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Predator and heterospecific stimuli alter behaviour in cattle

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ABSTRACT

Wild and domestic ungulates modify their behaviour in the presence of olfactory and visual cues of predators but investigations have not exposed a domestic species to a series of cues representing various predators and other ungulate herbivores. We used wolf (*Canis lupus*), mountain lion (*Puma concolor*), and mule deer (*Odocoileus hemionus*) stimuli (olfactory and visual), and a control (no stimuli) to experimentally test for differences in behaviour of cattle (*Bos taurus*) raised in Arizona. We measured (1) vigilance, (2) foraging rates, (3) giving up density (GUD) of high quality foods and (4) time spent in high quality forage locations in response to location of stimuli treatments. In general, we found a consistent pattern in that wolf and deer treatments caused disparate results in all 4 response variables. Wolf stimuli significantly increased cattle vigilance and decreased cattle foraging rates; conversely, deer stimuli significantly increased cattle foraging rate and increased cattle use of high quality forage areas containing stimuli. Mountain lion stimuli did not significantly impact any of the 4 response variables. Our findings suggest that domestic herbivores react to predatory stimuli, can differentiate between stimuli representing two predatory species, and suggest that cattle may reduce antipredatory behaviour when near heterospecifics.

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1. Introduction

Prey species have developed behaviours that aid the recognition, avoidance and active defense against predators (Brown, 1999; Laundré et al., 2001; Apfelbach et al., 2005). These behaviours, presumed intrinsically linked to “fearfulness” (typically measured as vigilance), have been shown to vary based on several predatory traits including predator size, speed, and numbers (Geist et al., 2005; Stancowich and Blumstein, 2005). Predators that induce higher levels of vigilance are likely to engender greater and longer standing modifications in antipredatory behaviour on both an individual and evolutionary scale. This may be especially prevalent in social animals as they are able to learn and modify their behaviour from their own experiences and those of conspecifics (Griffin, 2004). Further, antipredatory behaviour may be stronger when predator–prey species share a common natural history. For example, Parsons et al. (2007) recently demonstrated that a native predator stimulus [dingo (*Canis dingo*) urine] caused a much stronger fear response in grey kangaroos (*Macropus giganteus*) than a non-native predator stimulus [coyote (*Canis latrans*) urine]. They argued that an herbivore’s response to a predator can be marginal where predat-

tors and prey are “mismatched”, i.e., do not share a common natural history, referred to as a “leitmotif” (Apfelbach et al., 2005).

Prey species optimize conflicting demands between food and safety from predation in three basic ways that may increasingly reduce foraging efficiency. They may: (1) increase vigilance while continuing to feed in a high quality but potentially “risky” location (Berger and Person, 2001; Swanson et al., 2002), (2) temporarily move to another less threatening, but possibly lower quality, foraging location after a predation threat is detected (Arnould and Signoret, 1993; Kats and Dill, 1998), or (3) exhibit escape maneuvers to avoid being killed (Lima and Dill, 1990; Brown, 1999). In all of these cases, animals would ostensibly reduce feeding time and/or increase travel time to detect, or move away from, potential predation threats (see Quenette, 1990; Brown, 1999; Kie, 1999; Treves, 2000). However, recent studies suggest that prey animals may be able to reduce disruption of foraging activities by “multi-tasking” (i.e., chewing while remaining vigilant) (Fortin et al., 2004a,b).

“Giving up density” (GUD) is one metric researchers have used in controlled and semi-controlled field studies to gauge how animals optimize foraging behaviour and habitat use in response to predation risk (Brown, 1988; Altendorf et al., 2001; Olsson et al., 2002). Giving up density is the mass or amount of food abandoned by prey in a measurable food patch in response to a perceived threat by a predator (Brown, 1999). Prey species foraging in the presence of predators should exhibit higher GUDs than when foraging in areas where predators are absent. Research with small

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mammals and birds supports this contention (Brown et al., 1992; Bowers et al., 1993; Brown and Morgan, 1995; Olsson et al., 2002). Research involving wild ungulates and GUDs is limited, but a recent study showed that mule deer had higher GUDs near forest edges where they were more susceptible to predation by mountain lions (Altendorf et al., 2001).

