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Disentangling the roles of bottom-up and top-down drivers in the trade-off between food acquisition and safety in prey with multiple predators

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Authors' contributions

OP, PB, SCJ, MV, PD and HF conceived the ideas and designed methodology;

OP, PB, HF lead the creation of plots and collected data on vegetation;

OP, PB, SP collected data on impalas;

AJL, DWM, SP, EVM collected data on carnivores;

OP, HF analysed the data;

OP led the writing of the manuscript.

All authors have improved the manuscript with significant comments

data availability statement.

Data are available on [doi:10.5061/dryad.b5mkkwhbq](https://doi.org/10.5061/dryad.b5mkkwhbq) (Pays et al. 2020)

Disentangling the roles of bottom-up and top-down drivers in the trade-off between food acquisition and safety in prey with multiple predators

Abstract

1. Prey face a trade-off between acquiring food and avoiding predation, but food availability, and therefore its effect, is rarely measured in field studies investigating non-lethal effects of predation. The main aim of this study is to investigate the role of the presence of predators in the functional adjustments of feeding parameters with patch quality in a medium-size herbivore.

2. In Hwange National Park (Zimbabwe), we set up an experiment by manipulating, over two years, patch quality for impala (*Aepyceros melampus*), a medium-sized herbivore. We assess predation risk by monitoring the presence of three GPS-equipped predators: African lions (*Panthera leo*), spotted hyaenas (*Crocuta crocuta*) and African wild dogs (*Lycaon pictus*).

3. In enriched, fertilised plots the impalas reduced step rates (i.e. the rates of change in feeding stations), and increased their number of bites per feeding station while bite rates were not affected. Thus, the main adjustment of their feeding was the step rate. The total time the impalas spent vigilant appeared to be a good predictor of the variation of their bite rate. Although vigilance caused a reduction in bite rate when at a feeding station, the impalas reduced the relative costs of vigilance by continuing chewing and processing their food when scanning for predators.

23 4. When predators were in the vicinity, the impalas increased their exclusive vigilance
24 (high-cost vigilance) but not their vigilance while chewing (low-cost vigilance) and
25 decreased their bite rate while their step rate and the number of bites per feeding
26 station did not change significantly. The impalas were thus visually disconnected from
27 their patch, and reduced their bite rate when actually foraging. Exclusive vigilance
28 increased when both lions and hyaenas were in the vicinity, and when wild dogs were
29 nearby.

30 5. Patterns of vigilance that altered bite rate were linked to the presence of predators
31 during the previous 24h. Over the long term patch quality was the main determinant of
32 the feeding parameters (step rate and bite rate). This study shows how predators, by
33 affecting the time prey devote to predator detection, shape the functional adjustments
34 of food acquisition by prey to local patch quality.

35 **Key-words**

36 Antipredator response; Feeding rate; Foraging strategy; Herbivore; Patch quality; Risk effect;
37 Savanna; Vigilance

38

39

40 **Introduction**

41 Limitation of populations under natural conditions is driven by both bottom-up and top-down drivers
42 (Sinclair et al. 2000; Shurin et al. 2002; Hayward, O'Brien & Kerley 2007; Hopcraft, Olf & Sinclair
43 2010). Food abundance and quality have been reported to control herbivore biomass (Fritz & Duncan
44 1994) as they affect the physical condition of individuals and thus their capacity to survive and breed
45 (Mduma, Sinclair & Hilborn 1999). The role of predators in the limitation of prey populations through
46 numerical lethal effects (e.g. direct killing) has been demonstrated in numerous studies (Sinclair,
47 Mduma & Brashares 2003; Preisser, Bolnick & Bernard 2005; Heithaus et al. 2009). In addition,
48 antipredator behaviours of prey, such as changes in habitat use (e.g. Werner et al. 1983), changes in
49 temporal niches (Valeix et al. 2009a), vigilance (e.g. Dröge et al. 2017) and foraging strategies (e.g.
50 Barnier et al. 2014), may have energetic (e.g. Kotler, Brown & Bouskila 2004) and physiological
51 consequences (e.g. stress, Boonstra et al. 1998; Creel, Winnie & Christianson 2009), which can
52 adversely affect prey demography (e.g. Lima 1998; Creel & Christianson 2008; Zanette et al. 2011).
53 Although the antipredator responses of prey have been well described (Creel 2018), assessments of
54 the costs of these responses are scarce and little is known about the non-lethal effects of the
55 presence of predators on large mammalian prey populations (Creel et al. 2017, Say-Sallaz et al.
56 2019).

57 Vigilance is one behaviour that is central to the trade-off between food acquisition and
58 safety, and contributes to the indirect impact of predators on the fitness of prey through its link with
59 fitness-enhancing activities (Hopcraft, Olf & Sinclair 2010). Although maintaining high levels of
60 predator detection allows prey to reduce their probability of being killed, this strategy is likely to
61 reduce food acquisition and thus to incur fitness costs (Brown & Kotler 2004). Studies in birds (Fritz,
62 Guillemain & Durant 2002) and mammals (Fortin et al. 2004) have reported that an increase of
63 vigilance significantly reduced feeding efficiency (e.g. instantaneous intake rate) of foragers. This

64 trade-off between foraging costs and vigilance may be critical when food resources are of poor
65 nutritional quality, forcing foragers to maximise their foraging effort.

66 In studies investigating the non-lethal effects of the presence of predators, information on
67 the spatial and temporal variation in food availability for prey is often lacking, particularly in studies
68 of vigilance strategies in free-ranging animals. This makes it difficult or impossible to disentangle the
69 roles played by predation pressure and food quality in shaping the trade-off between food
70 acquisition and predator detection (McNamara & Houston 1994). When food biomass and quality are
71 not measured, it is uncertain whether vigilance behaviour of prey reduces food intake rate up to the
72 point where it jeopardizes fitness, as intake rates vary with patch quality and biomass (Cromsigt &
73 Olff 2006; Owen-Smith, Fryxell & Merrill 2010). Although the foraging strategies of herbivores have
74 been well studied (Spalinger & Hobbs 1992; Wilmshurst, Fryxell & Colucci 1999), the impacts of
75 variations in forage characteristics, particularly when they are seasonally driven, on the foraging
76 costs of vigilance are far from clear (Favreau et al. 2018). For instance, studies of short-grass grazers
77 have shown that higher grass biomasses are generally less digestible (Fryxell 1991), making the
78 relationship between food intake and the greenness and biomass of food (i.e. two proxies of patch
79 quality) complex to understand. However, an increase in vigilance is likely to affect food acquisition
80 differently if the animals are foraging in patches of different forage characteristics and quality: food
81 acquisition is affected by grass height and density (through their effects on bite sizes and rates), and
82 the chemical composition of grass affects its digestibility. Moreover, during antipredator vigilance,
83 many animals, including birds (Baker et al. 2011) and mammals (Blanchard & Fritz 2007), reduce
84 foraging costs by exhibiting vigilance while processing food (e.g. chewing) or moving (Illius &
85 Fitzgibbon 1994; Fortin et al. 2004). Vigilance with chewing contrasts with high-cost vigilance (called
86 exclusive vigilance) during which individuals stop handling food. Thus, the effects of predation risk on
87 food acquisition should be examined with attention to the way these two types of vigilance affect

88 functional adjustments in foraging parameters that influence intake rates (particularly bite rate and
89 step rate) in relation to patch quality.

90 Variations in prey animals' perception of predation risk (such as high vs low risk habitats)
91 affects the time prey allocate to foraging (Winnie & Creel 2007) and food acquisition (Sansom, Lind &
92 Cresswell 2009). Although some studies have investigated responses of prey to a single predator
93 species (Chamaille-Jammes et al. 2014; LaManna & Martin 2016), we know little about the effects of
94 the presence of more than one predator species on vigilance strategies and consequently on food
95 intake rates. Most natural ecological systems are multi-predator systems in which prey can be caught
96 by several predator species (Sinclair, Mduma & Brashares 2003, Thaker et al. 2011, Creel et al. 2017,
97 Montgomery et al. 2019). For a complete understanding of the trade-off between vigilance and food
98 acquisition in these multi-predator systems, it is important to determine how prey alter their intake
99 rate in response to specific predator species and the presence of single versus multiple predator
100 species. Finally, it is uncertain for how long after a predator is near the prey, it affects the trade-off
101 between food acquisition and predator detection by prey particularly when they do not encounter
102 their predators every day (Middleton et al. 2013, Courbin et al. 2016).

103 To examine the role of predators and food quality in shaping the trade-off between food
104 acquisition and predator detection, we studied vigilance and foraging strategies in impala (*Aepyceros*
105 *melampus*), a medium-sized herbivore, in Hwange National Park (HNP), Zimbabwe. Over a two-year
106 period, we used an experiment in which patch quality was manipulated by fertilising and mowing
107 plots in a grassland (cutting stimulates regrowth, Leriche et al. 2003), thus affecting both plant
108 biomass and its quality (the proportion of green plant material). Predation risk was investigated by
109 monitoring the presence of three predators, African lions (*Panthera leo*), spotted hyaenas (*Crocuta*
110 *crocuta*) and African wild dogs (*Lycaon pictus*) marked with GPS-collars.

