefore, at greater distances a wolf poses a greater threat than a mountain lion, and we would expect higher vigilance rates (monitoring) in response to a mountain lion (i.e., to keep the threat within site) and, if wolf recognition is retained, a greater probability of flight in response to a wolf. By determining marmot predator discrimination abilities for foxes, coyotes, wolves, mountain lions and a novel, nonthreatening control stimulus, a gray duiker, *Silvicapra grimmia*, we would be able to determine whether the complete loss of a predator (the wolf), but the persistence of other predators, leads to a loss of the ability to discriminate wolves from other predators and to respond fearfully to them.

METHODS

Subjects and Study Site

We studied yellow-bellied marmots in the Upper East River Valley in and around the Rocky Mountain Biological Laboratory (38°57′N, 106°59′W). Marmots at this site have been continuously studied since 1962 (Armitage 1991; Blumstein et al. 2006). Subjects were live-trapped in Tomahawk traps baited with Omolene 100 horse feed (Ralston Purina, St. Louis, MO, U.S.A.). Once caught, subjects were permanently marked with uniquely numbered ear tags, and a unique fur mark was dyed (using Nyanzol fur dye) into their dorsal pelage. Details of trapping and marking are published elsewhere (Blumstein et al. 2008a). Marmots were studied under research protocol ARC 2001-191-01, approved by the UCLA Animal Care Committee on 13 May 2002 and renewed annually, and trapped under permits issued annually by the Colorado Division of Wildlife.

Model Construction

We created a life-size photographic model of each species. Full-size two-dimensional model predators previously have been used effectively to study the antipredator responses of several different taxa (Coss & Ramakrishnan 2000; Ramakrishnan & Coss 2000a, b; Hollis-Brown 2005; Stankowich & Coss 2007). Following Stankowich & Coss (2007), images for the models were high-resolution digital images obtained from professional photographers (see Acknowledgments) and digitally manipulated to (i) achieve the same body and head orientation (i.e. lateral view of the body, head turned to face the observer), (ii) reconstruct legs and feet obscured by vegetation or snow, and (iii) remove blemishes. Images were sized according to average shoulder heights and body lengths reported in Nowak (1999). The images were printed on heavy-weight matte paper on a Hewlett–Packard Designjet 4000PS poster printer, mounted on foam board, spray painted green/brown camouflage on the reverse side, and sprayed with matte-finish polyurethane water repellent. Models were attached to a wooden base so that they would stand alone securely (Fig. 1).

Stimulus Presentation

Between 21 June and 19 July 2008, we presented three different visual stimuli to each of 24 subjects: 12 adult females (four with pre-emergent pups and five with postemergent pups), three yearling females, three adult males and six yearling males. The individuals were from five marmot colony sites: Marmot Meadow–Main Talus, Marmot Meadow–Aspen Burrow, Bench, Gothic Town Site, and Stonefield–South Mound.

We used a repeated-measures design in which each individual was presented with a duiker and two predatory stimuli according to a predetermined balanced order. We elected not to present each subject with all five stimuli to reduce order effects: marmots typically habituate to repeated experimental stimulus presentations (Blumstein et al. 2008b). We controlled for order effects experimentally (by balancing the order in which stimuli were seen) and assessed these effects statistically (by including order as a main effect in our statistical analyses).

For all experiments we placed the tarp-covered stimulus 20 m from a pile of bait (Omolene 300 horse feed; Ralston Purina) and the observer sat quietly an average of 41 m (SD = 18.1 m) away from the food. Once the subject began to forage, the observer started videorecording the subject. After a 60 s baseline period had elapsed, the observer pulled a string connected to the tarp and unveiled the stimulus. The subject was then recorded for an additional 3 min. Experiments were videorecorded with a Canon GL1 digital camcorder.

