

Spatial patterns of African ungulate aggregation reveal complex but limited risk effects from reintroduced carnivores

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1 **Spatial patterns of African ungulate aggregation reveal complex but limited risk effects**
2 **from reintroduced carnivores**

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16 **Abstract.** The ‘landscape of fear’ model, recently advanced in research on the non-lethal effects
17 of carnivores on ungulates, predicts that prey will exhibit detectable antipredator behavior not
18 only during risky times (i.e., predators in close proximity) but also in risky places (i.e., habitat
19 where predators kill prey or tend to occur). Aggregation is an important antipredator response in
20 numerous ungulate species, making it a useful metric to evaluate the strength and scope of the
21 landscape of fear in a multi-carnivore, multi-ungulate system. We conducted ungulate surveys
22 over a two-year period in South Africa to test the influence of three broad-scale sources of
23 variation in the landscape on spatial patterns in aggregation: 1) habitat structure, 2) where
24 carnivores tended to occur (i.e., population-level utilization distributions) and 3) where
25 carnivores tended to kill ungulate prey (i.e., probabilistic kill site maps). We analyzed spatial
26 variation in aggregation for six ungulate species exposed to predation from recently reintroduced
27 lion (*Panthera leo*) and spotted hyena (*Crocuta crocuta*). Although we did detect larger
28 aggregations of ungulates in ‘risky places’, these effects existed primarily for smaller-bodied
29 (<150kg) ungulates and were relatively moderate (change of ≤ 4 individuals across all habitats).
30 In comparison, ungulate aggregations tended to increase at a slightly lower rate in habitat that
31 was more open. Lion, an ambush (stalking) carnivore, had stronger influence on ungulate
32 aggregation than hyena, an active (coursing) carnivore. In addition, places where lions tended to
33 kill prey more strongly affected ungulate aggregation than places where lions tended to occur,
34 but an opposing pattern existed for hyena. Our study reveals heterogeneity in the landscape of
35 fear and suggests broad-scale risk effects following carnivore reintroduction only moderately
36 influence ungulate aggregation size and vary considerably by predator hunting mode, type of
37 predation risk, and prey species.

38 *Key words: antipredator behavior; carnivore predation risk; landscape of fear; predator-prey*
39 *interaction; risk effects; ungulate aggregation*

40 **INTRODUCTION**

41 Examinations of predator-prey ecology have focused on direct, lethal predation effects on
42 prey (Lima 1998), but recent work has expanded this view by quantifying non-lethal “risk
43 effects” (i.e., altered prey behavior due to risk; Creel and Christianson 2008). These risk effects,
44 which have been well-described in aquatic systems (e.g., Peacor and Werner 2001), are now
45 being assessed in vast carnivore-ungulate systems. From this research, we understand that
46 ungulates employ a variety of strategies to manage their interactions with carnivores. These
47 include migrating to areas with lower carnivore densities (Hebblewhite and Merrill 2007),
48 selecting habitat that provides cover (Valeix et al. 2009a, Thaker et al. 2011), and aggregating
49 into larger groups as a means of additional vigilance, dilution, and defense (Hamilton 1971,
50 Dehn 1990, Hebblewhite and Pletscher 2002). Predation-sensitive migration and habitat
51 selection has been relatively well-documented in a variety of carnivore-ungulate systems (e.g.,
52 Hebblewhite and Merrill 2007, Valeix et al. 2009a), although understanding the demographic
53 consequences of these behaviors remains a challenge. Comparatively, the factors shaping
54 ungulate aggregation are more poorly understood, largely due to the complexity of herding
55 behavior in heterogeneous environments (Pays et al. 2007, Fortin et al. 2009). For instance,
56 whereas larger aggregations of ungulates can reduce predation risk via dilution, they can also
57 result in decreased foraging efficiency (Molvar and Bowyer 1994). In addition, larger
58 aggregations offer improved predator detection, but they are also more easily detected by
59 predators (Caro 2005). Given that aggregation is one of the most common antipredator strategies
60 employed by ungulates (Caro 2005), a more thorough understanding of the degree to which

61 spatial variation in risk from multiple carnivores influences ungulate aggregation is crucial to
62 both predator-prey and behavioral ecology.

63 Several ungulate species in African systems modulate their group size in response to
64 carnivore predation risk (Valeix et al. 2009b, Thaker et al. 2010, Creel et al. 2014). Whereas
65 evidence suggests that ungulates aggregate when faced with predation risk in temporal
66 dimensions (e.g., Valeix et al. 2009b), it is unclear how spatial aggregation patterns relate to
67 predation risk. The “landscape of fear” model of predator-prey interactions (Laundré et al. 2001)
68 predicts that antipredator processes such as aggregation will be detectable not only during risky
69 times (i.e., when carnivores are in the immediate vicinity) but also in risky places (i.e., where
70 carnivores typically occur or kill prey; Valeix et al. 2009a, Valeix et al. 2009b, Thaker et al.
71 2011, Creel et al. 2014). Although the landscape of fear theory has been presented as a
72 framework for understanding broad-scale ecosystem dynamics (Ripple and Beschta 2004), the
73 strength and scope of carnivore-induced risk effects are highly variable. For example, in African
74 ecosystems, prey body size (Hopcraft et al. 2010), climate (Riginos 2015), and forage quality
75 (Anderson et al. 2010) have been found to influence ungulate behavior as much or more than
76 predation risk, while other work suggests interactive and context-specific effects of these factors
77 (Sinclair and Arcese 1995). Furthermore, risk effects depend on predator hunting mode, with
78 ambush predators generally eliciting the strongest prey responses (e.g., Schmitz 2008, Thaker et
79 al. 2010).