111 We first assessed how impalas adjusted their feeding behaviour to patch quality (biomass
112 and greenness) controlling for the presence of predators and perceived predation risk (visibility

113 around the individual impalas). Three parameters were used to describe impala feeding behaviour:
114 bite rate, i.e. the number of bites per min, step rate, i.e. the number of steps per min, and the ratio
115 between the number of bites and steps (the number of bites per feeding station), which is an
116 indicator of the number of bites per feeding station. Bite rate can be a proxy of intake rate, as it is
117 highly dependent on the rate of bite encounters, i.e. bite density, and on bite size, since bigger bites
118 take longer to chew hence lowering bite rate. In our study, grass biomass was mostly below 50g/m²
119 (see FigS1 Appendix1). Below this value, medium sized antelopes and gazelles are limited in their
120 adjustment of bite size (Wilmshurst, Fryxell & Colucci 1999; Wilmshurst, Fryxell & Bergman 2000).
121 Thus, bite size can vary but not in relation to patch biomass. Hence, we expected feeding parameters
122 in impalas foraging in our study area to respond more to the proportion of green tissues than
123 variation of grass biomass. This limited possibility to adjust bite size implies that bite rate was a
124 reasonable proxy of intake rate, and this intake rate was more dependent on encounter rate than
125 chewing rate (Process 2 of Spalinger & Hobbs 1992). Step rate while foraging gives an index of the
126 rate of change in feeding stations, with a greater rate of change when grass quality is low. While step
127 rate may affect the bite rates and the local density of acceptable bites, step rate can be influenced by
128 disturbance mechanisms unrelated to food. Thus, one metric that may directly translate the
129 perception of feeding patches giving a better description of the perceived patch quality is the ratio
130 bite rate/step rate (the number of bites per feeding station). If the amount of acceptable bites in a
131 given patch is high, the number of bites per feeding station is high. Thus we predicted that under low
132 predation risk, step rate should decrease with increases in patch quality while bite rate remains
133 stable, resulting in an increase in the number of bites per feeding station with patch quality i.e. in
134 enriched patches of tall grass (Fig 1a).

135 We tested the effects of perceived predation risk (measured by the level of vigilance) and the
136 recent nearby occurrence of predators on the feeding behaviour of impalas (bite rate) and how
137 impalas perceived and used feeding patches (indicated by the number of bites per feeding station).

138 We expected to find one or both of two patterns of adjustment to perceived predation risk (Pattern
139 1.1 and 1.2) and one pattern to the recent nearby occurrence of predators (Pattern 2) which are
140 presented in the Figure 1. Pattern 1.1 and 1.2 result from perceived predation risk that increases the
141 need for low-cost vigilance (while chewing or moving) and causes adjustment of step rate or bite
142 rate, respectively. In Pattern 1.1 the animal maintains selectivity for high quality bites. When the
143 cropping process is interrupted by vigilance before the mouth is full, the individual leaves the
144 partially depleted patch to go to a better patch with higher densities of acceptable bites, thus
145 increasing step rate. It is also consistent with vigilance interruption impairing searching for food
146 items in a partially depleted patch (Fritz et al. 2002). This would lead to a decrease in the number of
147 bites per feeding station mostly induced by higher step rate (Fig 1b). In Pattern 1.2, the animal
148 broadens the acceptability of bites in a given patch to achieve a full mouth before vigilance interrupts
149 it. This implies more bites per patch and smaller distances between bites, therefore higher bite rates,
150 leading to an increase of the number of bites per feeding station because of this increase of bite rate
151 for a given feeding station (Fig. 1c).

152 When predators are actually present, the level of vigilance should be higher for both low and
153 high-cost vigilance (Favreau et al. 2013). We expected a different pattern (Pattern 2) in which the
154 increase of high-cost vigilance visually disconnected the individual from its food patch, inducing a
155 greater cost of searching for acceptable bites. Under this scenario, we expected the number of bites
156 per feeding station to decrease because bite rate decreases (Fig 1d), particularly in the tall grass
157 where searching may be more difficult, but mainly because visibility while foraging with head down is
158 poor and thus perceived as risky (Pays et al. 2012). If the costs of resuming searching for remaining
159 bites is high, then stepping to another feeding station would be an alternative option allowing for
160 vigilance while moving. As in Pattern 1, this would cause an increase in step rate.

161 Previous observations in HNP reported that zebras, *Equus quagga*, encountered lions at night
162 every 35 days on average (Courbin et al. 2016). Thus observations with predators in the vicinity of

163 impalas may be rare compared to the ones without predators. From a statistical standpoint, this may
164 lead to failure to detect an effect of the recent nearby occurrence of collared predators on the
165 behaviours of the impalas. To avoid missing an effect of predation on the trade-off between food
166 acquisition and vigilance, we compared vigilance and bite rates and step rates of focal impalas on
167 days when collared predators had been in the vicinity during the previous 24 hours with observations
168 on days before their arrival (i.e. the preceding 24 hours). We also investigated whether behavioural
169 adjustments were more extreme when more than one predator species was present.

170

171 **Materials and methods**

172 Study site

173 Hwange National Park (HNP) hosts an exceptional diversity of mammals including most of the small
174 to large herbivores and carnivores observed in Southern African savannas (Fritz et al. 2011). The
175 fieldwork was conducted near Main Camp in the north of HNP (19°00'S, 26°30'E). The study site is an
176 open grassland area of 64 ha surrounded by *Acacia* and *Combretum* bushes, typical of the mixed
177 bushed grassland on nutrient-poor soils of the eastern Kalahari sands. Bushes form a natural and
178 visually obstructive boundary of the grassland. The long-term mean annual rainfall is 600 mm and the
179 rainy season occurs between October and April (Chamaillé-Jammes, Fritz & Murindagomo 2006). The
180 fieldwork was conducted from January to August in 2009 and 2010, which received 823.6 mm and
181 935.4 mm of rainfall respectively.

182 The density (\pm SD) of impalas around Main Camp was 1.43 impalas/km² (\pm 0.63) (Chamaillé-
183 Jammes et al. 2009). Impalas are expected to be top-down limited (Hopcraft, Olf & Sinclair 2010) as
184 their body mass averages 45 kg (Cumming & Cumming 2003), i.e. below the 180-200kg threshold
185 under which population dynamics of prey should be controlled by predation (Sinclair, Mduma &
186 Brashares 2003). Impalas are preferred by African wild dogs, cheetahs (*Acynonyx jubatus*), and

187 leopards (*Panthera pardus*) (Hayward & Kerley 2008) and other large carnivores such as spotted
188 hyaenas and lions also feed on impalas (e.g. impalas represent 17% and 8% of the total number of
189 prey found in lion and hyaena scats respectively in HNP (Davidson et al. 2013 and Périquet et al. 2015
190 respectively)). Impalas are mixed feeders and their feeding strategy varies seasonally (Jarman 1974):
191 they are predominantly grazers while grasses are green and growing, and browsers of foliage, forbs,
192 shoots and seedpods at other times. Here, we studied behavioural responses of impalas when they
193 were grazing. Focals when impalas browsed short bushes or trees were excluded from this analysis.

194 From 50 to 150 impalas (mainly adult females and juveniles) foraged each day at the study
195 site. All adult females in the study site formed a single herd (as described in Jarman & Jarman 1973)
196 which divided into a variable number of groups with marked fusion-fission dynamics. It was not
197 possible to capture and mark all individuals in the study population. However, since the year 2000
198 newborn fawns have been captured and tagged on an annual basis, it was possible to regularly
199 observe about 30 ear-tagged adult females. Ear-tagged individuals allowed us to confirm that
200 individuals randomly selected for observations (called 'focals' here) were rarely resampled and the
201 effect of potential pseudo-replication is therefore negligible.

202

203 Ethical Statement

204 The experiments complied with the laws (including animal welfare ethics) of Zimbabwe. They were
205 approved and conducted under permits from the Director General of the Zimbabwe Parks and
206 Wildlife Management Authority (Ref: DM/Gen/ (T), Permit numbers: 23(l) (c) (ii): 01/2009 and
207 01/2010 for the impala behavioural study and hyaena collaring, 03/2009 and 25/2010 for lion
208 collaring, and 09/2009 and 07/2010 for wild dog collaring). The long-term individual-based study on
209 impala population dynamics in HNP started in 2000 under permits from the same authorities cited
210 above.

211

212 Experimental design

213 We manipulated the impalas' food resources by spreading common fertiliser for pasture (N: 3.5%,
214 P₂O₅, 24.4%, S: 11.0% and Zn: 0.5%, at 70kg/ha) and by mowing (cutting) grass to increase both the
215 biomass and the proportion of grass that was green (and thus high quality) since herbivores select for
216 green tissues (e.g. Murray & Baird 2008). Four enriched and four control plots (60 × 120m), all
217 including strips of cut and uncut grass, were created at different distances from cover (Fig 2).
218 Fertilisation and mowing were performed in January 2009 and 2010, two weeks before the beginning
219 of the behavioural studies. We confirmed that fertilisation and mowing changed grass availability and
220 quality by measuring grass biomass, greenness and bare soil in all plots (192 samples in 2009 and 353
221 in 2010 for the three cited variables). Grass biomass was measured using a previously calibrated disk-
222 pasture meter and the proportion of green tissues and the average grass cover were estimated
223 visually by using photographs (as in Vanha-Majamaa et al. 2000, see Pays et al. 2012 for details, and
224 see Appendix 1 for statistical details and variations among seasons and between years and the
225 effects on patch quality). On average, during the 2-year experiment, biomass was 30% higher in
226 enriched plots compared to control plots in uncut strips while we did not detect any significant
227 difference in cut strips. The proportion of green tissues was 25 % higher in enriched plots than in
228 control plots in cut strips and 13% higher in uncut strips. In cut and uncut strips, the proportion of
229 bare soil was on average 17% lower in enriched plots compared to control plots.

230

231 Recording behaviour

232 We studied vigilance and foraging behaviours of impalas by videotaping focal adult females only
233 (hence avoiding adding sex-age effects), for 5-min periods chosen at random during the daytime
234 from February to August. Juveniles were present in all groups; it was not possible to say at which

235 female each juvenile belonged to. We filmed individuals in groups whose predominant activity during
236 the video sequence was grazing. 5-min focals were sufficient to obtain sequences during which both
237 foraging and vigilance behaviours could be studied. In total we recorded 740 sequences: 532 in 2009
238 and 208 in 2010.