Subjects were exposed to stimuli on different days (the average interval between stimuli was (mean ± SD) 55 h 24 min ± 37 h 44 min (minimum 19 h 27 min, maximum 154 h 39 min). Only four of the 24 subjects had previously seen a stimulus directed at another subject: on three occasions the focal marmot saw the duiker before its three stimuli, on one occasion one animal saw the mountain lion after its first stimulus (fox) and before the other two. In all cases the subject saw the extra stimulus for <1 min. Moreover, the average interval between the extra stimulus and the next targeted stimulus was 44 h 2 min ± 14 h 52 min). Thus, we assumed that the animals were not habituated by the extra stimulus presentation, and thus we included these animals in the final analyses.

Although we aimed to present a stimulus to only one subject at a time, on seven occasions there were multiple subjects at the bait (six times there were two animals and once there were three). Rather than risking habituation by exposing unintended targets to

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Figure 1. Photographs of the life-size stimuli presented to yellow-bellied marmots to study predator discrimination abilities. All stimuli were photographed at the same distance so that relative size was maintained.

a stimulus, we capitalized on this and scored the marmots' response and then ensured that the stimulus fit into one of the predetermined presentation orders. For all 72 experiments, the mean number ± SD of other adults at the bait during the first minute (the baseline time) was 0.57 ± 0.88 (median and mode = 0) and the mean number ± SD of adults within the vicinity in the first minute was 0.58 ± 0.88 (median and mode = 0). Thus, the vast majority of the presentations were to a single focal subject, and in all but the seven cases described above, we focused on only one subject at a time.

Data Analysis

Videotapes were scored using the event recorder JWatcher (Blumstein & Daniel 2007). We scored the following behaviours: forage (an individual stands quadrupedally and ingests food), stand look (an individual stands quadrupedally with its head elevated and motionless), lie look (the animal's belly was closer to the ground than in normal stand look and the head only slightly raised), rear look ('high vigilance': an individual stands bipedally with its head fixated), run, walk, burrow (when an animal returned to the burrow), out of sight (when the focal animal disappeared from sight into its burrow), social (these were rare and consisted mostly of nose-to-nose touching, which we refer to as greeting), self-groom (animal scratches or chews on its own pelage), and other. For analysis we combined lie look and stand look to form the new category 'low vigilance', walk and run to form the new category 'locomotion', burrow and out of sight to form the new category 'hide', and we created what we viewed as the highest level response: the proportion of time allocated to rear look along with out of sight and in the burrow.

We visually examined plots of baseline time allocation and time allocated to each behaviour in 15 s time bins after presentation. Marmots responded to all presentations by eliminating their foraging in the first 15 s after the unveiling of the stimulus and allocating time differentially. Over time, subjects resumed pre-stimulus presentation foraging.

We elected to focus our formal statistical analyses on the immediate response to the stimuli, the first 15 s after presentation, because we expected that discrimination of visual predators would happen quickly and that habituation to the novel presentation would happen quickly (most subjects resumed foraging after an immediate response). To do so, we fitted a series of linear mixed-effects models in SPSS-16 (SPSS, Inc., Chicago, IL, U.S.A.) with two main effects: stimulus and presentation order. Linear mixed-effects models (Lindskey 1993) are particularly good at dealing with unbalanced designs (every subject was exposed to the duiker and two of the four predatory stimuli). In no case was presentation order significant; however, we retained it in the analysis to remove its effect statistically. We calculated planned comparisons for the difference in response to each pair of stimuli because we explicitly wished to understand the pattern of responses and because each comparison would be meaningful (Ruxton & Beauchamp 2008), and we report unadjusted *P* values (Gotelli & Ellison 2004; Nakagawa 2004).

Experimental Questions and Predictions

Berger et al. (2001) reported rapid loss of predator recognition capacities after the loss of wolves. If wolf recognition were lost, we would expect a limited response to the wolf, and, because the duiker was novel yet nonthreatening, we expected lower-risk responses to the duiker compared with all other stimuli. However, if marmots responded fearfully to both the duiker and the wolf, we could not eliminate the hypothesis that marmots responded to novel stimuli. We expected that coyotes would elicit a larger response than foxes because they were more threatening to adult marmots. We also expected that if marmots generalized their coyote response to wolves they would respond similarly to both; different responses would suggest that wolves might be classified differently. Comparing the responses to the wolf and to the mountain lion allowed us to see if ontogenetic novelty was important: different responses would suggest that they were classified differently.

