

# Spatial and temporal changes in group dynamics and range use enable anti-predator responses in African buffalo

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**Abstract.** The reintroduction of large predators provides a framework to investigate responses by prey species to predators. Considerable research has been directed at the impact that reintroduced wolves (*Canis lupus*) have on cervids, and to a lesser degree, bovids, in northern temperate regions. Generally, these impacts alter feeding, activity, and ranging behavior, or combinations of these. However, there are few studies on the response of African bovids to reintroduced predators, and thus, there is limited data to compare responses by tropical and temperate ungulates to predator reintroductions. Using the reintroduction of lion (*Panthera leo*) into the Addo Elephant National Park (AENP) Main Camp Section, South Africa, we show that Cape buffalo (*Syncerus caffer*) responses differ from northern temperate ungulates. Following lion reintroduction, buffalo herds amalgamated into larger, more defensible units; this corresponded with an increase in the survival of juvenile buffalo. Current habitat preference of buffalo breeding herds is for open habitats, especially during the night and morning, when lion are active. The increase in group size and habitat preference countered initial high levels of predation on juvenile buffalo, resulting in a return in the proportion of juveniles in breeding herds to pre-lion levels. Our results show that buffalo responses to reintroduced large predators in southern Africa differ to those of northern temperate bovids or cervids in the face of wolf predation. We predict that the nature of the prey response to predator reintroduction is likely to reflect the trade-off between the predator selection and hunting strategy of predators against the life history and foraging strategies of each prey species.

**Key words:** Africa; bovid; Cape buffalo; group formation; habitat use; lion; *Panthera leo*; predator reintroduction; prey response; *Syncerus caffer*.

## INTRODUCTION

Large predators shape prey behavior in many ecosystems (Sinclair 1985, Berger 2007). The potential cost of anti-predator behavior (e.g., increased vigilance) leads to the prediction that, in the absence of predators, prey species will relax their investment in such behavior. Given that many ecosystems have lost their large predator assemblages, currently observed prey behavior, resource use, and ranging patterns may not reflect patterns that occur in the presence of large carnivores. The reintroduction of top predators, therefore, provides a powerful experiment to test the responses of prey species to large predators. These reintroductions may result in one of two outcomes: either the prey species will

be extirpated or the evolved predator-specific behavior will manifest itself in the population, enabling coexistence with the large predators and the predation pressure they exert (Laundre et al. 2001, Berger 2007).

The majority of studies investigating prey responses to predator reintroductions have involved North American cervids, and in particular, elk (*Cervus elaphus*; Fortin et al. 2005, Mao et al. 2005, Berger 2007), moose (*Alces alces*; Berger 2007), and caribou (*Rangifer tarandus*; Berger 2007) responses to wolf (*Canis lupus*) reintroductions. Elk are known to alter activity patterns (Fortin et al. 2005), feeding patterns (Ripple and Beschta 2003), vigilance behavior (Laundre et al. 2001, Berger 2007), and ranging patterns (Mao et al. 2005) following wolf reintroductions, which ultimately led to changes in the demographic structure of the elk population (Creel et al. 2007) and also trophic cascades (Ripple and Beschta 2003).

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The impact of large carnivore reintroduction on bovids has received considerably less attention, focusing predominantly on wolf reintroductions impacting bison (*Bison bison*) behavior and foraging (Laundre et al. 2001, Hernandez and Laundre 2005, Berger 2007, Fortin and Fortin 2009). Considering the diversity of African bovids and predators and the increasing numbers of large-carnivore reintroductions in Africa (Hayward et al. 2007), there is a dearth in research on the response of African bovids to the reintroduction of large predators. In South Africa, lion (*Panthera leo*) have been reintroduced into at least 37 reserves over the past two decades (Slotow and Hunter 2009), with little follow-up on how these large predators have impacted the behavior and demographics of prey species (but see Hunter and Skinner 1998, Tambling and du Toit 2005). It is, therefore, unclear whether African bovids would respond in a similar manner to northern hemisphere cervids and bovids.

