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Predator discrimination and 'personality' in captive Vancouver Island marmots (*Marmota vancouverensis*)

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Abstract

A major impediment to recovering declining populations successfully is the mortality of reintroduced or translocated animals. We generally assume that captive-born animals may lose their antipredator behaviour abilities in captivity, but studies rarely compare predator recognition abilities of captive-born and wild-captured animals to test this. To identify whether predator discrimination abilities of the critically endangered Vancouver Island marmots *Marmota vancouverensis* were lost in captivity, we presented wild-captured and captive-born marmots with taxidermic mounts of predators (a cougar *Felis concolor* and wolf *Canis lupus*) together with control stimuli (marmot, domestic goat *Capra aegagrus*, the cart on which all stimuli were presented and a 'blank' no-stimulus control). Regardless of specific predator discrimination abilities, for some species overall 'personality' may be associated with response to predators and subsequent survival. Thus, to quantify overall reactivity in the presence of a predator, we also conducted a mirror-image stimulus (MIS) presentation experiment where marmots were video-recorded with or without the presence of a wolf. Marmots discriminated among these stimuli, responding the most to the wolf and cougar. The MIS results suggest that marmots varied along a continuum of reactivity. The amount of reactivity was unaffected by the presence of a wolf, and was correlated with our highest level of responsiveness (vigilance at the burrow and time within the burrow) to the wolf. Taken together, we conclude that marmots differentiate predators from non-predators and that this ability has not been lost under the conditions in which they have been reared.

Introduction

Reintroduced and translocated animals are often killed by predators, and this mortality is often a significant impediment to successful population recovery (McCallum, Timmers & Hoyle, 1995). Some of this mortality may be expected because individuals vary in how they respond to predators and this variation may have fitness consequences (Wilson *et al*., 1994). Additionally, predator recognition abilities may be lost or modified when animals are brought into, or born into, captivity because animals may fail to develop appropriate recognition skills or lose these skills (within a generation or over evolutionary time; Griffin, Blumstein & Evans, 2000; McPhee, 2003). But predator recognition abilities, *per se*, are not the only factor that may explain variation in survival. A large body of literature has documented 'personality' differences among individuals (Wilson *et al*., 1994; Gosling, 2001; Sih, Bell & Johnson, 2004*a*; Sih *et al*., 2004*b*), and these differences may influence how animals respond, and fare, when they encounter predators (Wilson *et al*., 1994; Brick & Jakobsson, 2002; Réale & Festa-Bianchet, 2003; Sih *et al*., 2004*a*,*b*). Knowledge about antipredator abilities and personality differences is thus not merely of academic interest, but is an essential tool of conservation biology (Blumstein, 2000; Blumstein & Fernández-Juricic, 2004), particularly when animals suspected to lose predator recognition abilities in captive situations are re-released into the wild (Griffin *et al*., 2000).

Marmots are cat-sized ground-dwelling, semi-fossorial, sciurid rodents (Armitage, 2003). The critically endangered Vancouver Island marmot *Marmota vancouverensis* is endemic to Vancouver Island (Nagorsen, 1987) and has declined to near extinction (fewer than 35 remain in the wild; unpublished minutes, Vancouver Island Marmot Recovery Team, 9 November 2004). Predation by wolves *Canis lupus*, cougars *Felis concolor* and golden eagles *Aquila chrysaetos* has been implicated in their demise (Bryant, 2000; Bryant & Page, 2005). This decline has occurred despite the ability of free-living marmots to respond naturally to these natural predators (high predation rates are likely a consequence of greater predator abundance; Bryant & Page, 2005), dig numerous escape burrows and communicate in a sophisticated manner about predation risk (Blumstein, 1999; Blumstein, Daniel & Bryant, 2001). A successful captive breeding programme has begun (Bryant & Mcadie, 2003; Bryant, 2005) and a few animals have been reintroduced to the wild (unpublished minutes, Vancouver Island Marmot Recovery Team meeting, 9 November 2004). Four of the 13 released marmots were killed by predators the same season in which they were introduced. A reduction in mortality of introduced animals can be achieved in at least three non-mutually exclusive ways: (1) predator control (which may be socially and politically unacceptable; e.g. Patterson, 2004); (2) keeping predators away by physically shepherding the introduced animals (which may be labour intensive and ineffective); and (3) identifying behavioural patterns that predispose individuals to predation, and then either not releasing those individuals or attempting to modify their behaviour before release (e.g. Van Heezik, Seddon & Maloney, 1999; Mirza & Chivers, 2000).