80 Here, we aim to clarify the relative contribution of multiple forms of landscape-level
81 predation risk on patterns of aggregation for six species of African ungulates exposed to multi-
82 carnivore predation. A key objective of our study is to contextualize the top-down influence of
83 carnivores on ungulate aggregation by comparing its effect size with that of an established

84 relationship between ungulate aggregation size and habitat structure (i.e., aggregations tend to be
85 larger in more open habitat; Evans 1979, Gerard and Loisel 1995, Pays et al. 2007, Thaker et al.
86 2010, Marino and Baldi 2014). In addition, our study evaluates the hypothesis that carnivore risk
87 effects on ungulates will vary by hunting mode and by prey species, as has been indicated in
88 predator-prey systems across a diversity of taxa (Preisser et al. 2007).

89 To these ends, we conducted surveys over a two-year period in South Africa to quantify
90 average ungulate aggregation size. We then compared spatial variation in ungulate aggregation
91 to two types of risk associated with the primary carnivores in this system: 1) the probability of
92 carnivore occurrence (population-level utilization distributions (UDs)) and 2) the probability of
93 carnivore kill occurrence (probabilistic kill site maps). Given that both aggregation size and
94 predation risk vary by ungulate species (Thaker et al. 2011, Gervasi et al. 2013), we developed
95 this assessment at the level of each ungulate species.

96 **METHODS**

97 *Study Area*

98 We assessed spatial patterns in ungulate aggregation in the 132 km² fenced Main Camp
99 section of Addo Elephant National Park, South Africa (Addo; 33°30'S, 25°45'E; Appendix A).
100 The dominant habitat type in Addo is thicket with grassland sections in the east that are
101 derivative of an agricultural history (Tambling et al. 2012). Unlike typical African savanna
102 ecosystems, Addo lacks pronounced wet and dry seasons (e.g., average wet and dry season
103 rainfall only differs by ~20mm; South African Weather Service, unpublished data). Using
104 digital vegetation maps provided by South African National Parks, we identified six habitat types
105 within Addo, including bushclump, gully thicket, thicket, Zuurkop woodland, long grassland,
106 and short grassland (South African National Parks, unpublished data). The two primary

107 carnivores in the study area, lion (*Panthera leo*) and spotted hyena (*Crocuta crocuta*), were
108 reintroduced in the Main Camp following a 100-year absence (Hayward and Hayward 2006).
109 All lions (4M, 2F) and four hyenas (3M, 1F) were unrelated and were reintroduced in late 2003;
110 an additional four unrelated hyenas (2M, 2F) were reintroduced in the winter of 2004 following a
111 period of disease testing (see Hayward et al. 2007a, 2009). One leopard (*Panthera pardus*) also
112 occurred in the study area but was not included in the analysis due negligible predation on the
113 ungulate species of interest.

114 *Ungulate surveys*

115 Between December 2003 and November 2005, we conducted surveys to describe spatial
116 variation in aggregation size for Cape buffalo (*Syncerus caffer*; hereafter buffalo), eland
117 (*Tragelaphus oryx*), greater kudu (*Tragelaphus strepsiceros*; hereafter kudu), red hartebeest
118 (*Alcelaphus buselaphus caama*), warthog (*Phacochoerus africanus*) and zebra (*Equus quagga*).
119 These species occurred across the entire study area and were common prey of lion and hyena in
120 Addo (Hayward 2006, Hayward et al. 2007b). We conducted vehicle-based surveys on a
121 network of 51 transects (\bar{x} transect length = 913 m, range 567 – 1,029 m; Appendix A). We
122 conducted surveys three hours preceding and following dawn and dusk, using spotlights when
123 necessary. These time periods correspond with peak activity times for lions and hyenas in Addo
124 (Hayward and Hayward 2006). We conducted 30 surveys per year on randomly selected days
125 and varied the start location for surveys to eliminate temporal bias at any given location. We
126 recorded aggregation size at the start, middle, and end points of each transect. The same
127 observer conducted each survey alongside a scribe. Detections occurred without the aid of
128 binoculars, although counts were confirmed using binoculars. In most cases (i.e., >80%), only
129 one aggregation of a given species was present at a transect point during a given survey. When

multiple, distinct groups of the same species were seen at a given location, we first corrected group size via distance sampling to accommodate variation in visibility by regressing the log of group size against the estimated detection probability in each habitat type (Buckland et al. 2001). We then summed group sizes to obtain species-specific aggregation sizes. We considered groups distinct when individuals were closer to other members of their group than the nearest peripheral members of another group. We counted all individuals (i.e., adults and juveniles) and assumed counts close to the line were accurately recorded (Buckland et al. 2005). Thus, aggregations represent all individuals of the same species at a transect point at a given time, whether one distinct aggregation or an aggregation of two or more groups in close proximity to the transect point.

Carnivore occurrence models

We developed population-level UD models for lions and hyenas to model predation risk as a function of carnivore occurrence (Hebblewhite and Merrill 2007, Valeix et al. 2009, Thaker et al. 2011). We VHF-tracked the entire lion population ($N = 6$) and 75% ($N = 6$) of the adult hyena population for two years following release in Addo. Both lions and hyenas were consistently tracked throughout the two-year study period via continuous, 96-hour follows conducted on average once every six weeks; opportunistic observations of carnivore locations and kills were also recorded outside these times (see Hayward et al. 2009). As with ungulate surveys, carnivore location data were primarily collected during times when lions and hyenas were most active (i.e., within 3 three hours of dawn and dusk; Hayward and Hayward 2006, Hayward et al. 2009). In this way, we attained an average of 48 locations ($SD = 18$) per hyena ($N = 285$ total locations for 6 hyenas) and 103 locations ($SD = 23$) per lion ($N = 615$ total locations for 6 lions). Beginning in November 2003, we partitioned lion locations into three, four-month periods per year through

153 October 2005: summer (November – February), autumn/early winter (March – June), and late
154 winter/spring (July – October). We then mapped population-level lion UD_s for each period to
155 account for temporal variation in lion ranging patterns following reintroduction (i.e., range
156 expansion; Hayward et al. 2009). Given the lower sample size of hyena locations (N = 285), we
157 developed a pooled UD representing population-level hyena space use over the two-year period
158 (Seaman et al. 1999). We developed UD_s in R (R Development Core Team 2011) using a
159 bivariate plug-in matrix (Gitzen et al. 2006). We depicted the interpolated density estimates as
160 UD percentiles at a 30m² resolution such that the highest percentile (100) represented the very
161 core of the UD, while the lowest percentile (1) represented the periphery. Areas not
162 encapsulated by any portion of the UD_s had a value of 0, representing a negligible probability of
163 carnivore occurrence.