In African ecosystems, predation plays an important role in structuring ungulate communities (Sinclair et al. 2003); however, the relative impact of predation is dependent on the body size of the prey (Hopcraft et al. 2010). In the Serengeti ecosystem, predation pressure overrides interspecific competition as a determinant of spatial distribution in a number of species (Sinclair 1985). These observed patterns represent the evolutionary outcome of exposure to predation, confirming its strong selective pressure. Therefore, reintroductions of large predators should drive ungulate prey populations toward an evolved predator-prey relationship that would have been present prior to the extirpation of predators. Large African ungulates (i.e., buffalo, *Syncerus caffer*) are also well adapted to defend themselves against, or even kill, predators (Makacha and Schaller 1969). Therefore, we predict that the relatively unilateral response of northern hemisphere cervids (largely focused on avoiding predators) may not be expressed in those reintroductions where prey species include large, potentially dangerous prey, such as buffalo. We predict that buffalo will respond to the reintroduction of large predators by modifying their behavior to better utilize their fight response capability by increasing herd sizes and the use of open habitats. We used the reintroduction of top predators (lions in particular) into the Addo Elephant National Park (AENP) in the Eastern Cape, South Africa, to test this.

#### MATERIALS AND METHODS

The study was conducted in the AENP (33°31' S, 25°45' E), which encompasses 1400 km<sup>2</sup> and comprises six distinct fenced management sections. Two sections have substantial free-ranging buffalo populations, namely the Main Camp (130 km<sup>2</sup>) and Nyathi (140 km<sup>2</sup>) sections. The Main Camp has a relict population of 337 buffalo and Nyathi has had buffalo since 2003, when 71 buffalo were translocated from Main Camp. The Main Camp Section has been expanded numerous

times; most recently in 1994 and 2000, providing increased open vegetation for foraging buffalo. Large predators (lions and spotted hyaena, *Crocuta crocuta*) were reintroduced into Main Camp in 2003 following a 100-year absence (Hayward and Hayward 2006). Rainfall ranges between 260 and 530 mm per annum and peaks during the spring and autumn seasons (Landman et al. 2008). The principal vegetation type, covering >65% of the Main Camp Section, is the Sundays Thicket, dominated by dense stands of pork-bush, *Portulacaria afra* (Mucina and Rutherford 2006). Additionally, large areas of open, secondary grassland are present, a remnant of previous agricultural activity.

The buffalo population in the Main Camp Section has been monitored using aerial censuses since 1978, with detailed data including the size of each group counted between 1996 and 2009. We use this single snapshot of group size per year to investigate possible changes in group size over time by calculating the 0, 10, . . . , 90, 100 percentiles of each year's group size distribution from the count data. We expect the lower percentiles to represent single males and bachelor groups and the upper percentiles to represent breeding herds. For this analysis, we were interested in the size of the breeding herds as 90% of the population, including all recruitment, at any time found within these herds. Using a Davies test (Davies 1987) we assessed whether significant changes in percentile group size distributions existed between 1996 and 2009. To investigate possible drivers of group size changes for each percentile over time, we conducted a hierarchical partitioning analysis (MacNally and Walsh 2004) using a Poisson error distribution for the generalized linear model design. Potential drivers of group size at each percentile included (1) the rainfall during the year preceding the aerial census as an index of food availability (Robertson 1988), (2) the buffalo population size (group size is expected to scale linearly with population size; Pays et al. 2007), (3) the number of lions in the reserve (group theory suggests breeding buffalo should congregate into larger groups for protection; Caro 2005), and (4) the number of competitors indexed by the number of grazers counted during each year's census. The hierarchical partitioning proportions the variance explained in the overall model to each of the predictor variables (MacNally and Walsh 2004).