We focused on the third option. Our objective was to identify those behavioural factors that might predispose marmots to being killed by predators and how this differed between captive-born and wild-captured animals tested in captivity. We first evaluated whether marmots could discriminate between predators and non-predators by presenting wild-captured and captive-born marmots with taxidermic mounts of predators (a cougar and a wolf) and control stimuli to determine whether discrimination was lost in captivity. The control stimuli included an adult yellow-bellied marmot *Marmota flaviventris*, with its fur dyed to resemble a Vancouver Island marmot, a goat *Capra aegagrus*, which does not naturally occur on Vancouver Island and therefore represents a novel stimulus, and the cart on which all stimuli were presented. We also included a 'blank' stimulus presentation to quantify natural variation in behaviour. We then measured whether marmots altered their behaviour in terms of time spent foraging or being vigilant, or whether patterns of burrow use changed. In a second experiment, we documented personality by exposing marmots to a mirror with and without a taxidermic wolf mount present. We extracted principal components from the mirror-image stimulation (MIS) experiments and correlated these factors measures to identify marmot personality traits. Finally, we correlated factor scores with measures of responsiveness to the stimuli in the first experiment to determine whether a simple MIS test could be used as an overall metric of responsiveness to predators.

Materials and methods

Study sites

Studies were conducted at three of the four marmot breeding facilities: the Devonian Wildlife Conservation Centre of the Calgary Zoo (14 subjects between 2002 and 2004); the Tony Barrett – Mount Washington Marmot Recovery Centre near Courtenay on Vancouver Island (four subjects between 2002 and 2004); and Mountain View Breeding and Conservation Centre, a private facility near Langley, British Columbia (three subjects in 2002 only). Animals were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care. At all locations, marmots were housed in connected indoor/outdoor enclosures. The indoor enclosure was essentially their burrow and contained nest boxes. Marmots were fed outside, and this outdoor portion of the enclosure contained bales of hay or rocks that allowed resting. At each facility, keepers controlled access to the open slides between the outdoor and indoor enclosures. We were given independent access to the outdoor enclosures so that we could facilitate the experiments. This involved temporarily blocking marmot access to the outdoor enclosures with straw bales and plywood slide covers, until just before a stimulus presentation session. Experiments were conducted in the outdoor part of the enclosure, which varied in design among sites. All enclosures were surrounded by thick wire mesh. Calgary Zoo enclosures were 3.7 × 1.8 m or 3.6 × 3.4 m and Mount Washington enclosures were 2.4 × 3.1 m. Both had outdoor concrete pads lined with gravel. Mountain View enclosures were more naturalistic vegetated yards, *c.* 3.7 × 3.7 m, with large boulders on which marmots could rest. Details of the facilities can be found in Bryant & Mcadie (2003) and Bryant (2005).

Subjects were either wild captured (12) or captive born (nine) and ranged in age from 1 to 7 years (Table 1). Captive-born marmots were significantly younger when tested (median age = 2) than those wild captured (median age = 3; Mann–Whitney $P = 0.001$). Wild-captured animals were in captivity from 2 to 6 years before testing (mean ± SD = 3.5 ± 1.17 years). Five subjects were females and 16 were males. Subjects were typically housed in breeding pairs; in many, but not all, cases we were able to isolate them for testing in empty enclosures (15 subjects were housed singly for the experiments, and we had four pairs). If marmots were moved to new enclosures for testing, they had a minimum of 2 days to habituate to their surroundings. This was followed by a further 4 days of habituating them to the experimental protocol. When housed socially, we attempted to focus on only a single subject and attempted to perform experiments when the other animal was not in the outdoor part of the enclosure. There were two exceptions, where both animals living together were tested. All experiments were conducted in July, August or early September.

Predator discrimination

A single observer sat in a camouflaged (burlap) blind next to the enclosures. An identical second blind across from the observer's blind hid the experimental stimulus. A track in front of the enclosures ran between both blinds. One side of all enclosures was covered with opaque material (cardboard or plywood) to prevent marmots from seeing the person conducting the experiments and the stimuli before they were formally presented on a track in front of the enclosure. Each stimulus (Fig. 1) was presented on a cart, and was pulled from its enclosure along the track until it appeared in front of the marmot. Following presentation, the stimulus was pulled into the observer's blind, where it remained out of sight to the marmots.