In addition to fitting these models, we also calculated the difference from baseline in the proportion of time allocated to behaviours in the first 15 s after stimulus presentation, and we calculated the 95% confidence intervals for this difference. If the

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confidence intervals excluded 0, we could infer that marmots responded to the stimulus.

RESULTS

There were no significant differences in baseline behaviour (all $P > 0.176$) for subjects that were about to be exposed to the stimuli. Marmots responded to the presentation of all the stimuli. In the first 15 s after the stimuli were unveiled, marmots ceased foraging (95% confidence intervals of the difference between time allocated to foraging in the first 15 s and time allocated to foraging in the baseline period did not include 0). Because there were no differences in baseline behaviour, we focused on the response in the first 15 s.

Overall, we found statistically significant effects of stimulus on the proportion of time allocated to high vigilance ($F_{4,29.635} = 3.749$; $P = 0.014$; Fig. 2b) and the combined proportion of time allocated to high vigilance and time allocated to out of sight and in the burrow ($F_{4,24.661} = 3.104$; $P = 0.034$; Fig. 2d), two obvious antipredator behaviours, but not foraging ($F_{4,28.082} = 0.669$; $P = 0.619$; Fig. 2f), low vigilance ($F_{4,23.807} = 1.995$; $P = 0.128$; Fig. 2a), locomotion ($F_{4,23.765} = 1.201$; $P = 0.336$; Fig. 2e) or simply the time out of sight and in the burrow ($F_{4,19.815} = 1.959$; $P = 0.140$; Fig. 2c). Overall, we had no significant order effects (all $P > 0.086$ for locomotion).

Marmots spent significantly more time in low vigilance when exposed to the fox than to the mountain lion (Fig. 2a, $P = 0.038$). There were no significant differences in time spent in high vigilance between the duiker, the coyote and the wolf or between these models and either the fox or the mountain lion. The marmots spent significantly more time in high vigilance in response to the mountain lion (Fig. 2b) than to the duiker ($P = 0.044$), the fox ($P = 0.013$) or the wolf ($P = 0.030$). There were no significant differences between the mountain lion and the coyote or between the duiker, the fox, the coyote and the wolf. The subjects spent significantly more time hiding in response to the wolf than to the duiker (Fig. 2c, $P = 0.042$) or the coyote ($P = 0.025$), but not the fox or the mountain lion. There were no significant differences in time spent hiding in response to the duiker, fox, coyote and mountain lion. When we combined the time spent in high vigilance and the time spent in hiding, the marmots spent more time hiding from or being vigilant toward the wolf and the mountain lion than toward the duiker (Fig. 2d; wolf: $P = 0.048$; mountain lion: $P = 0.016$) or the fox (Fig. 2d, wolf: $P = 0.033$, mountain lion: $P = 0.011$). There was no difference between the wolf and the mountain lion, between the duiker and the fox, or between the coyote and any other model. The marmots spent less time in locomotion in response to the fox compared to the duiker (Fig. 2e, $P = 0.046$), but not to any other model. There were no other differences in locomotion among the models.

DISCUSSION

Together, our results suggest a unique set of responses to each stimulus. Marmots responded to the duiker by simply stopping foraging and engaging in low vigilance before moving off to a new area. When exposed to the fox, they stopped foraging, engaged in low vigilance, but did not flee or hide. In response to the coyote, they stopped foraging, engaged in moderate amounts of low and high vigilance and then moved away to a new area. The wolf model caused the marmots to stop foraging and immediately run and hide. Finally, the mountain lion elicited low levels of low vigilance, high levels of high vigilance (and on one occasion alarm calling), followed by flight and hiding.