Between September 2007 and August 2009, very high frequency (VHF) collared buffalo ( $n = 2$ , each associated with a breeding herd) were located at random times between one and six times a week. On location, the distance and bearing from the observer's position (GPS coordinate) to the middle of the herd associated with the known buffalo were recorded to estimate the exact location of the herd. If visual observation was not possible for a collared individual, the estimated coordinates were calculated using triangulation. Considering that habitat patch size is larger than the area encompassed by a single breeding herd at one time and that

road density is high (See Appendix A: Fig. A1), we are confident that triangulation efforts assigned herds to the correct habitat type. These breeding herd observations were used to assess the current habitat use of breeding herds in Main Camp. Habitat use was assessed based on six identified habitat types, varying in vegetation density, from a previously developed habitat map produced from satellite (Spot 5) imagery of the Main Camp during 2006 (Marietjie Landman, *unpublished data*). We ranked habitat preference using a compositional analysis (Aebischer et al. 1993) at two scales, representing the selection of the home ranges within the study area and the selection of the herds within the estimated home ranges (Johnson 1980). Aebischer et al. (1993) suggests that a minimum of six individuals be used in compositional analysis of habitat use. We, however, only had two individuals, but do not feel that this negatively influenced our ability to assess habitat use for breeding buffalo herds. Gregarious species pose problems for the analysis of habitat use, as the unit of sample; the individual will become correlated within the groups (Aebischer et al. 1993). During radio-tracking bouts in our study, the buffalo in breeding herds were separated into at most four herds, and most often separated into only two herds (each represented by one of our collars). Therefore, by tracking the two collared buffalo, we in essence were able to estimate habitat use for 63–93% of all buffalo in the park. By increasing collar numbers it is doubtful that habitat use estimates would change, as new buffalo's observed would have had identical locations as those already tracked. We handled the nonavailability of some habitat types by removing habitat types not found in the home ranges of either of the two collared buffalo from the within home range analysis (Aebischer et al. 1993). As a result, we used all six habitat types when conducting selection at the home range level, but only four habitat types when investigating selection within the home range. Using log-linked mixed-effects generalized linear models, we investigated possible drivers for our observed habitat preferences (i.e., the occupation of a habitat type). We included rainfall recorded over a short (30 days) and long (365 days) period prior to each collar relocation as a proxy for food availability (Robertson 1988). Micro-climatic variables, including temperature (indexed on a four point scale), cloud cover (indexed on a four point scale), and wind (indexed on a three point scale) were modeled to investigate if the localized environmental conditions affected where on the landscape buffalo were found. Finally, we classified time into one of four periods based on sun time (Nouvellet et al. 2012), namely night, day, evening (period of time around sunset), and morning (period of time around sunrise) to investigate temporal changes in habitat use associated with each relocation. We included the individual collared buffalo as a random factor to account for the habitat selection analysis being conducted at the individual level. To find the best fitting parsimonious

model to predict habitat use of buffalo breeding herds within the study area, we used a forward selection procedure with associated  $F$  tests (Efroymsson's algorithm), setting  $P < 0.01$  (Murtaugh 2009).

To assess calf survival during our study period, we recorded the composition of breeding herds at five time periods during the study; namely, in February–May 2004 (T3), October 2004–September 2005 (T4), February–May 2008 (T5), December 2008–February 2009 (T6), and May 2009 (T7). Buffalo in herds were classified as juvenile (0–1 years old, both sexes, 0–200 kg [Pienaar 1969]), yearling (1–3 years of age, both sexes), or adult (3+ years of age, separated by sex) age classes. The 71 buffalo translocated to the Nyathi Section in September 2003 (T2) were aged and sexed based on the above criteria and are used as a representative sample for Main Camp in 2003, prior to lion introduction (no age and sex structure data was collected during censuses immediately prior to the lion reintroduction). In addition, we obtained recorded herd structures from 1979 (T1; Hall-Martin 1979), resulting in seven demographic assessments between 1979 and 2009. We used a moving split window of chi-square statistic values to assess changes in consecutive age structures of breeding herds over time. We compared the proportion of juvenile buffalo to each corresponding period's monthly rainfall, as well as to a one-year lagged average monthly rainfall to account for lag effects in survival (Owen-Smith and Mason 2005), using linear models to assess if increased rainfall leading to increased forage production (Robertson 1988) was related to the juvenile percentage in breeding herds. During field observations, we opportunistically recorded the type of response (defensive or fleeing) buffalo employed when lions were encountered, and assessed changes in the number of flee vs. stand and defend interactions prior to 2006, and after 2006, where 2006 was identified as a critical point where buffalo breeding herd group size and juvenile survival increased (see *Results*). Finally, we compared the percentage of juvenile buffalo out of all buffalo killed by lions during the first two years after their reintroduction against the percentage of juvenile buffalo observed within the herds to assess if lions preferentially preyed on them following reintroduction.