Table 1 Details of the 21 Vancouver Island marmots *Marmota vancouverensis* for which we conducted visual predator discrimination tests

Year	Name	Origin	Facility	Sex	Years in captivity	Age tested	*n* housed with	MIS	MIS-wolf
2002	China	Wild	CZ	Female	3	7	0	Yes	Yes
2002	Gudron	Wild	CZ	Male	3	7	0	Yes	Yes
2002	Heather	Wild	CZ	Female	2	2	0	Yes	Yes
2002	Humphrey	Wild	MV	Male	3	3	1	Yes	No
2002	Mark	Wild	MV	Male	3	3	1	Yes	No
2002	Butler	Captive	MW	Male	2	2	0	Yes	No
2002	Hooper	Captive	MW	Male	2	2	0	Yes	No
2002	Moriarty	Captive	MW	Male	2	2	0	Yes	No
2003	Dylan	Captive	CZ	Male	1	1	1	Yes	Yes
2003	Franklin II	Wild	CZ	Male	3	3	0	Yes	Yes
2003	Houdini	Wild	CZ	Male	5	5	1	Yes	Yes
2003	Leonard	Captive	CZ	Male	1	1	1	Yes	No
2003	Macumba	Captive	CZ	Male	1	1	1	Yes	Yes
2003	Mirabel	Wild	CZ	Female	3	3	0	Yes	Yes
2003	Virginia	Captive	CZ	Female	1	1	1	No	No
2004	Hannibal	Captive	CZ	Male	3	3	0	Yes	Yes
2004	Ivan	Wild	CZ	Male	6	9	0	Yes	Yes
2004	Mel	Wild	CZ	Male	5	5	0	Yes	Yes
2004	Rani	Captive	CZ	Female	3	3	0	Yes	Yes
2004	Buck	Wild	MW	Male	3	3	0	Yes	Yes
2004	Oliver	Wild	MW	Male	3	3	0	Yes	Yes

CZ, Calgary Zoo; MV, Mountain View; MW, Mount Washington. MIS and MIS-wolf identify those subjects for which we also conducted mirror-image stimulation tests with and without a taxidermically mounted wolf present.

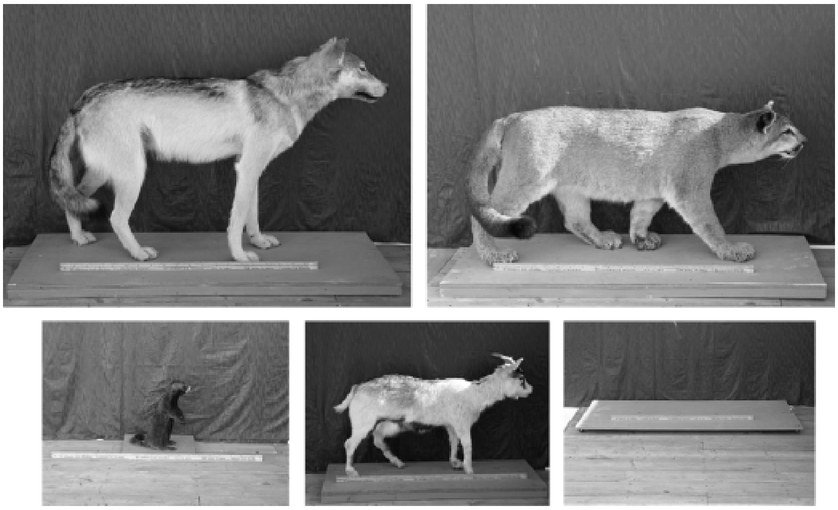

Figure 1 Stimuli used in a predator discrimination experiment (a metre stick is provided for reference). Clockwise from upper left: wolf, cougar, cart, goat, marmot.

The habituation phase began with 2 days in which only the tracks and blinds were in place. On the third and fourth days of habituation, the experimenter sat quietly in one of the blinds as she would on the day when the stimuli were presented. On experimental days, subjects were baited to a central location in each enclosure, where the marmots had an unobstructed view of the stage and the stimulus being presented.