164 *Kill occurrence models*

165 We identified carnivore-killed ungulates via continuous follows and incidental sightings.
166 We distinguished lion kills from those of hyenas based on observations of hunts and kills, signs
167 and direct observations of feeding on fresh carcasses. We saw no indication of intraguild
168 scavenging between lions and hyenas during continuous follows and have no other evidence of
169 its occurrence, as both species were at low densities during our study period.

170 We used the locations of killed ungulates to develop probabilistic spatial models of kill
171 occurrence throughout the study area as a function of landscape characteristics, which were
172 assigned using a lattice comprised of 250m² cells in ArcMap Version 10. We identified relevant
173 landscape covariates *a priori* for both lion and hyena kill occurrence models. These included the
174 proportion of each habitat type and the length of hard edge within a cell, in addition to the
175 Euclidean distance from kill site to fenceline, waterholes (N = 11), and campsites (N = 2). Given

176 that lions use cover to ambush prey (Loarie et al. 2013) and frequently kill near edge habitat
177 (Prins and Iason 1989), we defined hard edge as the boundary between open (short and long
178 grassland) and closed habitats (gully thicket, thicket, Zuurkop woodland, and bushclump). We
179 included the fenceline, waterhole, and campsite covariates to account for increased carnivore
180 hunting success near fences (Davies-Mostert et al. 2013), variation in ungulate water dependency
181 (Valeix et al. 2009b) and carnivore/ungulate avoidance of anthropogenic infrastructure (Howe et
182 al. 2013). For lions, we evaluated both a pooled model (using all locations of lion-killed
183 ungulates) and species-specific models (e.g., using only locations of lion-killed buffalo to
184 develop a lion-buffalo kill occurrence map) for ungulate species with sufficient sample size of
185 kill sites ($N \geq 25$; buffalo, kudu, and warthog). However, preliminary model analyses using
186 Akaike's Information Criterion corrected for sample size (AIC_c) indicated that, for each ungulate
187 species, the pooled model of lion-killed ungulates was better supported by the data than species-
188 specific models. Therefore, we used the pooled model in subsequent analyses for all six
189 ungulate species. For hyena, we did not have sufficient sample sizes to evaluate species-specific
190 models, thus we built the hyena kill occurrence model using pooled locations of all hyena-killed
191 ungulates. The smaller sample size of hyena-killed ungulates was unsurprising given that hyenas
192 exhibit non-specific predation tendencies and lower preference for our focal ungulate species
193 than lions (Hayward 2006).

194 Using a case-control design, we compared the landscape covariates of the locations of
195 each recorded lion ($N = 172$) or hyena ($N = 50$) kill site to landscape covariates associated with
196 20 random locations in k strata, where each stratum is a matched set consisting of the kill
197 location and 20 random locations (Hosmer and Lemeshow 2000, Manly et al. 2002). We
198 enforced a minimum distance of 500m such that none of the random controls were associated

199 with the exact habitat conditions of the kill sites (Gervasi et al. 2013). We used a mixed effects
200 logistic regression procedure and modeled the k_{ith} stratum as a random effect. We evaluated all
201 linear, non-interacting combinations of the *a priori* covariates described above and ranked
202 models according to AIC_c weight (w_i ; Burnham and Anderson 2002). Given that our primary
203 goal was prediction, we averaged parameter estimates over all models with a cumulative $AIC_c w_i$
204 of 0.95 (Burnham and Anderson 2002:150). We used the resultant averaged parameter estimates
205 to produce an odds ratio of kill occurrence (Keating and Cherry 2004) that took form:

$$206 \quad \Psi(\chi|\chi_R) = \exp [\beta_1(\chi_1 - \chi_R) + \beta_2(\chi_2 - \chi_R) + \dots + \beta_n(\chi_n - \chi_R)] \quad (1)$$

207 where $\Psi_{(x)}$ is the relative probability of kill occurrence in a given 250 m cell, χ_n is the covariate
208 value of that cell, and χ_R is the mean covariate value of all cells in the study area. Given that
209 predation events are rare throughout the study area, we can interpret the odds ratio as an
210 approximation of the relative probability of kill occurrence (Keating and Cherry 2004), where
211 $\Psi(\chi|\chi_R) = 1.0$ represents the mean probability of kill occurrence. Values lower or higher than
212 1.0 represent changes in the odds ratio of kill occurrence (e.g., $\Psi(\chi|\chi_R) = 2.0$ indicates a
213 location with twice the relative probability of kill occurrence than the mean; Fig. 1).

214 To assess the predictive ability of the kill occurrence models, we conducted k-folds cross
215 validation tests (Boyce et al. 2002). We divided the data between training and testing portions
216 maintaining an 80:20 ratio and fit kill occurrence models using the training data and validated
217 the predictions with the testing data. We conducted this test five times and partitioned the
218 predictive output into 10 categories. We compared the training and testing data using Spearman-
219 rank correlation coefficients (r_s ; Boyce et al. 2002).