## RESULTS

Breakpoints in the group size distribution were detected for all percentiles greater than 0.3 (Table 1, percentiles with no breakpoints omitted). Significant positive breakpoints (indicating a significant increase in group size) were detected between 2003 and 2006 for both the 90 and 100 percentiles (Table 1); whereas significant negative breakpoints (indicating a significant decrease in group size) were detected during the same period for the 60–80 percentiles (Table 1; Appendix B: Fig. B1). Hierarchical partitioning shows that positive significant breakpoints associated with the 90 and 100 percentiles were driven primarily (>50% of the variation

TABLE 1. Davies tests results for nonlinear regression of percentiles of group sizes against time for aerial census data in the Addo Elephant National Park, South Africa, between 1996 and 2009, indicating significant breakpoints (shown by asterisks) in percentile group size distributions and the direction of the change in group size.

Percentile	Davies test				Hierarchical partitioning (%)			
	Break	Direction	Year	<i>P</i>	Rainfall	Pop.	Lions	Comp.
30	yes	none	2004–2005	0.34	3.8	22	21.9	52.3
40	yes	none	2003–2004	0.29	10.1	13.1	33	43.9
50	yes	none	2004–2005	0.07	17	15	12.5	55.5
60	yes*	negative	2004–2005	<0.005	26.5	10.9	13.9	48.7
70	yes*	negative	2005–2006	<0.05	57.3	11.1	8.9	22.7
80	yes*	negative	2005–2006	<0.05	49.7	8.3	27.9	14.1
90	yes*	positive	2003–2004	<0.05	4.5	26.7	58.1	10.7
100	yes*	positive	2005–2006	<0.005	6.1	30.5	52.1	11.3

Note: Hierarchical partitioning represents drivers of group size percentiles with the percentage representing the percentage of variation explained by each predictor variable (Rainfall, rainfall during the year preceding the aerial census; Pop., buffalo population size during the census; Lions, number of lions in the reserve at the time of the census; and Comp., number of competing grazers counted at the time of the census).

explained) by the number of lions, with a positive scaling of group size with population size observed (25–30% of the variation explained; Table 1).

Over the course of the VHF tracking, the two collared buffalo were relocated 167 and 163 times, respectively, and only once were they relocated together. Cleared agricultural lands were the most preferred habitat type, ranking highest in preference both at and within the home range (Table 2a, b). Alternatively, thicket (the most dense habitat type) was the least preferred habitat type within the home ranges (Table 2b). When modeling the role of individual predictor variables, time of day was the strongest driver of habitat preference ( $P < 0.005$ ), with short- and long-term rainfall showing marginal impacts on habitat preference (both  $P < 0.01$ ). However, when proceeding with the Efronson algorithm, both long- and short-term rainfall were dropped from the model, with time of day the only remaining significant driver (Appendix B: Table B1). Buffalo breeding herds underwent a daily shift in habitat preference, moving from open cleared agricultural lands in the morning to more dense vegetation types during the day (morning–day,  $z = 4.383$ ,  $P < 0.005$ ), followed by a shift back toward the open areas in the evening, remaining in these open areas during the night and into the morning (day–evening,  $z = -2.938$ ,  $P < 0.005$ ; day–night,  $z = -3.795$ ,  $P < 0.005$ ; Appendix B: Fig. B2).