Stimuli were presented for a total of 1 min each, with an average interval between presentations of 20.8 h (SD = 26.11 h, median = 22.50 h, range = 0.22–221.53 h). We initiated a second test in the same day only after they had returned to baseline, relaxed behaviour. Stimuli were presented in a predetermined random order. We searched for (using repeated-measures general linear models with order as the within-subjects factor) and found no effects of stimulus presentation order on our various measures of responsiveness. Thus, we focus exclusively on describing stimulus effects. We video-recorded marmots for 1 min before stimulus presentation (i.e. a baseline period), during the 1 min stimulus presentation, and for 2 min following stimulus presentation. Videotapes were scored using JWatcher 0.9 (Blumstein, Evans & Daniel, 2000) by an observer unaware of the experimental treatment. We calculated the time allocated to foraging (head down and ingesting food or actively manipulating food into the mouth with front paws with head up), standing and looking at the burrow (quadrupedally standing on all four legs with head elevated, including chewing when not manipulating food with paws, while located at the burrow entrance), standing and looking away from the burrow (quadrupedally standing on all four legs with head elevated, including chewing when not manipulating food with paws, while located away from the burrow entrance), rearing and looking at the burrow (bipedally standing with head elevated, including chewing when not manipulating food with paws, while located at the burrow entrance), rearing and looking away from the burrow (bipedally standing with head elevated, including chewing when not manipulating food with paws, while located away from the burrow entrance), locomotion (either walking or running) and time spent within the burrow. We also noted the number of alarm calls emitted.

After fleeing to their burrows, marmots often spent time looking while locating either partially within or immediately adjacent to the burrow entrance. We considered vigilance at the burrow to be a higher-level response to a predator than vigilance away from the burrow (such as when a marmot raises its head to look without leaving the food dish), and thus scored looking while at the burrow as distinct from looking while away from the burrow. For subsequent analysis, we combined time spent within the burrow, time spent standing and looking at the burrow, and time spent rearing and looking at the burrow into a single new variable: time spent within or vigilant at the burrow. We view this response as the highest-level response.

We fitted repeated-measures general linear models with stimulus type as the within-subjects factor to study variation in time allocation. We first examined data from all 21 subjects to quantify whether the population as a whole responded to the stimuli. We then examined whether captive-born and wild-captured individuals responded differently. We analysed three response variables: proportion time allocated to foraging, proportion time spent within the burrow or vigilant at the burrow entrance, and proportion time engaged in rearing and looking away from the burrow (we view this as a measure of heightened vigilance). For each of these variables, we tested for (using a general linear model) and found no stimulus by time interaction for the presentation minute and the first minute post-presentation when subdivided into eight 15-s time bins; we therefore combined these periods into a single 2-min time period for analysis. The second post-presentation minute was excluded for analysis (in several cases, individuals moved out of sight and we were unable to score their behaviour reliably).

We set our α to 0.05, and report Bonferroni corrected *P*-values for all pairwise comparisons. We tested for sphericity (an assumption of repeated-measures analysis) using Mauchly's test for sphericity; in the few cases where sphericity could not be assumed, we report *P*-values based on Huynh–Feldt adjustments. We calculated *d*-scores (Cohen, 1988) to identify effect size of planned comparisons between treatments. We report partial η^2 values as a measure of effect size (Cohen, 1988) for the ANOVA examining origin effects.

Personality

Standardized methods to study individuality are based on Armitage's use of MIS (Svendsen & Armitage, 1973; Armitage & Van Vuren, 2003). Individual marmots had a mirror placed in their enclosure near their food, and we waited for the marmot to discover the mirror and interact with it. Individuals respond differently to a mirror and the nature of the response allows us to identify 'behavioural syndromes' (Sih *et al.*, 2004*a*,*b*) or 'personality profiles' (e.g. Gosling, 2001). Specifically, time allocation (or other measures of responsiveness) is quantified and principal components analysis is used to extract orthogonally rotated factors. Factor scores are then interpreted, and often reveal that individuals fall along a 'proactive–reactive' continuum or a 'shy–bold' continuum. Regardless of the precise interpretation, correlations within an orthogonal factor define the factor, and because factors are unrelated, behaviours that define a factor represent a set of correlated behaviours.

All experiments were videotaped. We then began scoring from 30 s before the marmot's discovery of the mirror, and continued to score behaviour, using JWatcher, for the next 10 min. We focused specifically on investigative-type behaviours and foraging. Additionally, because we aimed to quantify the response by individuals to the mirror, we scored behaviours such as vigilance and locomotion directed towards the mirror as distinct from those same behaviours directed to locations other than the mirror.