239 Observations were made from vehicles, maintaining a minimum distance of 100m between
240 the focal group and the observer to minimize disturbance. When several individuals were filmed
241 during the same day, the observer took care to avoid filming the same individuals to ensure
242 independence between observations. Finally, it was crucial that animals did not move long distances
243 (i.e. stayed in the same ecological conditions) during the 5-min video sequences to ensure that food
244 biomass and quality remained approximately stable during the focal. So we rejected focals during
245 which the individual left the plot and did not forage in the same mowed or uncut strips during the 5
246 min video sequence. We sampled 163 impalas foraging inside enriched plots, 58 in control plots and
247 519 outside plots (Fig 2c). We considered data collected outside plots as uncut controls.

248 An impala was considered vigilant when it raised its head above the horizontal, scanning its
249 surroundings, without moving its feet. Previous studies have shown that impala often chew when
250 vigilant, but it is assumed that this multitasking might reduce their ability to hear approaching
251 predators. Impalas have indeed been observed to stop chewing when hearing a threatening stimulus
252 (Blanchard & Fritz 2007; Favreau et al. 2013). Thus, we extracted the total time an individual spent in
253 vigilance, distinguishing high-cost vigilance when impalas stopped chewing their bites while vigilant
254 and low-cost vigilance when they continued chewing. From each focal, we also recorded when
255 individuals moved their left front leg to calculate the step rate and when they took a bite (easily
256 recognizable by jerky head movements) to calculate the bite rate. We then calculated the number of
257 bites per feeding station.

258 The observer recorded date, time of day and the location of the focal females on a field map.
259 Visibility around foraging individuals was categorized based on the height of the grass (Grass height),

260 which was visually estimated and classified in four classes: *short* when grass height was not above
261 the focal impala's hooves distinguishing between cut (*short cut*) and uncut (*short uncut*) strips,
262 *medium* when it was below the upper part of the impala's metacarpals, and *high* when it reached the
263 impala's tibia. In tall grass, how easily the focal impala could see the potential predators was
264 assumed to be strongly limited. The position of the individuals within a group (i.e. peripheral or
265 central) was impossible to determine during the video sampling because the animals moved
266 constantly when foraging. Although distance to cover was assessed through three classes: ≤ 50 , 50-
267 100, and >100 m, we did not detect any effect of this variable on any of the vigilance and foraging
268 behaviours of impalas (Chi-square tests, all $P > 0.54$), probably because we included plot identity as a
269 random factor and plots were set up at different distances to cover. Moreover, although group size
270 was assessed during video sampling, we did not detect any effect of the log-transformed group size,
271 considering the two way interactions on any feeding parameters (Chi-square tests, all $P > 0.080$) and
272 vigilance activities (Chi-square tests, all $P > 0.071$), probably because the range of group size was not
273 great enough since we avoided small group sizes (the mean group size (\pm SD) = 41.74 ± 32.70 , range
274 from 10 to 108 individuals). Thus, we did not consider these two variables in the final analyses.

275

276 Carnivore data

277 Long-term GPS-tracking studies of large carnivores in HNP allowed us to investigate how the
278 presence of carnivores influenced impala foraging behaviour. During the study period, 7 lions in
279 different groups (2 female adults from 2 different prides and 5 male adults from 5 different
280 coalitions), 5 spotted hyaenas distributed in 2 clans, and 2 wild dogs representative of 2 clans of 5
281 and 7 individuals were tracked around the study site, which they did use. Given the size of the
282 different predator groups, this leads to the following proportions of collared individuals for the local
283 populations of lions, wild dogs and hyaenas respectively: 0.50, 0.20, and 0.17. Collared individuals
284 visited the study site in 2009 and 2010 occasionally or regularly. We assumed that these individuals

285 were representative of the movements of their groups at least for lions (Valeix et al. 2009b) and wild
286 dogs (van der Meer 2011) (see Appendix 2 for more details). Although other predator species were
287 not collared, visits of cheetah and leopard were rarely observed during the study. We therefore
288 assumed that predation pressure at the study site was mainly driven by the three monitored
289 predator species. Because lions and hyaenas are active mainly at night and move little during the
290 day, GPS locations were acquired every hour from 18h to 6h hours, plus two fixes during the day. For
291 wild dogs, GPS locations were acquired every 100 minutes day and night (see van der Meer 2011;
292 Benhamou et al. 2014; Périquet et al. 2015 for details on captures and GPS-collars of wild dogs, lions
293 and hyaenas respectively). From GPS coordinates of collared predators, we determined whether
294 predators occurred in the vicinity of the focal impalas (i.e. within a radius of 2 km centred around the
295 focal impala) in the 24 hours preceding the focal. A previous study in the same area reported that
296 vigilance of prey including impala was affected by predators at this 2 km threshold (Périquet et al.
297 2012). Predators were present within 2 km of the focal impalas in 127 of the 740 video sequences,
298 including 97 sequences with lion only, 19 with wild dog only and 11 with both lion and hyaena. As we
299 observed only hyaenas only once, and the combination wild dog with lions only once, we discarded
300 these two sequences for the analyses.

301

302 Data analysis

303 Functional adjustment of foraging

304 We fitted linear mixed effect models to test for the effect of food quality or quantity on the
305 variations in bite rate. We included plot enrichment (whether the impala foraged on control or
306 enriched plots), grass height (contrasting the four classes, i.e. high, medium, short uncut, short cut),
307 predator within 2 km (whether GPS-collared predators were present in the 2 surrounding km in the
308 preceding 24 hours, i.e. no or yes) and two two-way interactions as independent variables:

309 $w(x) = \beta_0 + \beta_1(\text{Plot enrichment}) + \beta_2(\text{Predator within 2 km}) + \beta_3(\text{Grass height}) + \beta_4(\text{Plot enrichment} \times$
310 $\text{Predator within 2km}) + \beta_5(\text{Predator within 2km} \times \text{Grass height})$ (1)

311 With $w(x)$, the response variable (e.g. bite rate), β_0 , the intercept and β_k the coefficient estimated for
312 each predictor x_k . Because of the mowing of the grass, the two-way interaction Plot enrichment \times
313 Grass height could not be considered in the models. We included year (contrasting 2009 and 2010),
314 season (contrasting three periods i.e. Feb.-March, April-May or July-Aug.) and plot identity as nested
315 random factors to control for time and spatial correlations that might occur in the data set. To
316 capture the sequential structure of the data set, we converted the dates of focals to Julian days
317 cumulated over the two years and applied an autocorrelation function of order 1 using the function
318 *corAR1*. We tested the effect of each variable using likelihood ratio tests (i.e. χ^2). We used post-hoc
319 Tukey tests for multiple comparisons when necessary. The same procedure was applied to the log-
320 transformed step rate and the number of bites per feeding station. We paid special attention to
321 check the normality of residuals, the distribution of residuals against fitted values and the lack of
322 sequential autocorrelation in residuals (see Appendix 4).

323

324 Trade-offs between bite rate, the number of bites per feeding station and vigilant behaviour

325 To investigate how investment in vigilance affected bite rate in these impalas, we fitted linear mixed-
326 effect models including total time in vigilance as the predictor and bite rate as the dependent
327 variable. We log-transformed the total time spent in vigilance to achieve statistical requirements on
328 model's residuals:

329 $w(x) = \beta_0 + \beta_1(\text{Log}(\text{Total vigilance}))$ (2)

330 With $w(x)$, the response variable (e.g. bite rate), β_0 , the intercept and β_1 , the coefficient derived for
331 the predictor. Year, season and plot identity were included as nested random factors and an
332 autocorrelation function of order 1 on Julian day as described earlier. The same procedure was used

333 to test the effect of vigilance on the number of bites per feeding station and the effect of low and
334 high-cost vigilance on bite rate and the number of bites per feeding station.

335

336 Effect of the presence of collared predators in the surroundings

337 Although Eq. 1 allowed us to examine whether predator presence affected foraging and vigilance
338 over the whole period, we ran the same model (Eq. 1) comparing focals when collared predators
339 were in the surroundings in the 24h preceding the focals (N = 127) with focals the day before their
340 arrivals (N = 69). We used linear mixed-effect models including year and season as nested random
341 factors. To compare focals belonging to the same event, we created a variable called *predator event*
342 *identity* allowing focals during which a collared predator was present to be linked to focals collected
343 the day before their arrival and included it as a random factor nested into year and season. We
344 applied the same autocorrelation function of order 1 on the Julian day as described earlier. We
345 tested the effect of each variable using likelihood ratio tests (i.e. χ^2). The residuals of the model were
346 analysed and they fulfilled statistical requirements (see Appendix 4). The same procedure was
347 applied on bite rate, the log-transformed step rate and the number of bites per feeding station.

348 Finally, we tested for differences in vigilance including high and low-cost vigilance (log-
349 transformed), bite rate, the log-transformed step rate and the number of bites per feeding station
350 between different categories of predation risk within the surrounding 2km (lion only, wild dog only vs
351 lion with hyaena) using linear mixed effects models including predator species within 2 km and grass
352 height and including year, season and predator event identity as nested random factors:

$$353 \quad w(x) = \beta_0 + \beta_1(\text{Predator species within 2 km}) + \beta_3(\text{Grass height}) \quad (3)$$

354 With $w(x)$ as bite rate, the log-transformed step rate and number of bites per feeding station, β_0 , the
355 intercept and β_k the coefficient derived for each predictor x_k . The size of the data set did not allow us
356 to test for the effect of two-way interactions with each type of collared predator on foraging

357 parameters and vigilance, as each type of predator was not observed in each class of grass height.
358 We applied the same autocorrelation function of order 1 on the Julian day as described earlier. The
359 residuals of the model were analysed and they fulfilled statistical requirements.

360 Statistical analyses were performed using R 3.6.2 (R Development Core Team 2019). Models
361 were performed with the *nlme* package (Pinheiro et al. 2019) and multiple comparisons with the
362 *lsmeans* package (Lenth 2016).