Between 2004 and 2005 there was a significant change in breeding-herd structure ( $\chi^2_{2004-2004/2005} = 10.5$ ,  $df = 2$ ,  $P < 0.05$ ), with juveniles dropping from 20% to 10% during this period (Fig. 1). This drop was followed by a recovery in juvenile numbers between 2005 and 2008 ( $\chi^2_{2004/2005-2008} = 7.0$ ,  $df = 2$ ,  $P < 0.05$ ) with juvenile percentages rebounding to 22% (Fig. 1). There was no relationship between available forage (indexed by rainfall) during the period of demographic assessment ( $F_{1,5} = 0.11$ ,  $P = 0.76$ ) or prior to the period of demographic assessment ( $F_{1,5} = 0.72$ ,  $P = 0.43$ ; Appendix B: Table B2, Fig. B3) and the percentage of juveniles in the breeding herds. During observations on buffalo herd interactions with lions ( $n = 11$ ), we

witnessed buffalo groups resisting attempted predation in 100% of all observations later than 2007 ( $n = 5$ ), and fleeing from buffalo in 67% of all interactions between 2004 and 2007 ( $n = 6$ ). In the two years following lion reintroduction, 44% of observed lion kills were juveniles, significantly more ( $\chi^2 = 9$ ,  $df = 1$ ,  $P < 0.005$ ) than the percentage of juveniles observed concurrently in breeding herds (20%).

#### DISCUSSION

We detected a marked fluctuation in the survival of juvenile buffalo following the reintroduction of lions into Main Camp. Juvenile buffalo, along with adult males, is one of the main demographic classes killed by lions (Sinclair 1977, McBride 1984, Prins and Iason 1989, Funston and Mills 2006, Hay et al. 2008). High juvenile-buffalo mortality to lions is most probably related to a flee response by buffalo herds, exposing weaker, slower juveniles to predation. An indication of juvenile mortality resulting from flee responses is the extended distance (average =  $1090 \pm 1443$  m, range = 100–11 000 m) that lions pursued buffalo herds in the Southern Kruger National Park (KNP), resulting in high levels of juvenile mortality (Funston et al. 1998). Following lion reintroduction into Main Camp, juvenile buffalo were killed more often than expected by chance, and this corresponds with our observations of an initial majority flee response by buffalo when confronted by lions. The higher than expected juvenile mortality resulted in the reduced juvenile percentage observed in the herds in 2005. However, when buffalo herds do not turn and flee from lion presence, herds have the ability to resist lion predation (Mitchell et al. 1965, Sinclair 1977). An expectation resulting from any form of defense against lion predation is an increase in the percentage of juveniles per herd. During the 2004 aerial census in the KNP, the percentage of juveniles was recorded for each buffalo group observed (Whyte 2004), allowing a reanalysis of the data to assess herd size–juvenile percentage relationships. Buffalo herds with fewer than 60 buffalo (upper limit to group size prior to

TABLE 2. Simplified ranking matrices (Aebischer et al. 1993) for buffalo breeding herds based on (a) comparing proportional habitat use within minimum convex polygons (MCP) home ranges with proportions of total available habitat types, and (b) comparing the proportions of relocated observations within each habitat type within the home range in the Addo Elephant National Park between September 2007 and August 2009 (a higher ranking signifies a more selected habitat type).

Habitat type	Habitat type						Rank
	Alluvial	Coastal	Agricultural lands	Bontveld	Recovering thicket	Thicket	
a) MCP home range vs. total study area†							
Alluvial	0	-	---	-	+++	---	1
Coastal	+	0	-	+++	+	+	4
Agricultural lands	+++	+	0	+	+++	+++	5
Bontveld	+	---	-	0	+	+	3
Recovering thicket	---	-	---	-	0	---	0
Thicket	+++	-	---	-	+++	0	2
b) Radio locations vs. MCP home range‡							
Coastal		0	---	-		+++	1
Agricultural lands		+++	0	+++		+++	3
Bontveld		+	---	0		+++	2
Thicket		---	---	---		0	0

Note: A plus symbol represents that the habitat type in the row is used more often than the habitat type represented in the columns, whereas a minus symbol represents that the habitat type in the row is used less often than the habitat type in the columns. A triple sign (+ or -) represents significant deviation from random at  $P < 0.05$  (i.e., for part a, agricultural lands are used significantly more often than alluvial or thicket vegetation types).