We calculated the proportion of time allocated to foraging (head down and ingesting food or actively manipulating food into the mouth with front paws with head up), standing and looking towards the mirror (quadrupedally standing with head elevated, including chewing when not manipulating food with paws, body oriented towards the mirror), standing and looking away from the mirror (quadrupedally standing with head elevated, including chewing when not manipulating food with paws, body oriented away from the mirror), rearing and looking towards the mirror (bipedally standing with head elevated, including chewing when not manipulating food with paws, body oriented towards the mirror), rearing and looking away from the mirror (bipedally standing with head elevated, including chewing when not manipulating food with paws, body oriented away from the mirror), locomotion (walking or running) towards the mirror, locomotion (walking and running) away from the mirror, tail flagging directed towards the mirror, tail flagging directed away from the mirror, interacting with the mirror (sniffing and pawing the mirror) and time spent within the burrow. We also noted the number of alarm calls (if any were emitted). Each subject was also exposed to a mirror when the mounted wolf was present. The goal of this was to see to what degree 'personality' was context independent (Coleman & Wilson, 1998;

Brick & Jakobsson, 2002). The sample size for the MIS experiment was 20 marmots for which we also had data on the response to stimuli, and that for the MIS-wolf experiment was 14. All MIS studies followed predator presentation experiments. For historical reasons (we did not begin this MIS-wolf experiment until the end of 2002), all MIS-wolf experiments followed the basic MIS presentation (i.e. the presentation order was not randomized).

We used principal components analysis to extract two factors from the following combined behaviours: total time vigilant, total time in the burrow, total time foraging, total time engaged in locomotion, number of tail flags per minute and total amount of time interacting with the mirror. We rotated these component scores using a Varimax algorithm with Kaiser normalization and interpreted these orthogonal (i.e. unrelated) factors (e.g. Tabachnick & Fidell, 1996). Finally, to look for context independence, we correlated factor scores with each other and with time allocation measures during the stimulus presentation experiments.

Results

Predator discrimination

Using data from all 21 sampled individuals, marmots responded differentially to the various stimuli presented to them (Fig. 2). Marmots changed the amount of time spent foraging ($P<0.001$) and the time spent within the burrow or vigilant at the burrow ($P<0.001$), but did not change the amount of time allocated to vigilance away from the burrow ($P = 0.487$). Subjects significantly decreased foraging compared with the blank for all stimuli (cart $P = 0.012$; cougar $P<0.001$; goat $P = 0.001$; marmot $P = 0.005$; wolf $P<0.001$) and significantly decreased foraging compared with the cart for the cougar ($P = 0.022$) and the wolf ($P = 0.013$). Subjects spent significantly more time inside the burrow or being vigilant at the burrow for the cougar ($P = 0.002$) and the wolf ($P = 0.001$) compared with the blank, and for the wolf ($P = 0.036$) compared with the cart. Although not significantly different, the effect sizes of the comparisons for the responses of the two predatory stimuli (cougar and wolf) with the other controls (goat and marmot) were generally moderate to large (Table 2). Thus, if our sample sizes were larger, it is likely we would have been able to detect significant differences. There was no significant difference in baseline behaviour among stimuli for any of the response variables (forage $P = 0.946$; vigilance at or in the burrow $P = 0.422$; rear vigilance away from the burrow $P = 0.118$). There were no order effects for any of the response variables (forage $P = 0.347$; vigilance at or in the burrow $P = 0.845$; rear vigilance away from the burrow $P = 0.130$).

Subjects occasionally alarm called during and after stimulus presentation. However, alarm calling occurred so infrequently that we were unable to analyse formally the data (only five out of 21 individuals alarm called to at least one stimulus, with no obvious pattern detected).