Several studies have examined the effects of predatory stimuli on domestic animals (Terlouw et al., 1998; Hansen et al., 2001; Welp et al., 2004), but to our knowledge no studies have exposed animals to a combination of olfactory and visual cues representing various wild predators and herbivores, or measured GUD in response to such stimuli. Using domestic ungulates to investigate fear in prey offer several advantages in controlled studies that require confining animals in an experimental pasture during trials. Domestic animals are regularly handled by humans and routinely placed in pastures or enclosures (e.g., scheduled grazing, transporting, processing, health checkups). Thus, domestic animals are more habituated to captive situations than wild ungulates and offer a good model for investigating prey responses to predators in a controlled experimental setting. Although some research indicates animal husbandry lowers behavioural sensitivity to predators (Price, 1999), a great deal of work has shown that livestock respond to predator stimuli in ways similar to wild ungulates (Terlouw et al., 1998; Hansen et al., 2001; Welp et al., 2004). Furthermore, animal predators have increasingly preyed on free-ranging domestic cattle, accounting for 147,000 and 190,000 deaths in the United States in 2000 and 2005, respectively (US Department of Agriculture, 2001; National Agricultural Statistics Service, 2006). Research investigating the indirect impact of predators on livestock (i.e., influence on behaviour, movement, forage intake) is important for the fields of carnivore conservation, animal husbandry, human–wildlife conflict and animal behaviour.

Visual and olfactory stimuli that mimic the presence of predators can elicit similar behaviours by prey animals compared to the presence of an actual predator (Kats and Dill, 1998; Berger and Person, 2001; Apfelbach et al., 2005). The objective of our study was to compare the effects of predator and ungulate stimuli on the behaviour of range cattle. We examined how the presence of wolf, mountain lion, and deer stimuli (visual and olfactory) affected: (1) vigilance, (2) foraging rates, (3) intake and GUDs of high quality forage, and (4) use of high quality forage locations by cattle. We predicted that wolf stimuli would have the largest impact on cattle behaviour, mountain lion stimuli would have an intermediate impact, and deer stimuli would not differ from the control.

2. Materials and methods

2.1. Experimental pasture

All training and experimentation was conducted in a 0.25 ha dry-lot experimental pasture, located at the University of Arizona's West Campus Agriculture Center in Tucson, Arizona (IACUC certification # 7399). The experimental pasture was situated out-of-sight from the holding pens to prevent cattle from observing the pasture during experimental trials. We established a grid system within the experimental pasture by attaching labeled plywood squares to the fence at 10-m intervals. The grid system allowed us to divide the pasture into 4 readily identifiable quadrants and to record animal locations and activities during the experiment. The experimental pasture was large enough to allow cattle to exhibit exploratory behaviour but small enough for observers to record pertinent behavioural data.

2.2. Animals

Eighteen cattle were transported to the West Campus Agriculture Center in May 2006. All cattle were adult females (>3 years)

that reproduced at least once in their lifetime. Of these, 8 animals ($\bar{x} \pm \text{SE}$) (420 ± 24 kg) of Angus–Hereford breeding were from the Four Drag Ranch (FDR). Cows from the FDR (32°N , 109°W) were not lactating and came from an area in eastern Arizona where wolves had been established and interacting with the herd since 2000. The remaining 10 animals (5 Red Angus Cross, 5 Hereford Cross) (451 ± 15 kg) were from the V Bar V Ranch (VBV) (34°N , 111°W) located in central Arizona. VBV cows had calves (<4 months), were lactating and came from an area in Arizona where wolves were not established. Mountain lions and mule deer occurred at both ranch locations. Coyotes were also present at both ranches and were not known to kill any calves on the VBV (D. Schaefer, VBV manager, personal communication), but were known to kill an occasional calve on FDR (unpublished data). Herding dogs were occasionally utilized on both ranches to transport cattle from one pasture to another (D. Schaefer, VBV manager, personal communication; D. Ely, FDR permittee, personal communication).