363

364 **Results**

365 Functional adjustments of foraging parameters

366 On average, bite rate, step rate and the number of bites per feeding station (mean \pm SD) in impalas
367 foraging in our study area were 30 ± 9.60 , 4.5 ± 3.60 , and 15 ± 20 respectively. Plot enrichment and
368 grass height affected certain foraging parameters of these impalas. As expected, bite rate declined in
369 taller grass (22% reduction between tall and short cut grass, Fig. 3a), with the highest values when
370 impalas foraged in short cut strips (Table 1). We did not detect any significant effect of plot
371 enrichment on bite rate (Table 1), but step rate was lower by 27% and the number of bites per
372 feeding station higher by 18% in enriched than in control plots (Fig. 3b,d). On average, step rate
373 declined in the tall grass by 12% (Table 1, Fig. 3c) although we did not detect any difference between
374 medium and short- grass height for step rate (Appendix 3 for multiple comparisons). Contrary to step
375 rate, the number of bites per feeding station increased in tall grass by 53% (Table 1, Fig. 3e) with no
376 difference between medium and short grass height (Appendix 3). To conclude, when plot enrichment
377 increased patch quality (see Appendix 1), impalas reduced their step rate by 1 step per minute on
378 average and gained 3 bites per feeding station.

379

380 Trade-offs between bite rate, the number of bites per feeding station and vigilance

381 The impalas spent on average (\pm SD) 15% (\pm 13) of their foraging time in vigilance with 22% (\pm 20) of
382 their total vigilance spent in high-cost vigilance. Thus, while vigilant, individuals mostly continue
383 chewing and processing their food. Bite rate decreased with the log-transformed time spent in
384 vigilance ($\beta \pm$ SE = -11.213 ± 0.611 , $\chi^2 = 273.044$, df = 1, $P < 0.001$, pseudo $R^2 = 0.35$), high-cost
385 vigilance ($\beta \pm$ SE = -3.450 ± 0.289 , $\chi^2 = 131.586$, df = 1, $P < 0.001$, pseudo $R^2 = 0.16$) and low-cost
386 vigilance ($\beta \pm$ SE = -6.788 ± 0.631 , $\chi^2 = 100.988$, df = 1, $P < 0.001$, pseudo $R^2 = 0.18$). Figure 4 shows
387 that when individuals invested a lot in vigilance to detect predators (for instance 66% of their
388 foraging time, i.e. $\log(2.4)$), impalas could lose up to 20 bites per minute, falling from 40 to 20.

389 The number of bites per feeding station also decreased with the log-transformed time spent
390 in vigilance ($\beta \pm$ SE = -0.134 ± 0.033 , $\chi^2 = 16.045$, df = 1, $P = 0.001$, pseudo $R^2 = 0.01$) and high-cost
391 vigilance ($\beta \pm$ SE = -3.450 ± 0.289 , $\chi^2 = 42.007$, df = 1, $P < 0.001$, pseudo $R^2 = 0.05$) whereas low-cost
392 vigilance had no effect ($\chi^2 = 0.725$, df = 1, $P = 0.394$). Despite the significant patterns, the pseudo R^2
393 were low and the investment in vigilance was not a good predictor of the number of bites per
394 feeding station.

395

396 Effect of the presence of collared predators in the surroundings

397 Collared predators were present in the surroundings (within 2km) during 18 days of the 114 days of
398 data collection. Contrasting focals during these 18 days with the ones from the day before the
399 predator's arrival (controls) and controlling for the effects of grass height, showed that the presence
400 of collared predators (regardless of species) affected bite rate but did not affect step rate or the
401 number of bites per feeding station (Table 2). On average, impalas lost about 4 bites per minute
402 when predators were in the surroundings (14% reduction) with no difference of bite rate between a
403 single predator species or multi-predator species ($\chi^2 = 1.999$, df = 2, $P = 0.368$). Finally, the presence

404 of collared predators affected both the total time spent in vigilance and high-cost vigilance (Table 3)
405 but did not affect low-cost vigilance ($\chi^2 = 1.986$, $df = 2$, $P = 0.370$). Compared to days before the
406 predator's arrival (controls), impalas were more vigilant and increased their high-cost vigilance when
407 wild dogs were in surroundings by 101% and 167% respectively and when both lions and hyaenas
408 were present by 116% and 355% respectively although we did not detect any significant difference
409 when only lions were present (Table 4, Fig. 5).

410

411 **Discussion**

412 Functional adjustment of foraging parameters

413 As reported in other species of herbivores including warthog (*Phacochoerus aethiopicus*) and
414 white rhinoceros (*Ceratotherium simum*) (Cromsigt & Olf 2006), our study shows that local
415 patch quality shapes the feeding strategy of impalas. In enriched plots, impalas reduced their
416 step rate, the rate of change in feeding stations, and increased their number of bites per
417 feeding station while bite rate was not affected. The main adjustment parameter for the intake
418 rate is therefore step rate. By adjusting step rate to maintain bite rate, hence presumably intake
419 rate, impala decreased the number of bites per feeding station in control plots (for enrichment,
420 Fig. 3d) i.e. in places where there was a smaller proportions of green material. This analysis
421 of feeding parameters from the experimental plots suggests that intake rate is limited by the
422 encounter rate of acceptable bites, as occurs in the Process 2 in the theoretical framework of
423 Spalinger and Hobbs (1992). This result is consistent with both our prediction of the selective
424 feeding strategy in such medium-sized ruminants (see Fig. 1a) and other studies in the same
425 species (Fritz & de Garine-Wichatitsky 1996). Our results suggest that for medium-sized and
426 large herbivores that use step rate as an adjusting parameter of intake rate, individuals may

427 use low-cost vigilance (i.e. vigilance while chewing or moving) to minimise cost of predator
428 detection (Blanchard & Fritz 2007).

429 Grass height commonly shapes feeding parameters (e.g. bite size), and hence food
430 intake rate in grazing herbivores (Arsenault & Owen-Smith 2008). Our results show that in
431 tall grass bite rate and step rate were low and the number of bites per feeding station was high
432 indicating that the amount of acceptable bites was high in patches of tall grass. For a selective
433 herbivore like impala, the difficulty in finding high quality green blades in tall grass may lead
434 individuals to reduce their speed when they forage in tall patches when predators are absent.
435 However, as visibility around them is low, individuals may also reduce speed as the
436 perception of predation risk is high, investing more in vigilance (Pays et al. 2012). Thus more
437 studies are needed to clarify the functional adjustments with grass height in the trade-off
438 between feeding and detection of predators.

439 To improve patch quality, besides fertilization, we mowed grass to stimulate regrowth
440 and thus increase the availability of green leaves. Our results show that bite rate, step rate and
441 the number of bites per feeding station did not change significantly between short mown and
442 naturally short grasses. The impalas responded clearly to fertilisation particularly when they
443 foraged in tall grass. However, the effect of mowing on their feeding behaviour was not
444 significant. Indeed, although the percentage of green material was higher in cut strips, the
445 difference in biomass between cut (mown) and uncut strips was small, particularly in 2010,
446 even in fertilised plots (Appendix 1) and might have therefore limited the opportunity to
447 detect an effect of mowing on foraging.

448

449 Trade-offs between bite rate, the number of bites per feeding station and vigilance
450 Both high and low-cost vigilance have been examined here, and the total time spent in
451 vigilance was the best predictor of the variation in bite rate. Vigilance altered bite rate (and

452 potentially intake rates) as reported in previous studies (Fortin et al. 2004), although it had no
453 effect on the number of bites per feeding station. When at a feeding station, impalas reduced
454 the relative costs of vigilance by continuing chewing and processing their food (Pays et al.
455 2012). Our results show that impalas spent around 80% of their vigilance time in low-cost
456 vigilance, indicating how individuals can considerably reduce the potential costs of predator
457 detection when they are foraging.

458 Feeding with larger bites could mitigate foraging costs of vigilance in grazing
459 herbivores (see Spalinger & Hobbs 1992, and Wilmshurst et al 1999 for an example in
460 gazelles). Larger bites would induce longer chewing bouts, increase spare time and allow
461 individuals to use low-cost vigilance for longer periods. However, in our study, grass biomass
462 was mostly below the optimal value for impala (see Introduction) and it is unlikely that patch
463 biomasses on this site allowed individuals to take larger bite sizes. Our results suggest that
464 step rate was the adjusting parameter of intake rate, so we expect impalas to increase their
465 step rate between two feeding stations to improve bite quality (i.e. to detect patches with more
466 green tissues) and to increase encounter rates (Spalinger & Hobbs 1992). Finally, although we
467 did not detect a group-size effect on foraging and vigilance activities (as we mostly sampled
468 individuals in large groups), it has been commonly reported in gregarious species (Jarman
469 1974), including impalas (Pays et al. 2012), that individuals forage in large groups to reduce
470 foraging costs of vigilance and reallocate the time for predator detection to foraging
471 (FitzGibbon 1989, 1990).

472

473 Effects of the presence of predators and perceived predation risk

474 Creel et al. (2014) analysed the variation of antipredator behaviours and their foraging costs in
475 five ungulates (zebra, *Equus quagga*, Grant's gazelle, *Nanger granti*, wildebeest,
476 *Connochaetes taurinus*, impala and giraffe, *Giraffa camelopardalis*) in response to the

477 presence of lions and spotted hyaenas in the surroundings. They found that the increase of
478 vigilance in response to the presence of predators triggered a large reduction in time spent
479 foraging in four species including impala but not in wildebeest. In our study, we show that in
480 response to the presence of collared predators, impalas 1) were more vigilant, increasing their
481 exclusive (i.e. high-cost) vigilance and 2) on average they reduced bite rate while maintaining
482 their step rate and the number of bites per feeding station. These results suggest that the
483 presence of predators leads individuals to use more vigilance, which visually disconnects
484 foragers from their food and leads to lower bite rates (Fig. 1d). Thus our results may apply to
485 other herbivore prey species in which an increase in vigilance is likely to affect food
486 acquisition. This is particularly expected in tall grass where both bite rate and visibility are
487 low for individuals foraging head down. However, in tall grass bite rate and step rate were
488 low while the number of bites per feeding station was high, our results therefore fully support
489 the expected Pattern 2 as the decrease in bite rate did not lead to a decrease of the number of
490 bites per feeding station when predation risk was high. Finally, our results did not support the
491 hypothesis under which perceived predation risk would increase the need for low-cost
492 vigilance hence reduce the number of bites per feeding station (Pattern 1.1, Fig 1b) or broaden
493 the acceptability of bites in a given patch, leading to an increase of the number of bites per
494 feeding station (particularly in short grass) (Pattern 1.2, Fig 1c).