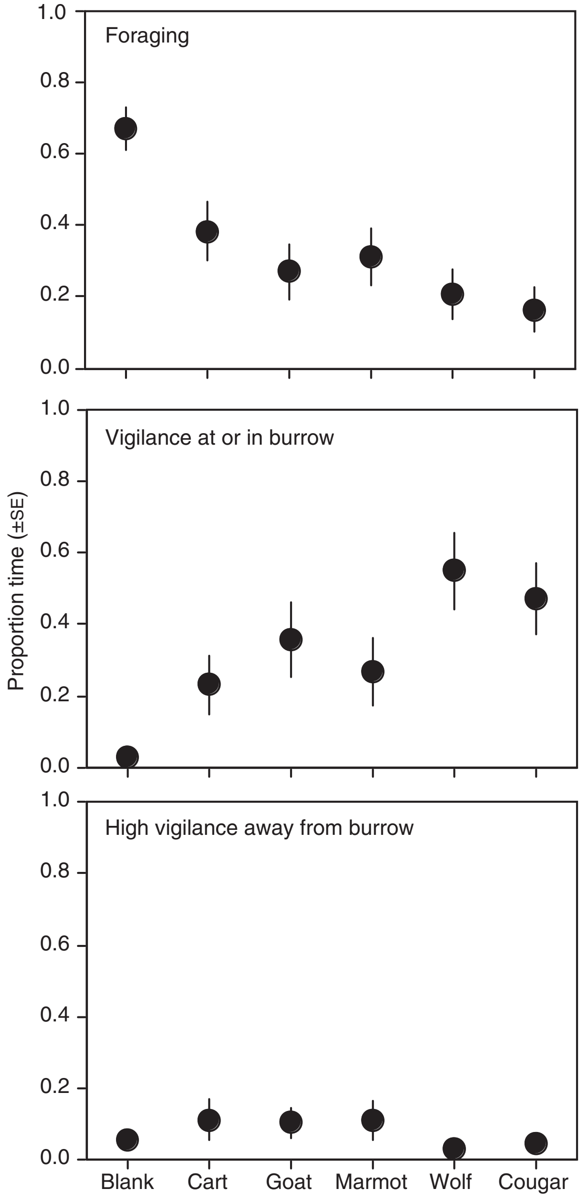

Figure 2 Average (± SE) proportion of time Vancouver Island marmots *Marmota vancouverensis* allocated to foraging, vigilance at or in the burrow, or high vigilance away from the burrow in response to experimental stimuli.

Repeated-measures ANOVA with origin as the between factor and stimulus as the within factor revealed no significant origin effect (Fig. 3; captive $n = 9$, wild $n = 12$; forage $P = 0.873$, partial $\eta^2 = 0.001$; vigilance at or in the burrow $P = 0.893$, partial $\eta^2 = 0.001$) nor was there a significant origin by stimulus interaction for either of these response variables (forage $P = 0.832$, partial $\eta^2 = 0.022$; vigilance at or in the burrow $P = 0.843$, partial $\eta^2 = 0.021$). An identical analysis applied to the baseline period revealed similar results. There was no significant origin effect (forage $P = 0.809$, partial $\eta^2 = 0.003$; vigilance at or in the burrow

Table 2 Effect size (*d*-scores) comparing the response of marmots to predators (cougar and wolf) with that of non-predators (goat, marmot)

Dependent variable	Non-predators	Predators	*d*-score
Forage	Goat	Cougar	0.33
	Goat	Wolf	0.33
	Marmot	Cougar	0.47
	Marmot	Wolf	0.47
Vigilance at or in burrow	Goat	Cougar	0.16
	Goat	Wolf	0.41
	Marmot	Cougar	0.34
	Marmot	Wolf	0.61

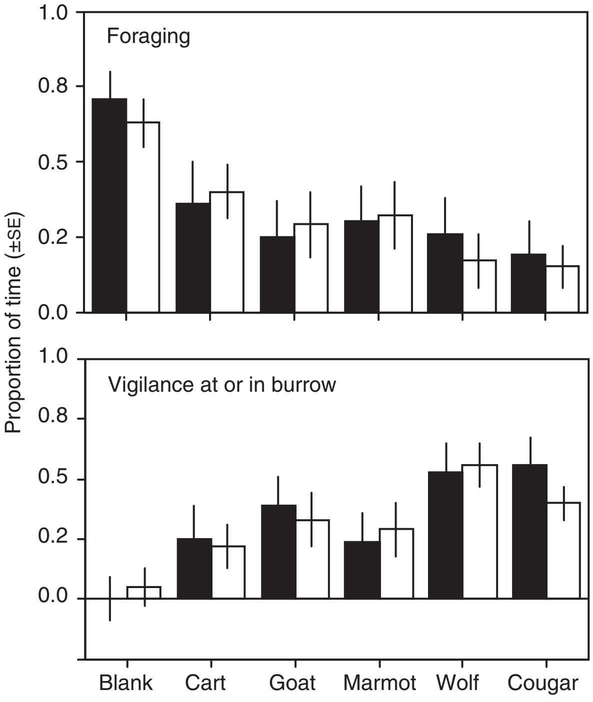

Figure 3 Average (± SE) proportion of time captive-born (black, $n=9$) and wild-caught (white, $n=12$) Vancouver Island marmots *Marmota vancouverensis* allocated to foraging and vigilance at or in the burrow in response to experimental stimuli.