2.3. Adaptation period

Cattle from the FDR and VBV ranches were housed in separate holding pens ($20\text{ m} \times 30\text{ m}$) located about 100 m from the experimental pasture. All cattle underwent a 12-day adaptation period when they were allowed to feed in the experimental pasture ($50\text{ m} \times 50\text{ m}$) for 10 min each day (Fig. 1). The purpose of the adaptation period was to simulate future 10-min experimental trials and to expose all animals to similar conditions that they would encounter during experimental trials (described later). Calves of VBV cows remained in their holding pen while their mothers were in the experimental pasture during all adaptation and experimental trials. We placed feed in all 4 quadrants of the experimental pasture. Three of the 4 quadrants contained a low quality food source (150–200 g wheat straw per quadrant) while the remaining quadrant contained a high quality food source (1000–1100 g steam flake corn and 250–300 g alfalfa). Foods were placed in rubber feed bowls (25.4 cm diameter, 10.2 cm depth) and placed in the center of each respective quadrant. The order in which each of the 4 quadrants contained the high quality food source was randomly selected during 3 consecutive 4-day intervals (Table 1). Once a quadrant contained the high quality food source during a 4-day interval it was not re-selected until the next 4-day interval. During the adaptation period, animals were

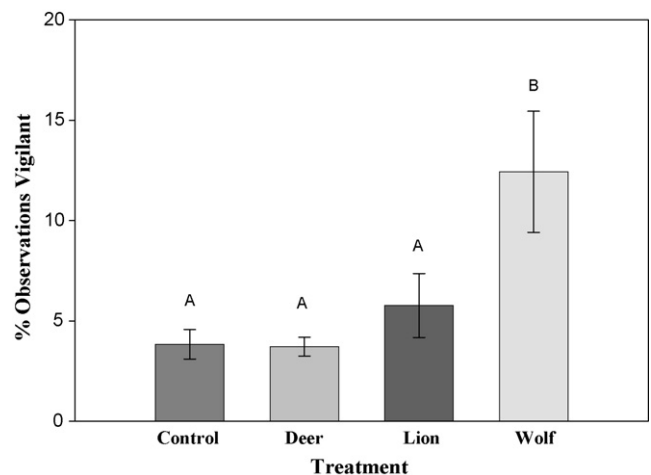


Fig. 1. Percentage of observations in which cattle exhibited vigilance (mean \pm SE) when exposed to visual and olfactory stimuli representing predatory and non-predatory animals. Treatments included a control (no stimuli), deer, mountain lion, and wolf stimuli (visual and olfactory). Means with different letters were different ($p < 0.10$) according to Tukey's HSD.

Table 1

Experiment schedule. During the 2-week adaptation period, animals were exposed to the experimental pasture in pairs during week 1 and as individuals during week 2. Animals were exposed as individuals during all 4 treatment weeks. Order of treatments was randomly balanced so that no treatment was repeated during any weekly session. Predator and deer treatments were randomly balanced so that each one (wolf, mountain lion, and deer) occurred in association with each high quality food location and so that each one appeared an equal number of times ($n=4$) during the experimental trials. High quality food locations were also balanced so that each quadrant was represented an equal number of times ($n=6$) throughout the experiment. H in Q1–4 = high quality food in quadrants 1, 2, 3, or 4.

Adaptation Week 1 Days 1–6	Adaptation Week 2 Days 7–12	Treatment Week 1 Days 13–18	Treatment Week 2 Days 19–24	Treatment Week 3 Days 25–30	Treatment Week 4 Days 31–36
H in Q1	H in Q1	Wolf H in Q4 Control	Deer H in Q1 Control	Lion H in Q2 Control	Deer H in Q3 Control
H in Q2	H in Q4	H in Q3 Lion	H in Q4 Lion	H in Q1 Wolf	H in Q2 Wolf
H in Q3	H in Q3	H in Q3 Control	H in Q4 Control	H in Q1 Control	H in Q2 Control
H in Q4	H in Q1	HQ in Q2 Deer	H in Q3 Wolf	H in Q4 Deer	H in Q1 Lion
H in Q3	H in Q2	H in Q2 Control	H in Q3 Control	H in Q4 Control	H in Q1 Control
H in Q2	H in Q4	H in Q1	H in Q2	H in Q3	H in Q4

exposed in pairs during days 1–6 and as individuals during days 7–12 (Table 1).

Cattle were familiar with alfalfa as a food source prior to the adaptation period but had no previous experience with steam flake corn or wheat straw. After the 12-day adaptation period, all cattle had sampled all food sources. To prevent animals from becoming satiated during adaptation and experimental trials, cattle were fed 25% of their average daily alfalfa hay ration (3.4 kg) in the morning (0500–0600) before trials, and then were fed alfalfa hay *ad libitum* (10.2 kg) in the evening (1800–1830) after trials were complete.