495 Several studies have reported that prey exhibit a large range of proactive behavioural
496 strategies including adjustment of space use, group size and time spent in risky habitat to
497 decrease overall predation risk and to invest in fitness-enhancing activities such as foraging
498 (Valeix et al. 2009b, Basille et al. 2015, Courbin et al. 2019). The interaction between
499 vigilance and proactive space use is complex and might make applying predictions to other
500 systems difficult (Patin et al. 2019). In addition, other studies have shown that prey can
501 reactively adjust their space use (Middleton et al. 2013, Courbin et al. 2016) or increase their

502 time allocated to vigilance in response to cues of predation risk (Pays et al. 2013, Dannock et
503 al. 2018), as was the case when impalas were stimulated by lion roars (Favreau et al. 2013) or
504 faeces of wild dogs (van der Meer, Fritz & Pays 2015). We show here that impalas increased
505 their vigilance by increasing their high-cost vigilance when two predators (i.e. lion with
506 hyaena) or when wild dogs were in the surroundings. Although our data on hyaenas did not
507 allow us to examine focals with only hyaenas in the surroundings, our results show that the
508 largest increase of high-cost vigilance in impalas was observed when two predators (lions and
509 hyaenas) were present at the same time in the surroundings. As the increase of vigilance with
510 lions only in the surroundings was small, we might expect that the presence of hyaenas
511 affected the vigilance of impalas. Overall, our results suggest that although impala is the main
512 prey of African wild dogs (Hayward & Kerley 2008, van der Meer et al. 2014), the presence
513 of two predators at the same time may be perceived as the most important threat. Although
514 our data did not allow us to investigate finer time and spatial scales (due to sample size
515 constraints), it would be very interesting to test for behavioural adjustments to predation risk
516 at other time lags.

517 Analyses over the whole study show that patch quality is the main determinant of
518 feeding parameters (step rate and bite rate). However, these impalas do respond to predators
519 in their vicinity by increasing their vigilance, and this reduced bite rate. This effect was clear
520 only when we compared focal samples from the 24 hour periods when predators were nearby
521 with focals from the days before. Although our experimental design focused on a large herd
522 of impalas (up to 150 individuals) foraging in one grassland area where many predators were
523 collared, some individual impalas may have been affected by uncollared predators. Our study
524 highlights the need to conduct fine scale analyses in order to understand the effect of patch
525 quality and predators on the trade-off between food acquisition and predator detection. In this
526 context, an important aspect of understanding the effect of the predators on feeding

527 parameters and ultimately the foraging costs of vigilance in prey is the frequency of
528 encounters of the prey with the predator. We suggest that this time scale issue merits specific
529 attention in future studies.

530

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Table 1. Factors influencing the bite rate (bite per minute), step rate (step per minute, log-transformed) and number of bite per step (Log-transformed) of impalas over the 2-year period $\beta \pm SE$ are indicated for significant variables. *Plot enrichment* indicated whether the impala foraged on control or enriched plots, *Predator within 2 km* indicated whether GPS collared predators were present within 2km (no and yes), grass height contrasted 4 classes (High, medium, short, short cut) and Log Group Size was the log-transformed group size in which the focal impala was studied with classes in italics that were considered as references in the linear mixed-effects model including Year, Season and Plot ID as nested random factors.

Dependant Variables	Predictors	χ^2	Df	P	$\beta \pm SE (P)$
Bite rate					(intercept: 30.944 \pm 1.392)
	Plot enrichment	0.023	1	0.878	
	Predator within 2km	1.1908	1	0.167	
	Grass height	14.106	3	0.003	Medium: 1.461 \pm 0.789 (0.065) Short: 4.060 \pm 1.409 (0.005) Short cut: 3.073 \pm 1.327 (0.021)
	Plot enrichment \times Predator within 2km	1.025	1	0.599	
	Predator within 2km \times Grass height	6.079	3	0.108	
Log (Step rate)					(intercept: 0.429 \pm 0.061)
	Plot enrichment	2.709	1	0.033	Enriched plot: -0.080 \pm 0.035
	Predator within 2km	0.003	1	0.957	
	Grass height	23.522	3	<0.001	Medium: 0.104 \pm 0.032 (0.001) Short: 0.195 \pm 0.054 (<0.001) Short cut: 0.186 \pm 0.053 (<0.001)
	Plot enrichment \times Predator within 2km	3.732	1	0.155	
	Predator within 2km \times Grass height	5.170	3	0.160	
Log (Bites per feeding station)					(intercept: 1.028 \pm 0.053)
	Plot enrichment	4.234	1	0.039	Enriched: 0.128 \pm 0.054
	Predator within 2km	0.279	1	0.598	
	Grass height	12.776	3	0.005	Medium: -0.117 \pm 0.037 (0.002) Short: -0.116 \pm 0.062 (0.060) Short cut: -0.147 \pm 0.058 (0.013)
	Plot enrichment \times Predator within 2km	5.119	1	0.078	
	Predator within 2km \times Grass height	6.346	3	0.096	

Table 2. Factors influencing the bite rate (bites per minute, BR), step rate (steps per minute, log-transformed, SR) and number of bites per step (log-transformed, B/S) of impalas when comparing the behaviour of focals when GPS collared predators were present and the day before the arrival of the predators. $\beta \pm SE$ are indicated for significant variables. Plot enrichment indicates whether the impala foraged on *control* or enriched plots, predator within 2 km indicates whether GPS collared predators were present within 2km of the impalas (*no* and *yes*), grass height contrasts 4 classes (*High*, medium, short, short cut) and Log Group size is the log-transformed group size in which the focal impala was studied with classes in italics that were considered as references in the linear mixed-effects model including Year, Season and Predator event ID as nested random factors.

Dependant Variables	Predictors	χ^2	Df	P	$\beta \pm SE$ (P)	
					(intercept: 30.610 \pm 1.281)	
Bite rate	Plot enrichment	1.354	1	0.245		
	Predator within 2km	7.080	1	0.008	Yes: -3.559 \pm 1.177	
	Grass height		11.904	3	0.008	Medium: 1.860 \pm 1.321 (0.161)
						Short: 6.252 \pm 2.430 (0.011)
						Short cut: 9.258 \pm 2.232 (<0.001)
	Plot enrichment \times Predator within 2km	0.147	1	0.701		
	Predator within 2km \times Grass height	6.221	1	0.101		
					(intercept: 0.548 \pm 0.084)	
Log (Step rate)	Plot enrichment	2.013	1	0.154		
	Predator within 2km	0.596	1	0.440		
	Grass height	0.618	3	0.893		
	Plot enrichment \times Predator within 2km	0.009	1	0.925		
	Predator within 2km \times Grass height	4.836	1	0.180		
					(intercept: 0.929 \pm 0.110)	
Log (Bites per feeding station)	Plot enrichment	0.574	1	0.449		
	Predator within 2km	0.181	1	0.671		
	Grass height	1.601	3	0.659		
	Plot enrichment \times Predator within 2km	0.013	1	0.910		
	Predator within 2km \times Grass height	4.797	1	0.187		

Table 3. Effect of the presence of a GPS-collared predator within the 2km surroundings when comparing focals on days when collared predators had been in the vicinity during the previous 24 hours with observations on days before their arrival on the log-transformed total time spent in vigilance (Total vigilance) and exclusive (high-cost) vigilance of impalas considering the effects of grass height (High, medium, short, short cut). We contrasted 4 classes (days before predators had been in the vicinity, lion only, wild dog only, lion with hyaena) with in italics, classes that were considered as references. Year, Season and Predator event ID were included as nested random factors. $\beta \pm SE$ are indicated for significant variables.

Dependent variables	Predictors	χ^2	Df	P	$\beta \pm SE$ (P)
					(intercept: 1.603 \pm 0.119)
Log total vigilance	Predator within 2 km	7.192	2	0.027	See table 4 for multiple comparison
	Grass height	5.245	3	0.157	
					(intercept: 0.188 \pm 0.122)
Log exclusive vigilance	Predator within 2 km	7.180	2	0.028	See table 4 for multiple comparison
	Grass height	1.605	3	0.658	

Table 4. Post-hoc Tukey test on the effect of the presence of GPS-collared predators within 2km, contrasting 4 classes (days before the predators' arrival, lion only, wild dog only vs lion with hyaena) on the log-transformed total time spent in vigilance (Log Total Vigilance) and high-cost vigilance (Log Exclusive Vigilance). The data on hyaenas were too sparse to allow the effect of this species to be analysed alone.

Contrast	Log(Total vigilance)			Log(Exclusive vigilance)		
	B	SE	P	β	SE	P
Lion only - Days before	0.131	0.071	0.070	0.377	0.253	0.138
Wild dog only - Days before	0.332	0.118	0.005	0.960	0.558	0.046
Lion with hyaena - Days before	0.476	0.148	0.002	1.023	0.317	0.001
Wild dog only - Lion only	0.220	0.114	0.041	0.261	0.245	0.288
Lion with hyaena - Lion only	0.344	0.145	0.018	0.908	0.311	0.004
Lion with hyaena - Wild dog only	0.144	0.172	0.404	0.647	0.370	0.082

Figure legends

FIGURE 1 Expected variations of functional parameters of feeding behaviour in impala with patch quality (as indicated by the interaction between grass height and enriched), and predation risk. BR is bite rate, i.e. the number of bites per min, SR is step rate, i.e. the number of steps per min, and B/S is the number of bites per feeding station i.e. the ratio between the number of bites and steps. The arrows and grey lines indicate how an individual would be expected to adjust its functional parameters of feeding behaviour to an increase of predation risk (see Introduction for more details on expected mechanisms): (a) when predation risk is low, the number of bites per feeding station increases with patch quality; (b) when perceived predation risk increases, the time spent grazing decreases so does the number of bites per feeding station at a feeding station (Pattern 1.1) or (c) increases the acceptability of bites (and thus the number of bites per feeding station) at the feeding station (Pattern 1.2); (d) when predators are present leading to an increase of high-cost vigilance altering the number of bites per feeding station (Pattern 2).