The pattern of responses was not explained simply by stimulus size, detectability, or stimulus similarity. If stimulus size were important, we would expect similar responses to both the wolf and the mountain lion because both were similarly sized (Fig. 1); we found different types of responses. Moreover, the duiker was much larger than the fox but the sight of the fox seemingly elicited a greater response than the duiker. Detectability is likely to be a function of both size and colour. To our eyes, the red fox stood out the most but elicited an attenuated response compared to that elicited by the coyote, mountain lion and wolf. Because diurnal sciurid rodents have dichromatic vision (Gurnell 1987), it is possible that the red fox's high chromatic colour was attenuated to the marmots. The wolf and coyote photographs superficially resembled each other but the wolf elicited a qualitatively different response. The fox, coyote and wolf were all canids, and thus superficially similar, but each elicited a qualitatively different response.

Marmots commonly see Rocky Mountain mule deer, *Odocoileus hemionus hemionus*, around their burrows, and they typically respond by becoming alert and moving off to a new area, which is similar to their response to the duiker (n.b. the duiker is about the size of a mule deer fawn). Although adult marmots are not routinely preyed upon by foxes, foxes do regularly take marmot pups. Adults, therefore, need not flee from foxes but simply maintain low vigilance. Because coyotes are major predators of adult marmots, marmots probably are quite savvy in their responses to coyotes; after assessing them through low and high vigilance, they move off to a new area out of harm's way.

Although our subjects have most probably not seen mountain lions in their lifetime, they have not lost their ability to recognize large felids as highly dangerous predators. Mountain lions are stalking predators, and it is exceptionally important to maintain visual contact with them at all times when detected, so that they cannot creep to within attack range. Because the distance between the model predator and the marmot (20 m) was outside the successful attack range for a mountain lion (5–10 m), the marmots were probably able to maintain greater perceptions of safety by keeping the model insight through high vigilance and moving away to a new area or hiding.

Finally, these marmots have been free from wolf predation for >70 years (>35 generations), but still respond fearfully to them. Upon detecting the wolf, the marmots typically monitored it through low vigilance followed by immediate flight and hiding out of site. The spatial margin of safety is probably much greater with wolves compared to mountain lions, as wolves are both coursing and sprinting predators that must chase down their prey. Marmots may have simply generalized their response to the wolf from coyotes, and the wolf may have appeared as a large coyote, thereby eliciting an even stronger reaction. Thus, it is possible that wolf recognition is being maintained by the presence of coyotes in this population. This hypothesis could be formally tested by comparing the responses of marmots in areas with no coyotes or mountain lions. However, we are aware of no locations where they are not sympatric with coyotes. Large ungulates that are not regular prey of extant local coyotes, but are susceptible to wolves, have lost their ability to recognize wolf odour after 130 years of isolation (Berger et al. 2001), but these animals are able to re-learn the danger of wolves within one generation of exposure to wolf predation. An alternative hypothesis is that the rapid flight response to wolves is being maintained by the presence of eagles and mountain lions in the environment, two species that create a need for rapid flight.

Taken together, our results are consistent with the main prediction of the multipredator hypothesis: visual predator discrimination for ontogenetically and evolutionarily novel predators may be maintained in yellow-bellied marmots by extant predation risk. These results have important implications for