220 *Ungulate aggregation models*

221 We used the average ungulate aggregation size for each species at each transect point and
222 within each period as the response variable in our ungulate aggregation models. We fit spatially-
223 explicit mixed effects linear regression models to predict spatial variation in average ungulate
224 aggregation in relation to carnivore occurrence and kill occurrence. These models took the form:

$$225 \quad Y_{ij} = X\beta_{ij} + Zu_j + e \quad (2)$$

226 where Y_{ij} is the log-transformed average ungulate aggregation size at the i th transect point in
227 period j , $X\beta_{ij}$ is a vector of the predictor covariates at the i th transect point in time period j (only
228 lion UDs were separated by period), and Zu_j is the random effect term for each time period in
229 the assessment (3 periods in each year such that $N_j = 6$). For all models, we accounted for spatial
230 autocorrelation among the i th transect points by using an exponential covariance structure, as
231 determined by AIC_c (Zuur et al. 2009). Prior to model fitting, we examined multicollinearity to
232 avoid excessive covariate correlation (0.7 tolerance level).

233 We took a two-step information theoretic approach to model selection to balance
234 precision and bias in our final models (Burnham and Anderson 2002). In the first step of model
235 selection, we built a global model *a priori* that included carnivore UDs, carnivore kill
236 occurrence, amount of hard edge (linear length in meters), and degree of openness (proportion of
237 open habitat within a 250m² cell). We included hard edge and openness covariates due to
238 associations between open habitats, increased visibility, and aggregations of African ungulates
239 (Evans 1979, Gerard and Loisel 1995, Pays et al. 2007, Creel et al. 2014, Marino and Baldi
240 2014). We then evaluated models developed from all possible linear combinations of these six
241 covariates. Interaction terms were not considered due to lack of clear justification and a desire to
242 keep the candidate model set as small as possible (Burnham and Anderson 2002:17). We ranked
243 models based on AIC_c and assessed models based on $AIC_{c w_i}$ (Burnham and Anderson 2002).

244 Aggregations of a given species might be influenced by the presence of other ungulates
245 (Scheel 1993). Accordingly, the second step of our model selection process tested whether the
246 top model for each ungulate species could be improved by the sequential addition of covariates
247 representing aggregations of other ungulate species at the i th transect point in the j th period.
248 These covariates were not considered in the first step of the model selection process because we
249 could not hypothesize ungulate species associations in an *a priori* fashion and because an all
250 combinations approach would have undermined model parsimony by resulting >2000 candidate
251 models (Burnham and Anderson 2002:174). Thus, we assessed whether the fit of the top-ranking
252 model from the first model selection step could be improved by the iterative addition of
253 covariates representing the other ungulate species, as assessed by a significant likelihood ratio
254 test ($\alpha = 0.05$ cutoff; Zuur et al. 2009). We concluded this process when the addition of
255 parameters no longer improved model fit and ranked final models using AIC_c and $AIC_c w_i$. We
256 averaged parameter coefficients across all models within $1/8^{\text{th}}$ $AIC_c w_i$ of the top-ranking model
257 (Burnham and Anderson 2002:171). We calculated the relative importance of covariates X_j by
258 summing Akaike weights across models where covariate j occurred (Burnham and Anderson
259 2002:168). Finally, we plotted model-averaged coefficients for all parameters with a
260 significance of $\alpha \leq 0.01$ to examine covariate effect size.

261 RESULTS

262 We recorded 4,964 observations of ungulates, 615 lion locations, and 285 hyena locations
263 during the two-year survey period. Population-level lion UD's varied by time period, with home
264 range expansion occurring over the two-year reintroduction period (Appendix B). Population-
265 level hyena UD's were focused around denning sites in the southwestern portion of the Main
266 Camp (Appendix B). Ungulate aggregation distributions were right-skewed; mean aggregation
267 sizes for the six species ranged from 2.8 to 16.7, with warthog forming the smallest aggregations

268 and buffalo forming the largest (Appendix C). We located 172 lion-killed ungulates and 50
269 hyena-killed ungulates. For both lion and hyena, kudu was the most commonly killed ungulate
270 (34.3% [N = 59] of all lion kills and 40.0% [N = 20] of all hyena kills) and zebra was the least
271 common (1.7% [N = 3] of all lion kills and 2.0% [N = 1] of all hyena kills).

272 Both the lion and hyena kill occurrence models revealed substantial spatial variation in
273 kill occurrence across the study area (Fig. 1). The k-folds cross validation tests indicated a good
274 fit of the models to the data, with an average correlation among the training and testing data of r_s
275 = 0.921 and $r_s = 0.916$ for the lion and hyena models, respectively. For the lion model, the
276 relative probability of lion kill occurrence was positively associated with length of hard edge and
277 proportion gully thicket and negatively associated with distance to campsites; the highest
278 probability of lion kill occurrence was where gully thicket habitat formed a hard edge with open
279 habitat (Appendix D, Fig. 1). For the hyena model, the relative probability of hyena kill
280 occurrence was negatively associated with distance to waterhole and distance to fenceline and
281 positively associated with length of hard edge (Appendix E). Hyena kill occurrence was greatest
282 in open habitat (Fig. 1).

283 For each ungulate species, the addition of covariates representing aggregations of the
284 other ungulate species failed to improve the top model and thus those covariates are absent in
285 final model sets. Buffalo aggregation size was best described by a univariate model representing
286 degree of openness and the open covariate was the most important covariate in the model set
287 (Table 1, Fig. 2a). No covariate was significantly associated with buffalo aggregation size at the
288 $\alpha < 0.05$ level (Appendix F). For eland, hyena occurrence featured as a covariate in each of the
289 top four models (Table 1) and had the highest relative importance in the model set (Fig. 2b). For
290 kudu and hartebeest, the top four models for both species featured the open, lion kill occurrence,