FIGURE 2 Experimental design for manipulating the quality of feeding patches for free-ranging impalas in Hwange National Park, Zimbabwe. (a) and (b) the location of our study area, (c) an overview of the experimental design, (d) plot features and (e) an aerial photograph of one plot.

FIGURE 3 Effect of patch quality on foraging parameters of impala over the 2-year experiment: (a) the effect of grass height on bite rate, (b) the effect of plot enrichment and (c) the effect of grass height on the log-transformed step rate, (d) the effect of plot enrichment and (e) the effect of grass height on the log-transformed bites per step. Lines of box plots indicate the lower quartile (25%), median in bold (50%) and upper quartile (75%). The black dot within the box indicates mean value.

Whiskers indicate the minimum and maximum values excluding outliers (open dots). Outliers are values less than 1.5 times the lower quartile and more than 1.5 times the upper quartile.

FIGURE 4 Trade-off between investment in vigilance and food acquisition in impalas. This trade-off is represented by the decrease of bite rate with the log-transformed time spent in vigilance in impala over the 2-year experiment.

FIGURE 5 Effect of the presence of GPS collared predators on investment in vigilance in impalas. The analysis contrasted focals sampled during days with predators and the ones sampled the day before the predators' arrival (called days before) distinguishing when lion, wild dog and both lion and hyaena were present within a 2km radius around the focal impala. See title of Fig. 3 for details on features of box plots. The data on hyaenas were too sparse to allow the effect of this species to be analysed alone.

Figure 1

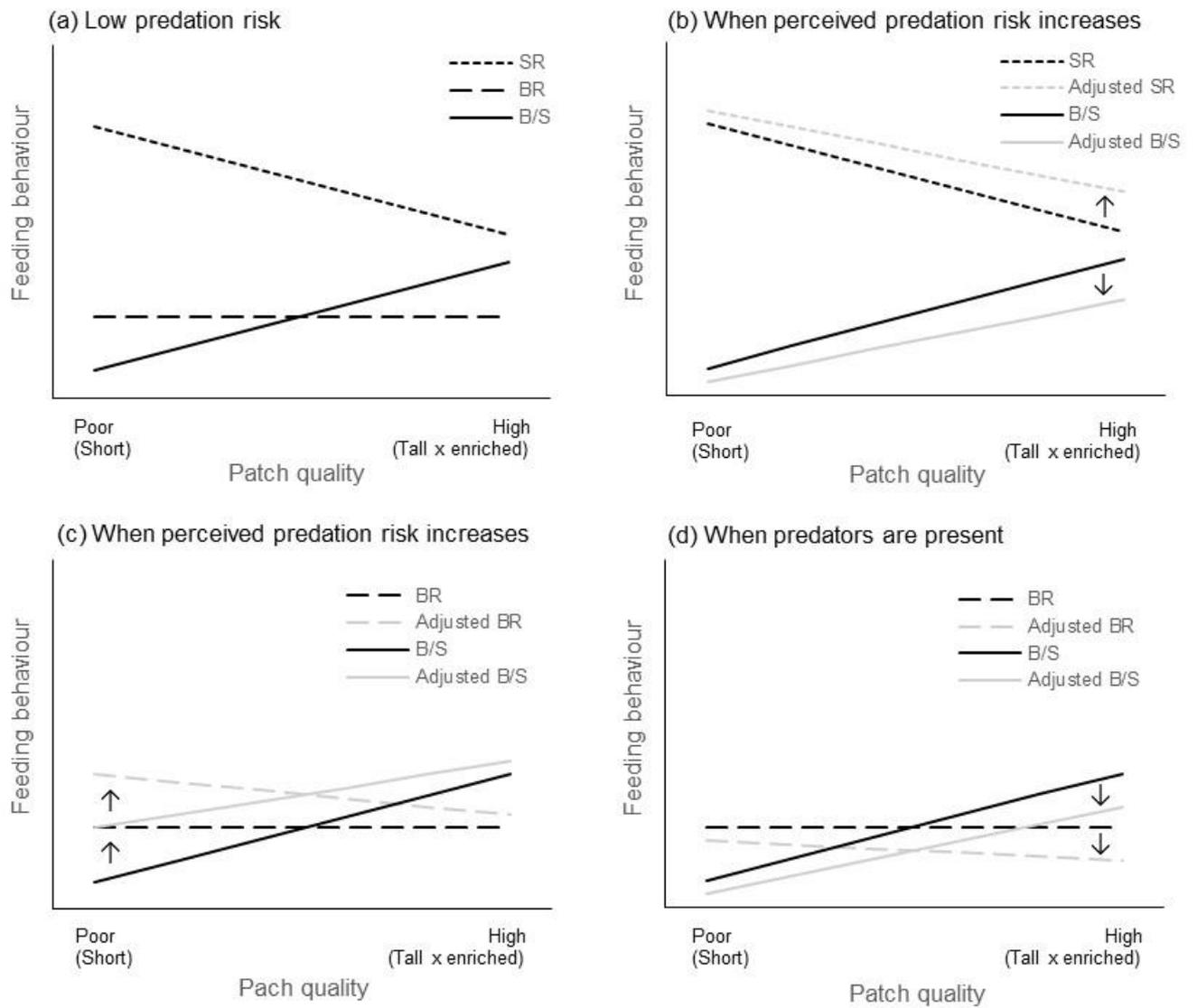


Figure 2

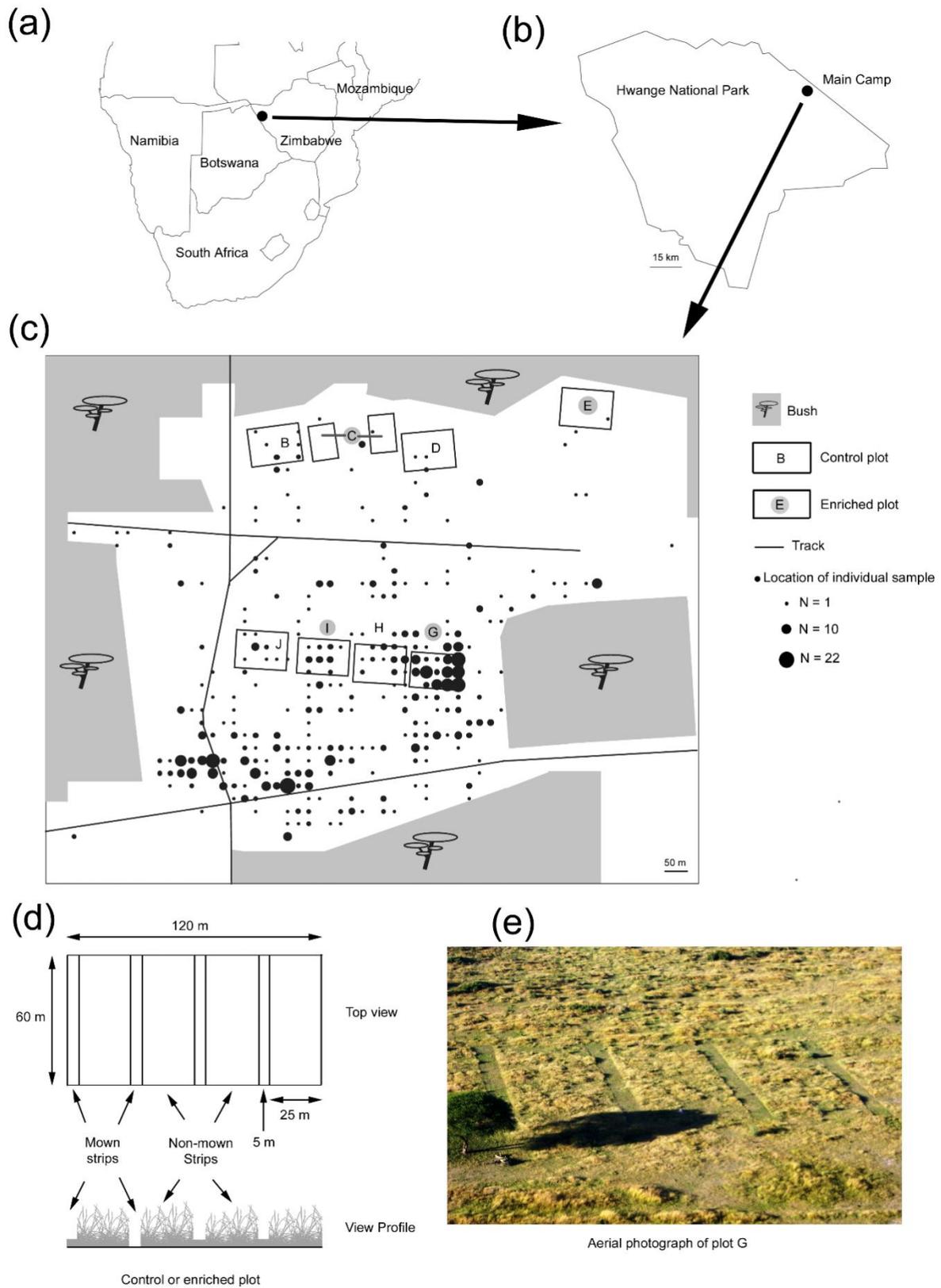
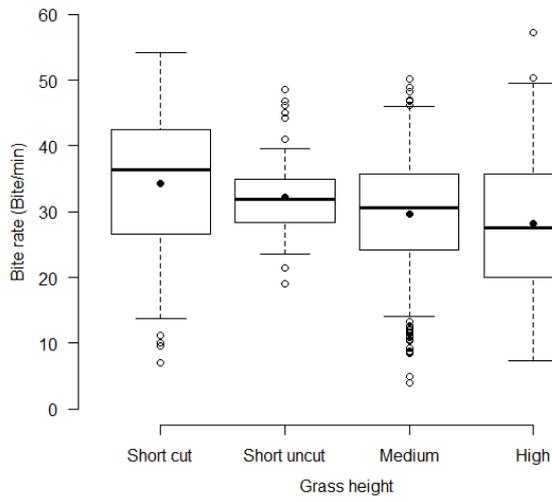
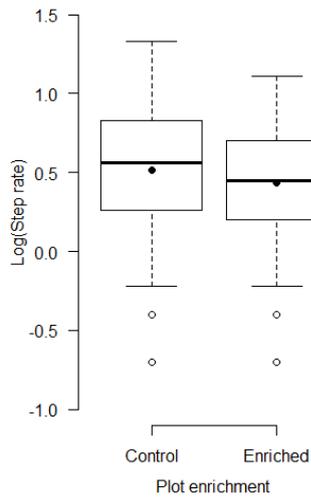