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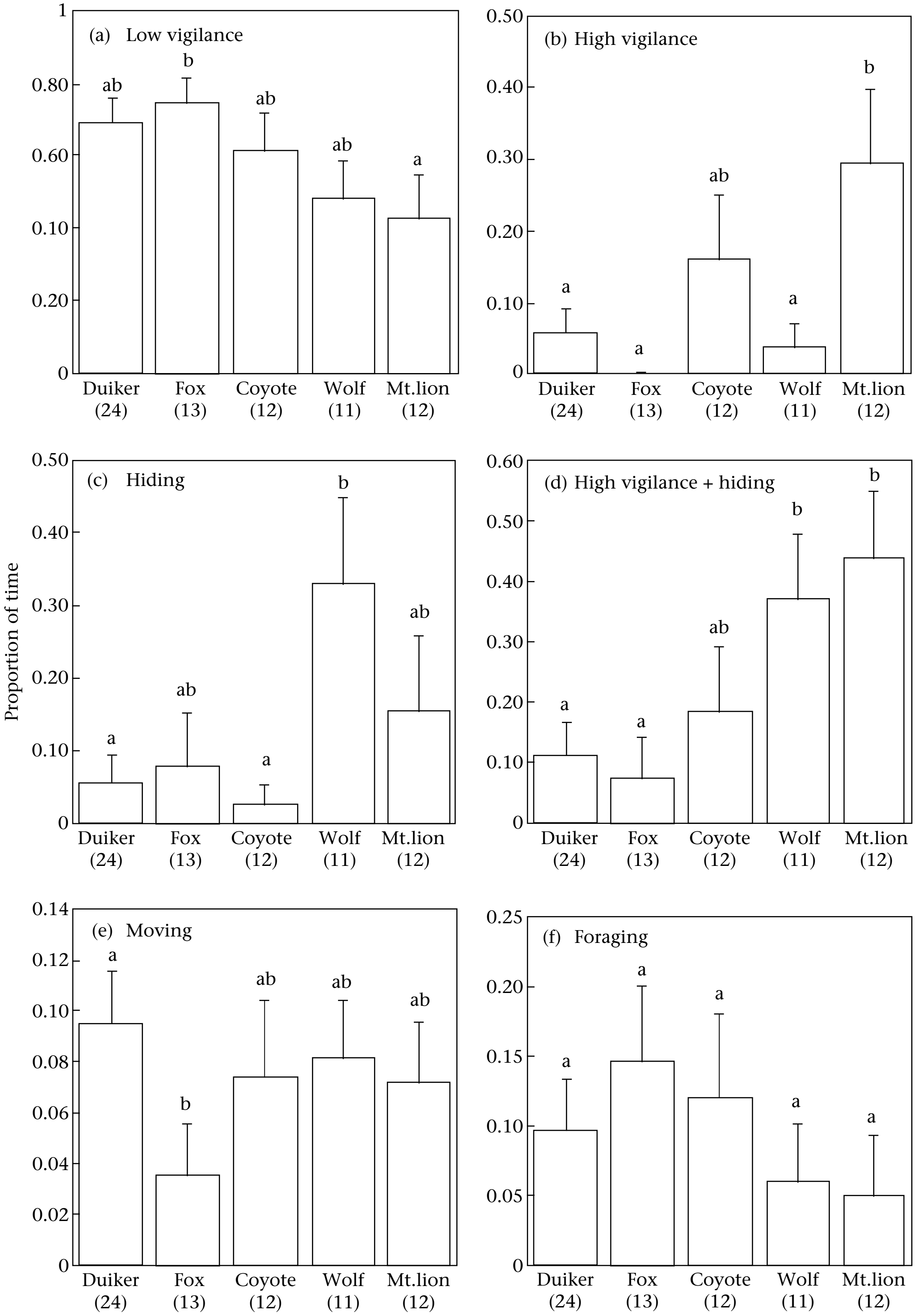

Figure 2. Responses (mean proportion of time + SE) of yellow-bellied marmots to the presentation of predatory and control stimuli in the first 15 s after stimulus presentation. Similar letters (e.g. a or b) above bars identify pairwise differences that are not statistically distinguishable ($P > 0.05$). Numbers refer to the number of experiments conducted with each stimulus.

conservation management of marmots and other species. Wolf extinction is not expected to have created an entirely predator-naïve marmot population, and we expect that marmots would survive wolf recolonization. Generally, systems such as these may be more resilient than systems with each antipredator trait assorting independently. Thus, the key assumption of the multipredator hypothesis, that selection will generate suites of antipredator traits (or antipredator syndromes), may make good design sense. If true, this is an important insight for designing robust defensive systems (Blumstein 2008).

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