2.4. Experimental trials

We simulated the presence of 2 predatory animals and 1 non-predatory animal using visual and olfactory stimuli simultaneously. Visual stimuli included three-dimensional target mounts of a wolf (HD Wolf, Delta Sports, LLC, Reinbeck, IA), mountain lion (3D Puma, Longhorn Targets, Orange, CA), and deer (HD 10 Deer, Delta Sports, LLC). Olfactory stimuli included fecal and urine samples and were obtained from Wildlife Science Center, Forest Lake, MN (wolf scat); Arizona-Sonora Desert Museum, Tucson, AZ (deer and mountain lion scat); Leg Up Enterprises Inc., Lovell, ME (mountain lion and wolf urine) and Mrs. Doe Pee/American Outdoors, Mt. Pleasant, IA (deer urine). All scats were frozen within 24 h of bowel movements and were stored frozen until used in trials. Approximately 300 g of scat and 250 ml of urine was used per trial day.

The purposes for using a non-threatening treatment (i.e., deer) were 2-fold: (1) to test for the possibility that cattle were reacting to the novelty of carnivore treatments rather than the perception of an actual predatory threat, and (2) to evaluate the reaction of cattle to stimuli representing a sympatric wild ungulate compared to the other treatments.

Animals were exposed as individuals during all 4 treatment weeks (Table 1). As during the adaptation period, a low quality food source was placed in 3 quadrants of the experimental pasture while a high quality food source was placed in the remaining quadrant. Type, mass, and orientation of low and high quality food sources were the same as the adaptation period. The location of the high quality food source was randomly selected among the 4 quadrants of the experimental pasture (Table 1). Order of treatments was also randomly selected with removal so that no treatment was repeated during a weekly session. Predator and deer treatments were ran-

domly balanced so that each one (wolf, mountain lion, and deer) occurred in association with each high quality food location, and so that each one appeared an equal number of times during the experimental trials (Table 1). Animal stimuli were systematically placed 2 m upwind from the high quality food source. Olfactory stimuli were placed directly beneath the visual stimuli. High quality food locations also were randomly balanced so that each location appeared an equal number of times during the experimental trials (Table 1). Control days, when no stimuli were introduced, were implemented between each treatment to reduce carry-over effect from treatments. For each control day, the location of the high quality food was the same as during the subsequent treatment to promote animals becoming accustomed to the high quality food source being located in the same area as it was for the next treatment (Table 1). Each cow was exposed to a treatment once per day during experimental trials lasting 10 consecutive minutes. Temperature was the only environmental variable (i.e., wind direction, temperature, cloud cover) that consistently varied throughout daily trials. Each individual was exposed to the experimental pasture 24 times during the experiment (428 total trials) and each animal was exposed to the range of temperatures that occurred over the course of the experiment. As during the adaptation period, calves of VBV cattle remained in their holding pens while their mothers were exposed to the experimental pasture during 10-min trials.

We defined sampling units as focal animal trials lasting 10 min where animal location and behaviour was recorded every 15 s for a total of 40 observations per trial. We divided cattle behaviour into 5 categories that were immediately discernable at 15 s intervals: foraging, scanning, traveling, standing/not scanning, and resting. We defined foraging as standing or walking slowly with the head below shoulder level. Scanning was standing with the head at or above shoulder level. Traveling was walking, trotting, or running with the head at or above the shoulder level. Standing/not scanning was licking or scratching. Resting was any behaviour that took place while an animal was lying. We recorded animal location by noting which quadrant the animal was in during each 15-s observation. We calculated GUD as the percentage mass of high quality food remaining after each 10-min trial.

We used scanning behaviour to estimate vigilance. We defined vigilance as when an animal stood with its head raised while looking around, and was not lying, feeding, moving to another feeding spot, or engaged in a maintenance behaviour (e.g., grooming) (Hunter and Skinner, 1998; Laundré et al., 2001; Kluever et al., 2008). Although animals may be engaged in activities other than vigilance while scanning (e.g., chewing, ruminating, monitoring young and other herd mates), scanning behaviour as defined in our study has been the most common behaviour used to measure vigilance in ungulates (Hamel and Coté, 2008; Jayakody et al., 2008; Li and Jiang, 2008; Lung and Childress, 2006).