291 and hyena occurrence covariates and these three covariates had the highest relative importance
292 over the model set (Table 1, Fig. 2c,d). In the case of kudu, lion kill occurrence and proportion
293 open habitat were both highly significant predictors of aggregation size ($P < 0.0001$, Appendix
294 F). For example, kudu aggregations increased from an average of ~ 2 individuals in completely
295 closed habitat to ~ 4.5 individuals in completely open habitat (Fig. 3a). Similarly, as the odds
296 ratio of lion kill occurrence increased twelve-fold from 0.5 to 6.0, the average aggregation size of
297 kudu increased from ~ 2 individuals to ~ 5 (Fig. 3b). For red hartebeest, these two covariates
298 (proportion open habitat and lion kill occurrence) were also highly significant ($P < 0.01$,
299 Appendix F) and showed a similar positive association. For example, average hartebeest
300 aggregations increased from an average of ~ 3 individuals in completely closed habitat to ~ 5
301 individuals in completely open habitat (Fig. 3c) and from ~ 3 individuals to ~ 7 as the odds ratio
302 of lion kill occurrence increased from 0.5 to 6.0 (Fig. 3d). For warthog, the open and lion kill
303 occurrence covariates featured in all of the top four models (Table 1) and both had a relative
304 importance near 1.0 over the model set (Figure 2e). The positive association between warthog
305 aggregation size and lion kill occurrence was highly significant ($P = 0.01$, Appendix F); as the
306 odds ratio of kill occurrence increased from 0.5 to 6.0, warthog aggregations increased from an
307 average of ~ 2 individuals to ~ 3 (Fig. 3e). Finally, for zebra the open and edge covariates
308 featured in all of the top four models (Table 1) and these two metrics both had a relative
309 importance near 1.0 over the model set (Fig. 2f). Of these, the open covariate had a highly
310 significant ($P < 0.01$) positive association with zebra aggregation size; zebra aggregations
311 increased from an average of ~ 3 individuals in completely closed habitat to ~ 4 in completely
312 open habitat (Fig. 3f).

313 **DISCUSSION**

314 A recent wave of research has advanced our understanding of non-lethal effects of
315 carnivores on ungulates, but generalizing these risk effects over broad terrestrial scales has
316 proven difficult (e.g., see Kauffman et al. 2010). Over a two-year period, we found that ungulate
317 aggregation size was positively associated with increased predation risk and habitat openness,
318 but the effects of both of these factors were moderate and varied by carnivore hunting mode and
319 prey species (Preisser et al. 2007). The final models predicting ungulate aggregation size were
320 largely multivariate and often contained several important covariates (Fig.2), highlighting the
321 idea that no single influence drives ungulate aggregation (Creel et al. 2014). Given that top
322 predators were absent from Addo for 100 years preceding our study and that reintroduced
323 carnivores existed in low densities, the risk effects we observed might be smaller in magnitude
324 when compared to systems with non-naïve prey (Berger 2001) or high predator densities (Peacor
325 and Werner 2001). Moreover, given the coarse-grain scale of our study (i.e., population-level
326 spatial tendencies of carnivore occurrence and kill sites over two years), we view our
327 conclusions as relevant to broad spatial scales of predation risk rather than finer-scaled responses
328 (e.g., increased vigilance as a predator approaches; Périquet et al. 2010). Therefore, despite the
329 established general principle that prey tend to aggregate in response to heightened predation risk
330 (Caro 2005), application of this antipredator defense strategy is scale-specific and dependent
331 upon habitat structure, the type and duration of predation risk, prey naiveté, and the ungulate
332 species in question. We do not view our study as an explicit test of top-down versus bottom-up
333 effects on ungulate aggregation. However, given the correlation between habitat structure and
334 forage availability and quality, our study suggests that complex top-down effects act in tandem
335 with bottom-up habitat features to shape prey response to predation risk (Jarman 1974, Anderson
336 et al. 2010, Hopcraft et al. 2010).

337 Our results suggest that, like a complex physical landscape, the landscape of fear can be
338 highly heterogeneous. We note two sources of variation in the landscape of fear in Addo: 1)
339 carnivore identity, and 2) the nature of predation risk. In our study, spatial variation in lion kill
340 occurrence was a more important factor for predicting ungulate aggregation size than lion
341 occurrence, the latter having generally low importance (Fig. 2). Others have found the presence
342 of lions influences ungulate behavior, either by increasing vigilance (Hunter and Skinner 1998,
343 Périquet et al. 2010), altering habitat selection and space use (Valeix et al. 2009a, Thaker et al.
344 2010, 2011), or limiting access to quality forage (Barnier et al. 2014). Taken in context with our
345 results, this suggests that ungulates employ multiple strategies to mitigate interactions with lions.
346 For example, whereas ungulates might prefer more open habitats and increase vigilance in
347 response to fine-scale risk (e.g, a lion in close proximity; Valeix et al. 2009b), they might
348 aggregate in especially dangerous locations at broader scales (Thaker et al. 2010, this study).
349 Moreover, in the face of consistent, long-term (i.e., >3 years) exposure to predation, some
350 ungulates might form large herds (i.e. > 100 individuals; Tambling et al. 2012) or migrate to
351 areas of lower risk (Hebblewhite and Merrill 2007).

352 In contrast with these lion-related effects, the influence of hyena on ungulate aggregation
353 was weaker and more strongly linked to where hyenas tended to occur rather than where they
354 tended to kill (Fig. 2). This difference appears to be driven in part by the opposing patterns of
355 kill occurrence of lions and hyenas in our study (Fig. 1). Given that covariates for lion and
356 hyena kill occurrence often occurred in top models together (Table 1) but did not always have
357 opposing coefficients (Appendix F), the effect of the opposing patterns in kill occurrence on
358 ungulate aggregation likely arose from differences in hunting behavior rather than as a mere
359 artefact of negatively correlated spatial kill patterns between lions and hyenas. Thus, our results

360 corroborate the disparity of influence from active (coursing) versus ambush (stalking) predators
361 that has been shown in smaller systems (e.g., Schmitz 2008). Creel et al. (2014) found that
362 African ungulate group size was more influenced by hyena presence than lion presence and
363 suggested ambush predators might have weaker effects in carnivore-ungulate systems than in
364 invertebrate systems (e.g., Schmitz 2008). Our study sheds light on this discrepancy by
365 decomposing risk from carnivores with differing hunting modes into two distinct expressions,
366 namely, where they tend to occur and where they tend to kill. With this level of resolution, our
367 results suggest that the active carnivore (hyena) tends to influence ungulate aggregation via
368 occurrence while the ambush carnivore (lion) tends to influence via a tendency to kill in specific
369 locations. However, as in Creel et al. (2014), the influence of these factors varied considerably
370 among our focal ungulate species, highlighting the need for additional research to test this
371 generalization in carnivore-ungulate systems