Figure 3

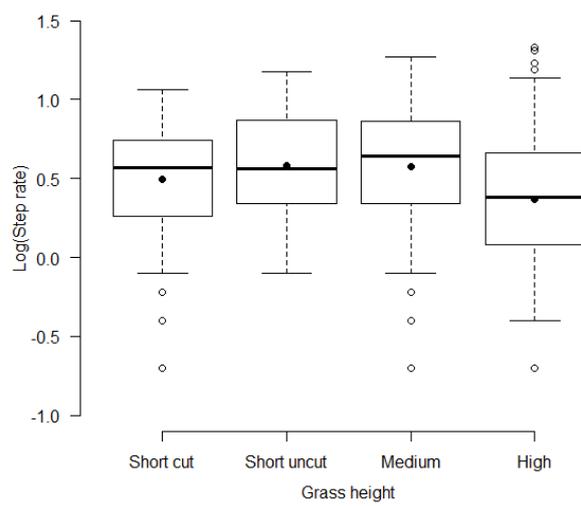
a)



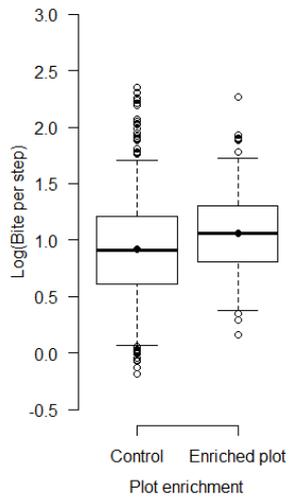
b)



c)



d)



e)

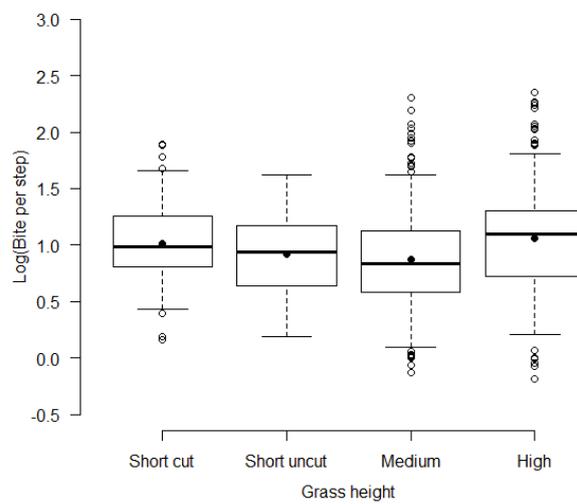


Figure 4

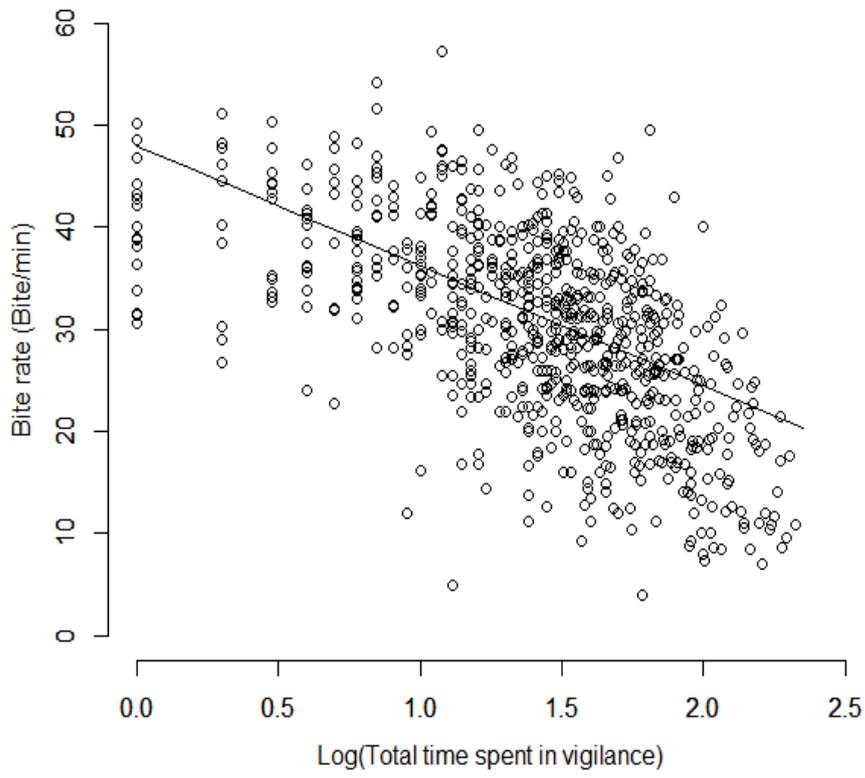
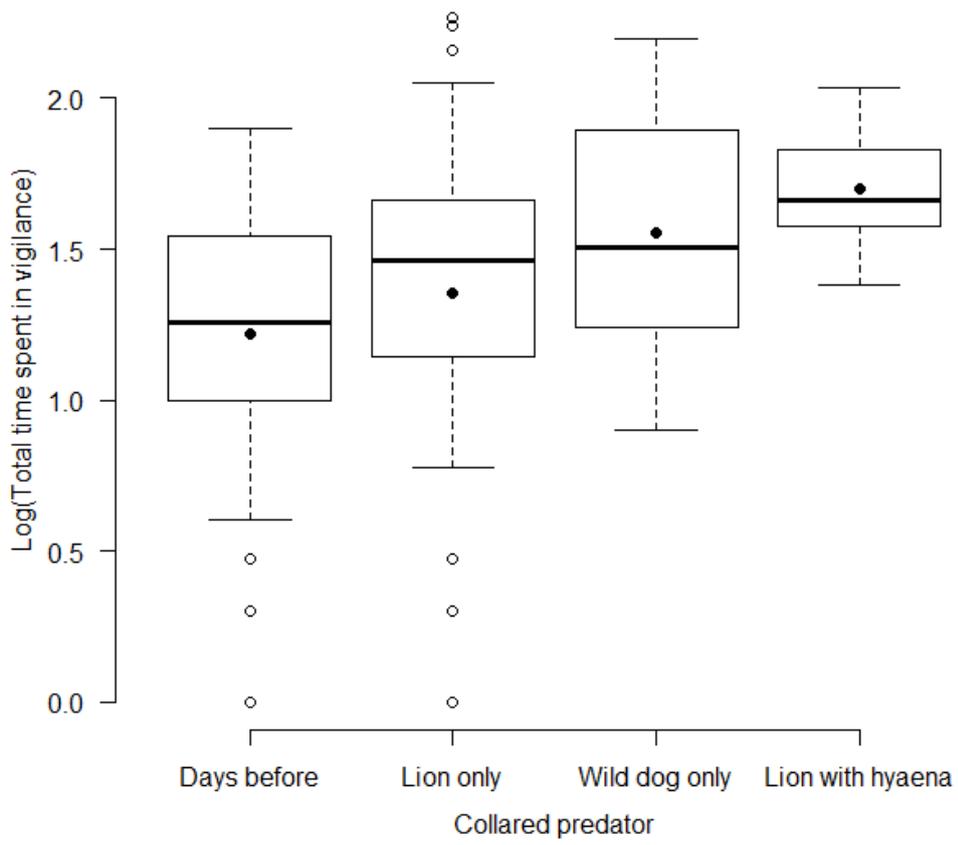


Figure 5



Appendix 1

We tested for differences of biomass and proportions of green tissues and bare soil between enriched and control plots, cut and uncut strips controlling for season and year.

In the uncut strips, biomass was on average higher in enriched plots compared to control plots in 2009: February ($\beta_{\text{enriched}} \pm \text{SE} = 0.070 \pm 0.030$, $P = 0.019$), March ($\beta_{\text{enriched}} \pm \text{SE} = 0.059 \pm 0.039$, $P = 0.127$) and May ($\beta_{\text{enriched}} \pm \text{SE} = 0.079 \pm 0.042$, $P = 0.060$) 2009; March ($\beta_{\text{enriched}} \pm \text{SE} = 0.140 \pm 0.033$, $P < 0.001$) and July ($\beta_{\text{enriched}} \pm \text{SE} = 0.098 \pm 0.057$, $P = 0.048$) 2010 (Fig 3). In the cut strips, biomass did not differ between enriched and control plots in February ($P = 0.156$), March ($P = 0.674$), May ($P = 0.940$) 2009 and in March ($P = 0.237$) and July ($P = 0.280$) 2010 (Fig S1).