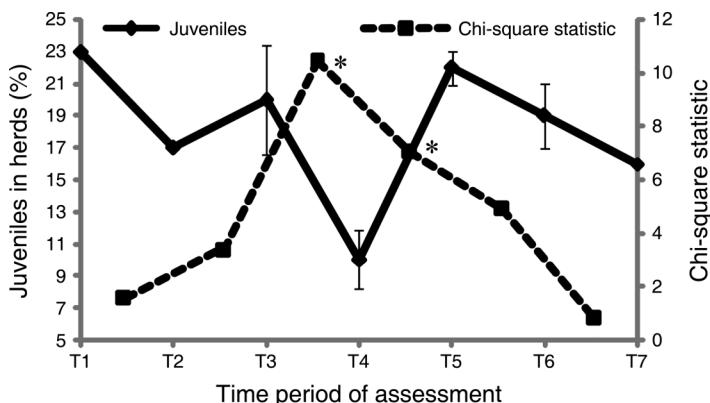
† Agricultural < Coastal ≪≪ Bontveld < Thicket ≪≪ Alluvial ≪≪ Recovering thicket. The < symbols signify the direction of the overall order of habitat use, with a triple sign signifying a significant shift in preference for a particular habitat type (most preferred on the left, least preferred on the right).

‡ Agricultural ≪≪ Bontveld < Coastal ≪≪ Thicket.

lion reintroduction in Main Camp) had a significantly lower percentage of juveniles ( $9.7\% \pm 1.3\%$ ; similar to the lowest juvenile percentage observed in Main Camp in 2005) in comparison to buffalo herds between 60 and 220 (buffalo group sizes after lion introduction; juvenile percentage =  $12.9\% \pm 0.6\%$ ,  $F_{1,55}$ ,  $P < 0.05$ ). This suggests that buffalo in smaller herds had either (1) lower reproductive ability or (2) reduced juvenile survival. However, putting the current herd size observations in Main Camp into perspective, under threat of lion predation, buffalo herds tend to average in excess of 100 individuals (Eltringham and Woodford 1973, Sinclair 1977, Halley et al. 2002, Cross et al. 2009). Therefore, buffalo herd sizes prior to lion reintroduction were either an anomaly and herd sizes have now returned to expected for buffalo, or buffalo that do not suffer predation occur in smaller herds.

Buffalo populations in the absence of lions in the thicket biome of South Africa are characterized by smaller herds, generally fewer than 20 individuals, as shown with the following: (1) AENP's Main Camp, current study prior to lion reintroduction; (2) Nyathi Section of AENP, where the maximum group size during 2009 aerial census was 17 (South African National Parks, unpublished data), and (3) Great Fish River Reserve, where the average breeding herd size was  $14.4 \pm 1.37$ ,  $n = 51$  (Eastern Cape Parks Board, unpublished data). Similarly, in the lowland forests of Congo and the mixed forest-savanna of Gabon, both areas expected to be predator free (Bauer et al. 2003), buffalo herds average fewer than 50 individuals (Sinclair 1977, Korte 2008). The majority of the abovementioned populations were estimated to be a similar size to the current population in Main Camp, so population size effects cannot explain the differences observed currently

FIG. 1. Moving-window analysis using a chi-square statistic (dashed line) to determine shifts in the yearly consecutive population structure of buffalo (adult, subadult, and juvenile [ $< 1$  year old; solid line, mean  $\pm$  SE]) at the Addo Elephant National Park Main Camp Section, South Africa. Asterisks signify a significant change in the population structure ( $P < 0.05$ ). Time periods are: T1, 1979; T2, September 2003; T3, February–May 2004; T4, October 2004–September 2005; T5, February–May 2008; T6, December 2008–February 2009; and T7, May 2009.



in Main Camp. Consequently, our results suggest a mechanism whereby buffalo in Main Camp, originally characterized by small herds, have switched from a flee to fight response in handling lions, and this response has been associated with increased herd sizes, such that current herd sizes are characteristic of localities that have co-occurring lion and buffalo populations.