372 Habitat structure was also associated with ungulate aggregation for several species. Early
373 research posited that ungulates aggregated in open habitat to decrease predation risk via dilution
374 (Jarman 1974). However, more recent theoretical (Gerard and Loisel 1995) and experimental
375 (Pays et al. 2007) studies have shown that open areas facilitate aggregation simply by virtue of
376 improved visibility and conspecific detection. In our study, the degree of habitat openness
377 consistently featured in the top models for most species (Table 1, Fig. 2). However, with respect
378 to lion kill occurrence, open habitat was relatively safe (Fig. 1). Therefore, our work
379 corroborates the notion that predation and openness can act independently to shape group size in
380 ungulates (Marino and Baldi 2014), although these factors might be interactive for some species
381 (Thaker et al. 2010). The edge formed between open and closed habitat is especially dangerous
382 for African ungulates (Prins and Iason 1989). However, the amount of hard edge was generally a

383 less important aspect of habitat structure for ungulate aggregation compared to the level of
384 openness (Fig. 2), emphasizing the importance of visibility over access to cover, as has been
385 reported for other African ungulates (Riginos 2015).

386 Our models for buffalo suggest that neither predation risk nor habitat structure were
387 strongly related to aggregation size (Table 1, Appendix F). This lack of effect corroborates the
388 notions that buffalo “basically ignore lions” (Prins and Iason 1989:290) and that risk-induced
389 behavioral modifications are weaker in large-bodied ungulates (Hopcraft et al. 2012). Rather
390 than aggregating, buffalo might shift habitat selection to avoid risky areas (Valeix et al. 2009a,
391 2009b), a pattern that has also been recorded for giraffe (*Giraffa camelopardalis*; Creel et al.
392 2014). Recent work in Addo using long-term (i.e., 14 years) data found that, following lion
393 reintroduction, small buffalo herds amalgamated into a large herd that provided protection for
394 juvenile buffalo; however, this change required more than three years to take place (Tambling et
395 al. 2012). Hence, behavioral adaptations in ungulates following reintroduction might need
396 several years to actualize for naïve prey (Berger 2001). Understanding how risk effects vary over
397 time, especially in relation to naïve ungulate prey facing reintroduced carnivores, is an important
398 topic for future research.

399 Species-specific strategies for minimizing predation risk are poorly understood in multi-
400 carnivore systems (Thaker et al. 2011, Creel et al. 2014). We noted distinct responses among six
401 ungulate species. The two largest ungulates, buffalo and eland, showed the least response to risk
402 and had the highest model uncertainty (Table 1, Fig. 2, Appendix F). These two species had the
403 largest aggregations on average (Appendix C) and both can successfully defend against lion
404 attacks (Caro 2005), thus their response to predation risk is perhaps more closely tied to a few
405 very large herds capable of self-defense rather than smaller aggregations of individuals

406 throughout the study area (Tambling et al. 2012). Moreover, the lack of risk effects on buffalo,
407 eland, and zebra (Fig. 2a,b,f) support the conclusion of Sinclair et al. (2003) that the influence of
408 top-down predation rapidly declines as prey body size increases beyond 150kg (zebra, the
409 smallest of these three species, has an average body size of 175kg; Stuart and Stuart 2000). The
410 final models for red hartebeest, kudu and warthog (Table 1, Fig. 2c,d,e; Appendix F), further
411 corroborate stronger influence of predation risk on small-bodied (<150kg) ungulates (Sinclair et
412 al. 2003, Hopcraft et al. 2012). However, whereas the associations between lion predation and
413 aggregation in these three smaller-bodied species were significant ($P \leq 0.01$, Appendix F), the
414 magnitude was moderate (Fig. 3b,d,e). For example, the greatest degree of association between
415 spatial aggregation and lion kill occurrence among these three species was in red hartebeest, with
416 aggregations increasing from ~3 to ~7 individuals on average across the full range of risk (e.g.,
417 the odds ratio of lion kill occurrence in the most dangerous locations was >10 times that of the
418 safest places, Fig. 1, Fig. 3d). Nominal effects of predation risk on ungulate group size have
419 similarly been reported in both experimental (Hunter and Skinner 1998) and observational
420 studies (Valeix et al. 2009b, for exception see Thaker et al. 2010). However, more pronounced
421 risk effects might be expected in systems with non-naïve prey or higher predator densities
422 (Peacor and Werner 2001). For instance, lion density in our study was 0.045 lions/km², which is
423 lower than systems such as Kruger National Park (0.07 lions/km²) or the Serengeti (0.14
424 lions/km²; Hayward et al. 2007c). Similarly, prey response to risk might be more pronounced at
425 finer spatial scales (e.g., when a predator is in the immediate vicinity of prey). Risk effects from
426 wide-ranging carnivores vary over spatial scales (Hebblewhite and Merrill 2007), suggesting
427 that, like many ecological processes, comparisons of risk effects are likely scale-dependent
428 (Levin 1992). Accordingly, our inferences apply at a relatively coarse spatiotemporal scale (i.e.,

429 analogous to Johnson's (1980) second or third order) and do not necessarily preclude stronger
430 risk effects at finer-scales.