We collapsed our data to individual animals and treatments where each animal had 1 mean response for each of the 4 treatments. Response variables were vigilance, foraging rates, GUD of high quality food, and time spent in high quality quadrant. Analysis of variance (SAS Institute Inc., Cary, NC, USA) was used to evaluate a 4×2 factorial design. Factors were the 4 stimuli treatments (control, wolf, deer, mountain lion), and the 2 physiological conditions (lactating vs. non-lactating cattle). Interactions between stimuli treatments and physiological condition were also analyzed in the model. We performed least square mean comparisons (i.e., Tukey's Honestly Significant Differences—Tukey's HSD) to examine differences between individual treatments when the p -value of the main effects were ≤ 0.10 . When making least square means comparisons we also choose an $\alpha \leq 0.10$ to designate differences among means. We chose $p < 0.10$ to test differences among main effects and to test differences among means because were more comfortable with committing an error of false discovery than an error of a false

negative. We refer to figures when effect size demonstrates potential biological differences among treatments as recommended by Ramsey and Scafer (2002). We transformed proportional response data to a logit scale to meet the assumptions of parametric statistical tests.

3. Results

3.1. Physiological condition

Physiological condition influenced GUDs ($\bar{x} \pm SE$) between cattle ($F_{1,70} = 37.4, p < 0.0001$). VBV cattle (lactating) consumed $93\% \pm 0.01$ of high quality forage while FDR cattle (non-lactating) consumed only $76\% \pm 0.03$ of high quality forage. However, there was no interaction between physiological condition and stimuli treatments ($F_{3,68} = 0.272, p = 0.98$). As expected, lactating cattle consistently consumed a higher percentage of the high quality food across all stimuli treatments compared to non-lactating cattle. However, because lactating (VBV) and non-lactating (FDR) cattle did not differ in vigilance ($F_{3,68} = 1.82, p = 0.153$), foraging ($F_{3,68} = 0.867, p = 0.463$), or time spent in the high quality quadrant ($F_{3,68} = 0.544, p = 0.65$), our data support that lactation, not familiarity with wolves (i.e., ranch origin), was the causal factor influencing higher overall foraging rates by VBV animals. Therefore, we pooled data from each of the 4 response variables across ranches for the remainder of the analyses.

3.2. Experimental treatments

We found significant treatment effects for 3 of the 4 response variables (vigilance, foraging rates, and high quality space use) toward predatory and/or heterospecific ungulate stimuli (Figs. 1–4). We found a significant difference in cattle vigilance ($\bar{x} \pm SE$) among treatments ($F_{3,68} = 3.9, p = 0.0125$; Fig. 1) with the greatest response resulting from wolf stimuli ($12\% \pm 0.03$; Linear Contrast, $F_{1,64} = 11.42, p = 0.001$). Cattle vigilance for the mountain lion treatment did not differ from controls or deer stimuli (Linear Contrast, $F_{1,64} = 1.03, p = 0.31$; Fig. 1).

We found a significant difference in cattle foraging rates ($\bar{x} \pm SE$) among treatments ($F_{3,68} = 3.59, p = 0.018$; Fig. 2). Cattle foraged least in the presence of wolf stimuli ($76\% \pm 0.01$; Linear Contrast, $F_{1,64} = 3.31, p = 0.07$) and the most in the presence of deer stimuli

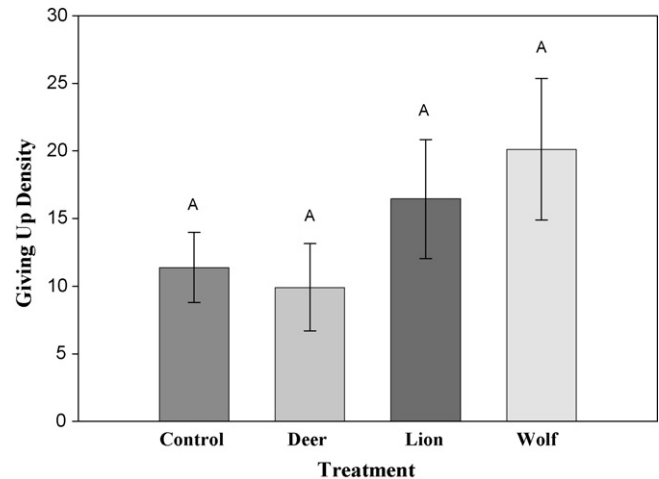


Fig. 3. Percentage mass of high quality food remaining after each 10-min trial (i.e., GUD mean \pm SE) when exposed to visual and olfactory stimuli representing predatory and non-predatory animals. Treatments include a control (no stimuli), deer, mountain lion, and wolf stimuli (visual and olfactory). Means with different letters were different ($p < 0.10$) according to Tukey's HSD.