$P = 0.258$, partial $\eta^2 = 0.067$) nor was there a significant origin by stimulus interaction (forage $P = 0.361$, partial $\eta^2 = 0.055$; vigilance at or in the burrow $P = 0.247$, partial $\eta^2 = 0.067$).

Splitting the data set by origin (i.e. captive born or wild captured) revealed that captive-born subjects foraged significantly less in response to the cougar ($P = 0.032$) compared with the blank, whereas wild subjects foraged significantly less in response to the cougar ($P = 0.003$) and the wolf ($P = 0.005$) compared with the blank. Wild-captured subjects tended to spend more time either vigilant at the burrow or within the burrow in response to the wolf ($P = 0.052$) compared with the blank. There were no other significant pairwise comparisons for this variable (all P-values > 0.111).

Comparing the response between captive born and wild captured for each stimulus separately (that is, six separate analyses, one each for blank, cart, cougar, goat, marmot and wolf) revealed no significant differences for either forage (all P-values > 0.514, all partial $\eta^2 < 0.023$) or time spent within the burrow or vigilant at the burrow (all P-values > 0.400, all partial $\eta^2 < 0.038$).

Personality

Two factors explained 72.4% of the variance in the MIS and 72.1% of the variance in the MIS-wolf experiment (Table 3). Lack of vigilance and high rates of interaction of the marmot and the mirror and foraging characterized factor 1 in the MIS experiment, whereas high rates of locomotion and interaction and low rates of burrow use characterized factor 1 in the MIS-wolf experiment. Factor 1 in the MIS experiment was positively correlated with factor 1 in the MIS-wolf experiment ($r = 0.530$, $n = 14$, $P = 0.051$), whereas none of the other correlations between factors were significant (F1, F2-wolf: $r = -0.216$, $P = 0.458$; F1-wolf, F2: $r = 0.348$, $P = 0.222$; F2, F2-wolf: $r = 0.054$, $P = 0.853$). Overall, because interaction loaded highly on both measures of factor 1, we interpreted factor 1 as a 'reactivity' factor (e.g. Sih *et al*., 2004*a*). Thus, marmots can be described as having a contextually independent interactive personality trait. Factor 2 was more difficult to interpret because it varied across situations. In the MIS experiment it could be interpreted as a 'fearful' factor because animals engaged in locomotion, tail flagged and used their burrow a lot. However, when the wolf was present, it appeared to be more of a 'foraging and not vigilant' factor.

Because factor 1 was correlated across predator and no-predator contexts, we focused only on the sample size of 20 subjects for which we had data from stimulus presentations and factor analyses. We then correlated factor 1 with the proportion of time marmots allocated during each stimulus presentation to foraging, being vigilant at the burrow or in the burrow, and being vigilant away from the burrow. The only significant relationships (Table 4) were

Table 3 Rotated component scores from the mirror-image stimulation experiment without and with the wolf present

	MIS		MIS-wolf	
Behaviour	Factor 1	Factor 2	Factor 1	Factor 2
Total vigilance	−0.916	0.027	0.291	−0.877
Interact with mirror	0.873	0.045	0.794	0.265
Total foraging	0.772	−0.443	0.293	0.872
Total locomotion	−0.171	0.831	0.837	0.057
Tail flags/min	0.438	0.781	0.702	−0.364
Total time in burrow	−0.398	0.520	−0.765	0.094

In the MIS, factor 1 explained 44.7% of the variation and factor 2 explained an additional 27.7% of the variation. In the MIS-wolf, factor 1 explained 43.1% of the variation and factor 2 explained 29.0% of the variation.

MIS, mirror-image stimulation.

Table 4 Pearson correlations between factor 1 and measures of time allocation during stimulus presentation ($n=20$ subjects who had both MIS and all stimulus presentations)

	Foraging		Rear vigilant		Vigilance at or in burrow	
Stimulus	*r*	*P*	*r*	*P*	*r*	*P*
Blank	0.275	0.241	−0.220	0.351	0.044	0.854
Cart	−0.063	0.792	0.073	0.759	0.635	0.003
Goat	−0.0.66	0.784	0.002	0.992	0.321	0.168
Marmot	−0.153	0.520	−0.167	0.482	0.668	0.001
Wolf	0.171	0.471	−0.127	0.592	0.186	0.432
Cougar	0.063	0.791	−0.218	0.356	0.471	0.036

MIS, mirror-image stimulation.

found with our highest measure of fearful response (vigilance at or in the burrow). Thus, very interactive marmots were highly responsive to the cart, marmot and cougar but, surprisingly, not to the wolf. We interpret this as suggesting that factor 1 provided some ability to predict how marmots might respond to cougars.