A confounding variable is that most predator-free buffalo populations occur in areas characterized by dense vegetation (with Main Camp being no exception), and small herds may allow selective grazing by individual buffalo where resources are dispersed (Sinclair and Gwynne 1972, Jarman 1974). Prior to lion reintroduction into Main Camp, buffalo were similarly thought to remain in the dense vegetation characteristic of the thicket biome (Winterbach and Bothma 1998), which may explain the presence of small breeding herds. However, buffalo are more vulnerable to predation by lions in areas with greater cover (Funston et al. 2001) as a result of lions being primarily ambush predators (Hopcraft et al. 2005). It is, therefore, not surprising that current observations show that buffalo breeding herds use open areas far more than would be expected based on the available vegetation. Our data also shows that, in addition to the overall preference buffalo herds display for open areas, there is an increase of this preference during the evening and night with a peak in the morning when lions are most active (Hayward and Hayward 2006, Hayward and Slotow 2009). Thus, in Main Camp, lion reintroduction has resulted in what appears to be a shift into open habitats, with a concomitant increase in herd size, which resulted in an increased herd defense. The net result of these changes was an increase in juvenile buffalo survival rates in Main Camp.

Laundre et al. (2001) suggest that behavioral changes are required by prey species to adapt to new "landscapes of fear" following predator reintroductions. However, these "landscapes of fear" will differ when considering different predator-prey combinations. The best known example of ungulates altering behavioral and ranging patterns in the face of predation comes from the Yellowstone ecosystem following wolf reintroductions. Our results, viewed in association with observations from the Yellowstone system, suggest contrasting factors shaping the response of prey species to predator reintroductions. Following the reintroduction of wolves, elk did not increase group sizes in response to increased predation risk, but rather shifted their utilization of the landscapes to avoid regions perceived as dangerous (Hernandez and Laundre 2005, Mao et al. 2005). Increasing herd size is not always advantageous, as elk are more often encountered and attacked by wolves once in larger herds (Creel and Winnie 2005). Similarly, once in large herds, buffalo are easily encountered (Hayward and Kerley 2005). In the case of buffalo, larger herds offer an advantage that defense against predation is improved. Bison show little habitat or group size response to wolf presence or absence (Hernandez and

Laundre 2005, Fortin et al. 2009), and this could be a consequence of bison not being considered a preferred prey species of wolves across a range of studies (M. Hayward, *unpublished data*).

Predator hunting mode (ambush [i.e., lions] vs. coursing [i.e., wolves]) has a profound impact on prey anti-predator responses (Schmitz 2007, Kauffman et al. 2010). Ambush predators are expected to have a larger impact on prey responses (Schmitz 2008), as they generally hunt in environments that provide concealment (Hopcraft et al. 2005). The use of these ambush environments creates a landscape with large variations in risk to prey species. According to the predation risk allocation hypothesis (Lima and Bednekoff 1999), prey species are then expected to alter their activity and ranging behavior more so than if predation risk was uniform (i.e., as provided by coursing predators). Therefore, evident shifts in buffalo range use, group size, and activity patterns (C. J. Tambling, *unpublished data*) support the hypothesis that lion (ambush predators) reintroduction will drive these observed changes in behavior and that these responses to predation should be greater in magnitude than responses to wolf reintroductions.

These contrasting approaches by prey to avoid predation highlight the multifaceted strategies that prey species employ to counter reintroduced predators. Just as the response of temperate and tropical ungulates varied as a function of predator-prey combination, the response of other African bovids will undoubtedly vary depending on the predator-prey combination investigated, with the degree of selection and hunting strategy that each predator has for each specific prey species playing an important role. Nonselected prey species and prey species responding to coursing predators are expected to display less pronounced shifts in behavior. Combining this relationship of predator specific responses with the life history patterns associated with foraging strategies of different prey species provides an ideal framework for the investigation of the predictive understanding of the response of African bovids to a multitude of predator threats.

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#### SUPPLEMENTAL MATERIAL

##### Appendix A

A figure showing the different vegetation types within the Addo Elephant National Park, South Africa (*Ecological Archives* E093-114-A1).

##### Appendix B

Additional results related to buffalo herd size distributions over time, buffalo habitat use within the Addo Elephant National Park, and the relationship between juvenile buffalo survival and rainfall (*Ecological Archives* E093-114-A2).