($85\% \pm 0.01$; Linear Contrast, $F_{1,64} = 6.89, p = 0.01$). There was no difference between lion and control treatments (i.e., $80\% \pm 0.02$ and $79\% \pm 0.03$, respectively; Linear Contrast, $F_{1,64} = 2.17, p = 0.15$).

Cattle visited the high quality food source in 100% of the trials but ignored the low quality food sources in 73% of the trials. Therefore, we used only high quality forage intake data in the GUD analyses. There was no statistical difference among the 4 treatments for GUD ($F_{3,68} = 1.91, p = 0.136$; Fig. 3). However, GUD effect sizes followed a similar trend as was found for vigilance rates (i.e., highest for wolf stimuli and lowest for deer stimuli). We performed a post hoc analysis including GUD data only from the wolf and deer stimuli and found a significant difference ($F_{1,34} = 5.61, p = 0.024$) between these two treatments.

We found a significant difference among treatments in the amount of time cattle spent in the high quality quadrant ($F_{3,68} = 4.58, p = 0.006$; Fig. 4). Cattle spent the most time ($\bar{x} \pm SE$) in the high quality quadrant ($90\% \pm 0.02$) during the deer treatment (Linear Contrast, $F_{1,64} = 4.32, p = 0.041$), and the least amount of time in the high quality quadrant ($81\% \pm 0.06$) during the wolf treatment.

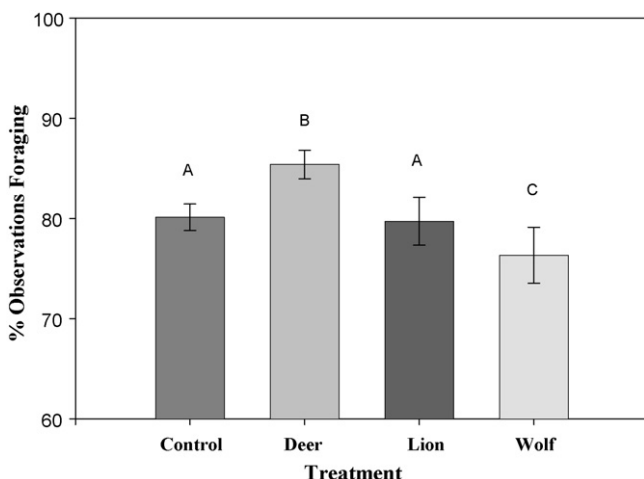


Fig. 2. Percentage of observations in which cattle foraged (mean \pm SE) when exposed to visual and olfactory stimuli representing predatory and non-predatory animals. Treatments included a control (no stimuli), deer, mountain lion, and wolf stimuli (visual and olfactory). Means with different letters were different ($p < 0.10$) according to Tukey's HSD.

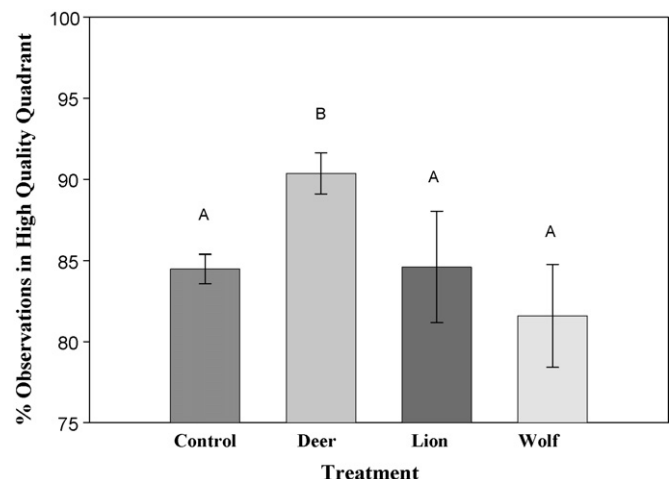


Fig. 4. Percentage of observations cattle spent in the quadrant containing a high quality food source when exposed to visual and olfactory stimuli representing predatory and non-predatory animals. Treatments included a control (no stimuli), deer, mountain lion, and wolf stimuli (visual and olfactory). Means with different letters were different ($p < 0.10$) according to Tukey's HSD.