Subjects occasionally alarm called during these trials. However, alarm calling occurred so infrequently that we were unable to analyse formally the data (only two individuals called during the trials, both cases occurring when the wolf was also present).

Discussion

Animals raised in captivity need not inevitably fail to develop their antipredator behavioural abilities. Although our wild-captured animals were older than our captive-born subjects when tested, we detected no effect of captivity on the development of antipredator behaviour. Our results suggest that Vancouver Island marmots are able to distinguish predators from non-predators, and that captive-born animals respond as well as wild-captured animals under the captive conditions in which they have been housed. The effect size of being captive born on the response to various stimuli was uniformly small. This is important because it suggests that animals reared at these three facilities are likely to have adequate abilities to respond to predators upon release.

Importantly, the three facilities where we studied marmots all provided access to natural predators or other potentially alarming stimuli that walked or flew near the cages. Specifically at the Calgary Zoo, there were free-living coyotes *Canis latrans*, American badgers *Taxidea taxis*, striped skunks *Mephitis mephitis*, cats *Felis catus*, Swainson's hawks *Buteo swainsoni*, red-tailed hawks *Buteo jamaicensis* and Northern harriers *Circus cyaneus*. At Mountain View, marmots could have been exposed to cats and coyotes. At Mount Washington, marmots could conceivably have been exposed to wolves, cougars and golden eagles. In addition, free-living ungulates walked by the marmot enclosures and were observed alarming marmots at all sites.

We were unable to demonstrate, with any certainty, whether marmots are able to 'recognize' predators rather than simply discriminate among the various stimuli presented. Importantly, the magnitude of the foraging and vigilance at or in the burrow responses were associated with the relative size of the stimulus presented. Thus, it is possible that marmots simply responded to relative stimulus size as a cue of risk. In nature, this mechanism would likely be sufficient to allow marmots to respond to predators.

The mirror-image experiment strongly suggests that marmots vary in their reactivity in consistent ways. Support for this comes from the correlation of the factor scores between MIS and MIS-wolf, and from the moderately strong relationships between factor 1 and the vigilance at or in the burrow during the stimulus presentations. Interestingly, the relationship between factor 1 and the response to the stimuli varied; factor 1 was a strong predictor of the response to the marmot, cart and cougar, but less so for the goat and (surprisingly) the wolf. At this point, we cannot explain this discrepancy with the relationship to different predators, but it might hinge on the ways in which marmots naturally respond to different predators. Many species have predator-specific escape strategies (Cheney & Seyfarth, 1990; Macedonia & Evans, 1993), and cooperatively hunting wolves might elicit different responses than solitary hunting cougars.

Although our results suggest that marmots should be able to discriminate and respond to predators upon release, released marmots are nevertheless being killed by predators (Bryant & Page, 2005). Thus, our results suggest that future research should focus on the fate of introduced animals and search for a relationship between variation in recognition abilities, reactivity and subsequent survival. We know that variation in antipredator abilities can affect later survival (Ellis, Dobrott & Goodwin, 1977; Miller *et al.*, 1994; Van Heezik *et al.*, 1999; Mirza & Chivers, 2000). Bremner-Harrison, Prodohl & Elwood (2004) have found some support for the hypothesis that variation in the survival of reintroduced swift foxes *Vulpes velox* was explained by variation in their level of 'boldness'. At this point, only four of our subjects have been released, all were captiveborn, and two were killed by cougars. The male that scored highest of our 20 test subjects (reactivity factor score = 2.21) was killed by a predator, as was one that scored −0.51. Reactivity scores for the non-predator fatalities were 0.87 (died in accident) and 0.26 (died over winter) (unpublished minutes, Vancouver Island Marmot Recovery Team, 9 November

2004; A. Bryant, pers. comm.). If individual variation in responsiveness or discrimination ability influences survival, then pre-release training (McLean, Lundie-Jenkins & Jarman, 1995; McLean *et al*., 2000; Mirza & Chivers, 2000; Griffin, Evans & Blumstein, 2001) could be instituted. If variation in reactivity influenced later survival, subjects that were predicted to die could be withheld from introduction. If there is no effect of predator discrimination abilities or variation in reactivity on later survival, we seem to be able to do little with natural variation in recognition abilities to increase survival upon release and other methods will have to be used to decrease predator-related mortality.

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