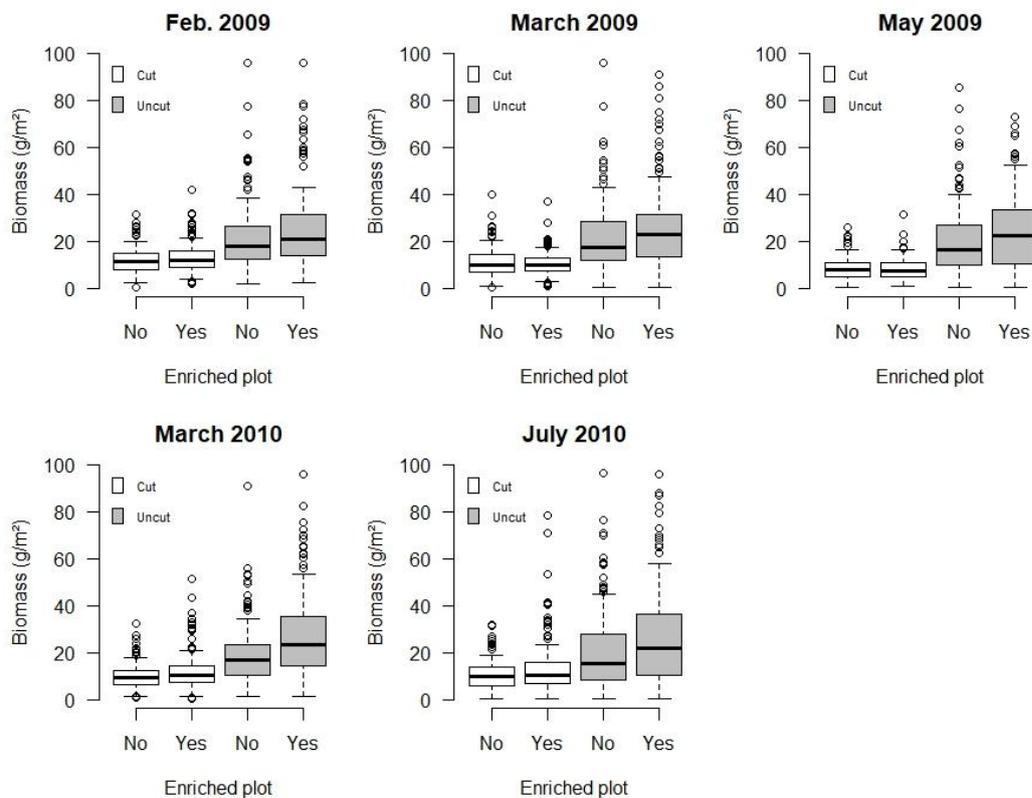


Fig. S1. Variation of grass biomass between enriched and control plots, cut and uncut strips over the 2 years of the experiment.

In the cut and uncut strips in 2009, the proportion of green tissues was higher in enriched plots compared to control plots in April ($\beta_{\text{enriched in cut}} \pm \text{SE} = 0.078 \pm 0.036$, $P = 0.032$, $\beta_{\text{enriched in uncut}} \pm \text{SE} = 0.131 \pm 0.041$; $P = 0.002$) as well as in July 2010 ($\beta_{\text{enriched in cut}} \pm \text{SE} = 0.032 \pm 0.014$, $P = 0.019$) while we did not detect any difference in green tissues among the uncut strips ($P = 0.456$) (Fig S2). The

proportion of green tissues was higher in April 2009 compared to July 2010 ($\beta_{\text{April}} \pm \text{SE} = 0.188 \pm 0.011$, $P < 0.001$) and in cut compared to uncut strips ($\beta_{\text{Cut}} \pm \text{SE} = 0.025 \pm 0.009$, $P = 0.009$) (Fig S2).

In cut and uncut strips, the proportion of bare soil was less in enriched plots compared to control plots in April 2009 ($\beta_{\text{enriched in cut}} \pm \text{SE} = -0.116 \pm 0.039$, $P = 0.003$, $\beta_{\text{enriched in uncut}} \pm \text{SE} = -0.123 \pm 0.048$, $P = 0.012$) as well as in July 2010 ($\beta_{\text{enriched in cut}} \pm \text{SE} = -0.178 \pm 0.028$, $P < 0.001$; $\beta_{\text{enriched in uncut}} \pm \text{SE} = -0.187 \pm 0.028$, $P < 0.001$) (Fig S2). We did not detect any difference in the proportion of bare soil between April 2009 and July 2010 ($P = 0.793$) while the proportion of bare soil was higher in the cut compared to uncut strips ($\beta \pm \text{SE} = 0.069 \pm 0.018$, $P < 0.001$) (Fig S2).

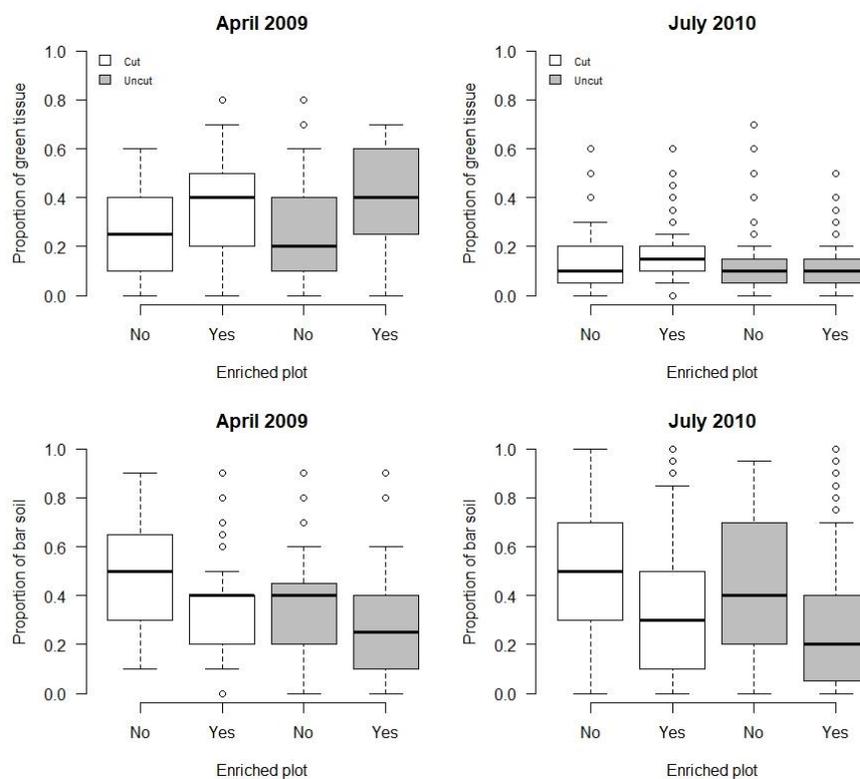


Fig. S2. Variation of the proportion of green tissues and bare soil between enriched and control plots, cut and uncut strips over the 2 years of the experiment.

Appendix 2

Lions are known to live in a fusion-fission society but the frequency of pride fission increases with increase in pride size (Mbizah et al. 2019. Applying the resource dispersion hypothesis to a fission-fusion society: a case study of the African lion (*Panthera leo*) Ecology and Evolution 9: 9111-9119). In the Main Camp area, where the study site is located, prides are rather small and composed of up to 4 female adults and previous work has revealed that lionesses from the same pride stay together most of the time, with females from a pride sighted together in 89.2% of sightings (Valeix et al. 2009. article in Ecology cited in the manuscript). Therefore, for lions, we can be rather confident that the movements of the collared individuals are quite representative of the movements of almost all lions around the study site (only dispersing individuals were missed).

Regarding wild dogs, members from a pack always stay together except during the denning period when some individuals become helpers at the den. So overall, the individuals that have been GPS collared per pack were representative of the movements of all individuals in their pack around the study site.

Regarding spotted hyaenas, because clans are characterized by a very high level of fission-fusion, we have to acknowledge that the movements of the collared individuals cannot be considered representative of the members of the monitored clans. Hence, the results about hyaenas must be interpreted with caution, as it is very likely that the movements of uncollared individuals were missed. However, we believe that the effect of undetected hyaenas should mainly reduce our capacity to detect differences.

Appendix 3

Post-hoc Tukey tests on the effect of grass height on bite rate (bites per minute), step rate (steps per minute) and number of bites per step (Log-transformed) over the 2-year period ^(a) and when comparing focals when equipped predators were present with the days before their arrival ^(b).

Contrast	Bite rate ^a			Bite rate ^b			Log(Step rate) ^a			Log(Bite per step) ^a		
	β	SE	P	β	SE	P	β	SE	P	B	SE	P
High - Medium	1.461	0.789	0.065	1.389	1.340	0.301	0.104	0.032	0.001	-0.117	0.037	0.002
High - Short uncut	4.060	1.409	0.005	5.507	2.469	0.026	0.195	0.054	<0.001	-0.116	0.062	0.060
High - Short cut	3.073	1.327	0.021	9.471	2.278	<0.001	0.186	0.053	<0.001	-0.147	0.058	0.013
Medium - Short uncut	2.606	1.363	0.056	4.117	2.318	0.077	0.091	0.053	0.085	0.001	0.060	0.992
Medium - Short cut	4.642	1.037	<0.001	8.082	2.113	<0.001	0.082	0.054	0.126	-0.029	0.060	0.615
Short uncut- Short cut	2.036	1.555	0.191	3.964	2.961	0.182	-0.009	0.071	0.899	-0.030	0.079	0.703

Appendix 4

Fig. S3. Diagnostic plots on the structure of residuals from the linear mixed-effects model investigating the plot enrichment, predator within 2 km, grass height and their two-way interactions and including year, season and plot ID (a-c) or predator event ID (d-f) as three nested random factors on bite rate in the impalas over the 2-year experiment (a-c) and contrasting focals sampled during days with predators and focals on the days before predators' arrivals (d-f). An autocorrelation function of order 1 ("corAR1") was also considered in models to control for the sequential structure of the data set (see Methods). The residuals against fitted values in (a) and (d) show that the variance remains approximately constant as the fitted values increased. (b) and (e) show that the distribution of residuals was consistent with normality. (c) and (f) show the autocorrelation function (ACF) estimated on residuals. The horizontal dotted lines provide an approximate 95% confidence interval for the autocorrelation estimate at each lag and reveal that sequential correlation was controlled.