Cattle arithmetically spent the least time in the high quality quadrant when wolf stimuli were present but there was no statistical difference between wolf and lion treatments or the control (Linear Contrast, $F_{1,64} = 1.23$, $p = 0.27$).

4. Discussion

4.1. Deer stimuli

Contrary to our predictions, when deer stimuli were placed in the high quality forage quadrant, cattle showed less vigilance, spent more time foraging, had the lowest GUD effect size, and spent more time in the high quality quadrant compared to the wolf stimuli treatment (Figs. 1–4). Although several African ungulate species have exhibited decreased vigilance as the number of heterospecifics increased under field conditions (Scheel, 1992), our study may be the first to corroborate this general phenomenon under controlled conditions. Herbivores that graze in mixed-species groups apparently confer the advantages of “many eyes” or “safety in numbers” as a means to minimize predation risk (Hamilton, 1971; Pulliam and Caraco, 1984). Cattle may have perceived deer stimuli as a non-threatening, familiar stimulus, which would explain their “comfort response” when another ungulate (albeit a replica) was in the high quality quadrant of the experimental pasture. A comfort response could be an innate response to another ungulate or it could be that cattle in our study had learned to become familiar with deer on their respective ranches prior to our experiments. Cattle and mule deer are known to forage in similar areas (Willms et al., 1979; Torstenson et al., 2006) and were common on both ranches.

4.2. Predator stimuli

Our results partially corroborate other studies that have shown foraging and vigilance rates in wild and domestic ungulates can be influenced by the presence of predator stimuli (Poindron, 1974; Pfister et al., 1990; Lima and Dill, 1990; Arnould and Signoret, 1993; Hunter and Skinner, 1998; Laundré et al., 2001). An important finding from our study was the overall lack of response of cattle to mountain lion stimuli (i.e., lion never differed from control treatments; Figs. 1–4) and a relatively stronger response of cattle to wolf stimuli (i.e., 2 response variable showed significant differences, Figs. 1 and 2, and the other response variables showed similar trends though did not differ statistically, Figs. 3 and 4).

The reasons for the more profound response to wolf vs. mountain lion stimuli are unknown but could be attributed to at least 2 factors. First, the auroch (*Bos primigenius*), cattle's wild ancestor, evolved with wolves in Eurasia (Van Vuure, 2005), but remains of mountain lions have not been found outside of North and South America (Nowak, 1999). Thus, ancient cattle evolved with and were preyed upon by wolves over the millennia (Van Vuure, 2005) and natural selection may have engendered an innate behavioural response by cattle to wolves. Our results, like Parsons et al.'s (2007) study with grey kangaroos, provide evidence that the scent of predators that share a common natural history with a prey species elicit stronger behavioural responses than scents from non-sympatric predators (i.e., the “leitmotif” effect).

Alternatively cattle reaction to wolf stimuli may have been due to a generalized learned response to all canids including wolves, domestic ranch dogs, and coyotes. This explanation is predicated on the idea that canids (stalking predators) incite more fear and therefore more indelible learning experiences in prey compared to mountain lions that are ambush predators (Nowak, 1999). More dramatic (i.e., fearful) events can cause more profound learning in animals (Griffin, 2004; Forkman et al., 2007) and work from Yellowstone National Park on elk supports the notion that wolves cause

a greater fear response than other predators including mountain lions (Laundré et al., 2001).

In our study cattle from FDR had significant interaction with a suite of predators including wolves, mountain lions, and coyotes (Breck et al., 2007; Darcy Ely, personal communication; John Oakleaf, personal communication). Thus, it is tempting to draw the conclusion that wolves caused a more profound learned response that carried over into our experiment. However, VBV cattle had no history of interacting or being preyed upon by wolves and yet also showed a strong response to the wolf treatment. We speculate that reaction of VBV cattle in our experiment resulted from a generalized reaction to a wild candid rather than a specific reaction to wolves. Calves from both ranches occasionally were preyed upon by coyotes and more commonly interacted with ranch dogs that were used to rotate cattle between pastures. Thus, familiarity with coyotes and dogs may have been why VBV and FDR cattle responded similarly to wolf stimuli in our experiment. However, anecdotal observations made on both ranches indicate that cattle are likely able to discriminate between wild and domestic canids. For example, we observed cattle lying (i.e., ruminating and resting) near ranch dogs while located in holding pastures on the FDR, and VBV cattle did not exhibit antipredatory behaviour toward herding dogs (Kluever, 2007, unpublished data). An important direction for further research will be to examine the effects of different canid stimuli (i.e., wolf, coyote, dog) on cattle/domestic ungulate behaviour.