431 Our findings highlight the complexity inherent in broad-scale, multi-carnivore, multi-
432 ungulate systems and suggest that understanding the strength and scope of carnivore risk effects,
433 along with associated implications for ungulate demography and ecosystem function, remains a
434 substantial challenge. Moreover, evaluating the numeric prey response to reintroduced predators
435 is also important, both for understanding patterns in ungulate aggregation (Hebblewhite and
436 Pletscher 2002) and predicting the long-term impacts of top predators on trophic interactions
437 (Peterson et al. 2014). Hence, we view our findings of moderate, coarse-grain risk effects on
438 naïve prey over a two-year period as reason to echo the call of Tambling et al. (2012) for robust,
439 long-term monitoring of African carnivore reintroductions in order to place non-lethal behavioral
440 responses within the context of the numeric and functional responses in multi-predator, multi-
441 prey systems. Studies that disentangle the effects of 'risky times' (carnivores in close proximity)
442 and 'risky places' (locations of probable carnivore occurrence or kills) at multiple spatial scales
443 (sensu Johnson 1980) would be particularly insightful. Lastly, we encourage researchers to build
444 upon our study by incorporating explicit measures of forage into evaluations of carnivore risk
445 effects on ungulates.

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615 **SUPPLEMENTAL MATERIAL**

616 **Ecological Archives**

617 Appendices A-F are available online: URL

618 Appendix A. Study area and transect locations.

619 Appendix B. Utilization distributions (UDs) of lions and hyenas.

620 Appendix C. Ungulate aggregation sizes.

621 Appendix D. Lion (*Panthera leo*) kill occurrence model.

622 Appendix E. Spotted hyena (*Crocuta crocuta*) kill occurrence model.

623 Appendix F. Model-averaged coefficients for ungulate aggregation models.

624 Table 1. Models describing aggregation of ungulates exposed to multi-carnivore predation in the
 625 Main Camp section of Addo Elephant National Park, South Africa (2003-2005) after a two-step
 626 information theoretic model selection procedure. Top four models shown for clarity.

	Model covariates [†]	k	ΔAIC_c	w_i
Buffalo	Open	6	0	0.13
	HyenaKill	6	1.23	0.07
	Open + LionKill	7	1.43	0.06
	Null (Intercept only)	5	1.45	0.06
Eland	LionKill + HyenaUD	7	0	0.07
	LionUD + HyenaUD	7	0.35	0.06
	HyenaUD	6	0.42	0.05
	LionKill + LionUD + HyenaUD	8	0.48	0.05
Kudu	Open + Edge + LionKill + LionUD + HyenaKill + HyenaUD	11	0	0.21
	Open + LionKill + LionUD + HyenaKill + HyenaUD	10	0.37	0.17
	Open + Edge + LionKill + HyenaKill + HyenaUD	10	0.79	0.14
	Open + LionKill + LionUD + HyenaUD	9	1.78	0.09
Red	Open + Edge + LionKill + HyenaUD	9	0	0.36
hartebeest	Open + Edge + LionKill + HyenaKill + HyenaUD	10	1.28	0.19
	Open + LionKill + HyenaUD	8	1.7	0.15
	Open + Edge + LionKill + LionUD + HyenaUD	10	2.11	0.13
Warthog	Open + LionKill	7	0	0.28
	Open + LionKill + HyenaUD	8	1.84	0.11

	Open + Edge + LionKill	8	1.93	0.11
	Open + LionKill + LionUD	8	1.94	0.11
Zebra	Open + Edge	7	0	0.2
	Open + Edge + LionKill	8	0.76	0.14
	Open + Edge + LionUD	8	1.49	0.1
	Open + Edge + HyenaKill	8	1.57	0.09

627 *Notes:* k = number of model parameters; w_i = AIC_c weight for the i th model.

628 †Covariate definitions: Open = proportion open habitat, Edge = length of hard edge, LionKill =
 629 odds ratio of lion kill occurrence, LionUD = lion UD percentile, HyenaKill = odds ratio of hyena
 630 kill occurrence, HyenaUD = hyena UD percentile.

631 **FIGURE LEGENDS**

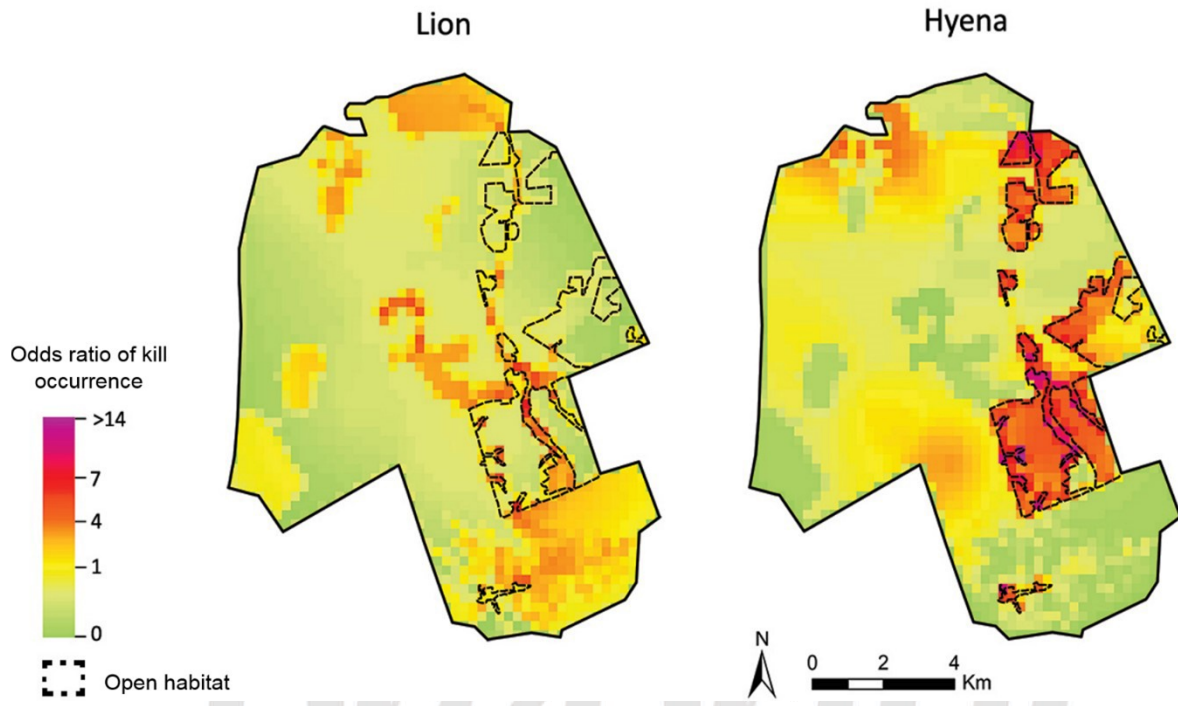
632 Figure 1. Odds ratios of lion and hyena kill occurrence of six ungulate species (buffalo, eland,
633 kudu, red hartebeest, warthog, and zebra) at 250m² resolution in the Main Camp section of Addo
634 Elephant National Park, South Africa (2003-2005). The odds ratio scale of predation applies to
635 both maps, but given the higher prevalence of lion predation, risky areas in the lion map are
636 riskier than similarly colored areas in the hyena map. Green and red/purple areas represent the
637 lowest and highest odds ratios of kill occurrence, respectively. Open habitat is identified by the
638 overlaid dashed polygons; all other habitat was classified as closed.