4.3. Optimizing foraging vs. vigilance behaviour

Productivity of wild and domestic ungulates is largely a function of forage intake ($I = \text{g/min}$ or kg/day), which has been characterized as the product of bite rate ($BR = \text{bites/min}$), bite size ($BS = \text{g/bite}$), and foraging time ($FT = \text{time foraging/day}$), i.e., $BR \times BS \times FT = I$ (Stuth, 1991). Ungulates may increase, decrease, or maintain intake by adjusting any of these 3 variables in response to changing foraging conditions and predation threats (Howery and Deliberto, 2004). Animals that consume more food in relation to energy expended traveling and searching for food are said to forage more efficiently, and typically gain more weight and produce more young than animals with lower intake levels and higher energy outputs (Osugi, 1974; Sevi et al., 1999).

Foraging efficiency for ungulates in the wild has been demonstrated to be higher in the absence of predators apparently because prey species occupy high quality habitats without fear of predation and exhibit more selectivity among plants and plant parts (Laundré et al., 2001). Conversely, when herbivores sense or encounter predators, foraging efficiency may decrease due to increased vigilance and corresponding lower intake, being forced into lower quality habitats where nutrients are less available or digestible, or due to increased energy expenditures caused by escape maneuvers (Brown, 1999; Lima and Dill, 1990). Wildlife researchers have demonstrated that small mammals may abandon or reduce use in high quality habitats when predation risk outweighs the forage benefit of remaining in the patch (Brown, 1988; Brown et al., 1992).

Cattle in our study showed marginal evidence of this trend when mean GUD effects were higher for wolf and lion stimuli compared to the deer treatment and the control (Fig. 3). Similarly, the mean effect for amount of time spent in the high quality quadrant was lowest when wolf stimuli were present in that quadrant (Fig. 4). Conversely, a recent study indicated that female bison (*Bison bison*) and elk (*Cervus elaphus*) compensated for increased vigilance by taking larger bites and continuing to chew while scanning their environment (Fortin et al., 2004b). Fortin et al. (2004b) acknowledged that while increased vigilance rates impart substantial foraging costs (e.g., decreased bite rates and reduced forage selectivity), these costs were not as high as reported in previous studies due to the ability of wild herbivores to “multi-task”. Obvi-

ously, the degree to which animals are able to “multi-task” via simultaneous chewing and vigilance will depend upon the gravity of an impending predator threat.

5. Conclusion

The objective of this study was to determine if cattle react differently to stimuli representing different predator and prey species in a highly controlled study. Overall, cattle reacted most negatively to wolf stimuli because they were most vigilant and foraged least when wolf stimuli were present compared to all other treatments. Cattle did not react negatively or positively to mountain lion stimuli (i.e., there was no difference from controls for all 4 dependent variables studied). Cattle reacted most positively to deer stimuli because they foraged most and spent the most time in high quality when deer stimuli were present compared to all other treatments.

These results shed new light on the relationship between cattle, predators, and heterospecifics. This information will help researchers and managers to better understand the role of a shared natural history between predator and prey species and to plan future studies in behavioural and management oriented fields (e.g., the efficacy of wolf stimuli as a cattle repellent, integrating wild and domestic ungulate herds to increase foraging efficiency).

Our controlled study was limited in scope because it was conducted in an experimental arena, with experimental rations, and with artificial predator and heterospecific stimuli. Future studies that investigate vigilance behaviour in natural foraging environments must address how seasonal changes in forage quantity and quality (e.g., plant nutrients, toxins), as well as how site specific conditions (e.g., topography, hiding cover), bite rate, and bite size can confound vigilance, foraging behaviour, and intake measurements (Laundré et al., 2001; Childress and Lung, 2003; Wolff and Van Horn, 2003; Fortin et al., 2004a). There will be an ongoing need for additional field and controlled studies to discover the underlying mechanisms of predator–prey and prey–prey behavioural relationships, and to provide management recommendations on how predator–prey problems can be resolved.

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