639 Figure 2. Relative importance of covariates in final model sets describing ungulate aggregation
640 in Addo Elephant National Park, South Africa (2003-2005). The numbers above each bar are
641 relative importance values of a given covariate rounded to two decimal places.

642

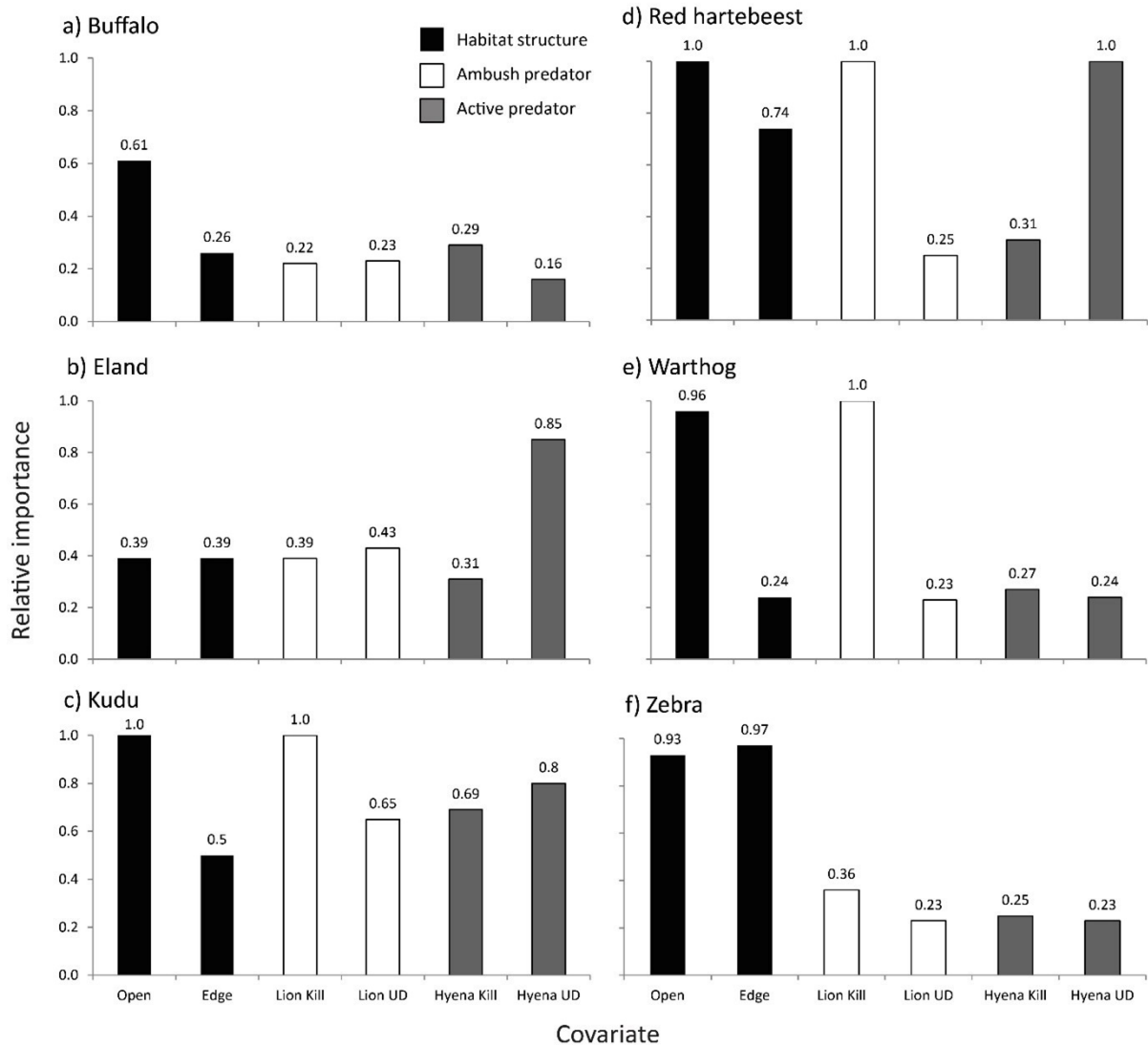
643 Figure 3. Statistically significant ($\alpha \leq 0.01$) spatially-explicit mixed effects regression trends
644 derived from model-averaged coefficients from models describing ungulate aggregation in Addo
645 Elephant National Park, South Africa (2003-2005). Shaded areas represent 95% confidence
646 intervals.

647 Figure 1.



648

649 Figure 2.



650

651 Covariate definitions: Open = proportion open habitat, Edge = length of hard edge, LionKill =

652 odds ratio lion kill occurrence, LionUD = lion UD percentile, HyenaKill = odds ratio of hyena

653 kill occurrence, HyenaUD = hyena UD percentile.

654 Figure 3.

