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1 **Challenges of foraging on a high-quality but unpredictable food source: the dynamics of**
2 **grass production and consumption in savanna grazing lawns**

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25
26 **Running title:** The dynamics of grass consumption in grazing lawns

27 **Summary**

28

29 **1.** Grazing lawns are short grassland areas where intense grazing maintains grass in an early
30 growth stage. These areas represent a source of high-quality forage for herbivores. However,
31 as herbivores continually remove nearly all the newly accumulated biomass, instantaneous
32 resource availability depends on the dynamics of grass growth.

33 **2.** In this paper, we investigate how production and consumption inside grazing lawns are
34 synchronized. We then explore how that synchronization affects the ability of large
35 herbivores to use these lawns. We also provide a critical comparison between grazing lawns
36 and intensively managed grasslands in livestock farms.

37 **3.** We investigated vegetation production and herbivore grazing activity during a wet and a
38 dry season using clipping experiments and direct observation in two grazing lawns in a South
39 African savanna.

40 **4.** Weekly total grazing activity by unit area was strongly and positively related to short-term
41 primary production. This indicates a close synchronization between these two processes. In
42 contrast, grazing activity was poorly related to standing biomass. Primary production had a
43 threshold response to the weekly pattern of rainfall, implying a stochastic dynamics of grass
44 growth.

45 **5.** The dynamics of grass production and consumption of grazing lawns is similar to the one
46 of continuously stocked grazing systems from intensively managed grasslands. But the
47 mechanisms regulating the two systems lead to different equilibrium points between
48 production and consumption. The two systems also have opposed nutritional functions within
49 the animal diet.

50 **6. *Synthesis.*** The close synchronization between resource production and consumption inside
51 grazing lawns indicates that instantaneous resource availability is a direct function of the
52 short-term rate of grass growth. In tropical savannas, the main source of variability of lawn

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53 grass primary productivity is the stochastic nature of short-term rainfall. As a result,
54 herbivores' ability to use grazing lawns is poorly predictable in time. This has important
55 consequences on the degree of information herbivores can use in the elaboration of their
56 foraging strategies, and on the potential interest of grazing lawns.

57

58

59 **Key-words:** climatic variability, continuous stocking, grazing systems, intensively managed
60 grasslands, large herbivores, primary production, rainfall, white rhino

61 **Introduction**

62 Sustainable food resource use is critical in plant–herbivore systems supporting intense levels
63 of consumption. At a regional scale, vertebrate herbivores from most native terrestrial
64 ecosystems only remove a limited proportion (10–20% on average) of the annual net above-
65 ground primary production (NAPP) (Wiegert & Evans 1967). At a local scale, however,
66 levels of consumption can be much higher. By enhancing local resource attractiveness,
67 repeated grazing can lead to the formation of intensively grazed, short-cropped sward areas
68 called grazing lawns (McNaughton 1984). Grazing lawns exist in a large variety of terrestrial
69 ecosystems, including North-American tall or mixed grass prairies (Coppock *et al.* 1983;
70 Knapp *et al.* 1999), European grasslands (Menard *et al.* 2002), alpine tundra (McIntire & Hik
71 2002), subarctic salt marshes (Person *et al.* 2003) and African savannas (Vesey-Fitzgerald
72 1965; McNaughton 1984). In these lawns, herbivores can consume up to 80–95% of the
73 annual NAPP (e.g. McNaughton 1985; Person *et al.* 1998). Such intense levels of
74 consumption involve a dynamics of resource production and consumption completely
75 different from that in less intensively grazed areas. Understanding this dynamics is of critical
76 importance for evaluating the potential interest of large herbivores in grazing lawns as a food
77 resource.

78 Grazing lawns are generally reported to be highly profitable grazing areas (e.g.
79 McNaughton 1984; Person *et al.* 2003; Verweij *et al.* 2006). Maintaining a short-cropped
80 sward allows herbivores to keep grass tissues in a phenologically young state of high
81 nutritional value (Waite 1963). In addition, primary production remains at remarkably high
82 levels, sometimes exceeding 10 tonnes dry matter ha⁻¹ year⁻¹ in tropical areas (McNaughton
83 1985). However, continually removing nearly all NAPP has a strong impact on instantaneous
84 food availability: it does not allow the build up of standing crop. As a result, the ability of
85 herbivores to use grazing lawns at any one time is probably strongly dependent on the short-

86 term rate of primary production of these areas.

87 Results from past studies have emphasized the importance of temporal changes in
88 primary production on the pattern in which herbivores use grazing lawns. For instance, in the
89 Serengeti Plains (Tanzania), the localized distribution of rainfall leads to levels of primary
90 production that are highly stochastic in space and time (McNaughton 1985). Nomadic
91 populations of Thomson's gazelle (*Gazella thomsoni*) and wildebeest (*Connochaetes*
92 *taurinus*) closely track these changes in the large-scale spatial distribution of lawn grass
93 production (Wilmshurst *et al.* 1999; Fryxell *et al.* 2004). But at a more local scale, the
94 temporal link between primary production and grass consumption in grazing lawns remains
95 poorly documented.

96 Continuously stocked grazing systems, optimized for livestock production in
97 intensively managed grasslands, have a dynamics of grass production and consumption
98 remarkably similar to the one of grazing lawns. Indeed, they were designed to maintain a
99 relatively constant short sward canopy by letting domestic herbivores continually remove
100 newly accumulated biomass (Spedding 1965). Whereas the two systems remain
101 fundamentally different in their overall functioning (i.e. continuously stocked grazing systems
102 are closed and carefully managed by farmers, whereas grazing lawns are open, with
103 herbivores free to move in and out), established fine-scale processes on the dynamics of grass
104 production and consumption in intensively managed grasslands (e.g. Bircham & Hodgson
105 1983; Parsons *et al.* 1983; Johnson & Parsons 1985) can usefully enlighten patterns observed
106 in grazing lawns.

107 The objective of this study was first to determine the strength of the temporal link
108 between primary production and grass consumption inside grazing lawns. Secondly, it was to
109 evaluate how this link affects the ability of large herbivores to use grazing lawns as a food
110 resource. Specifically, we determined for grazing lawns the relationships at a weekly time

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111 scale between: (i) primary production and rainfall; (ii) large herbivore grazing activity and
112 primary production and (iii) large herbivore grazing activity and standing biomass. We
113 interpret and discuss our results relative to the principles of grass production and consumption
114 established in continuously stocked grazing systems in farms and provide a critical analysis of
115 this comparison. We then discuss implications of our results in a context of highly stochastic
116 distribution of rainfall.

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117 **Materials and methods**118 **STUDY SITE**

119 We conducted the study in the Hluhluwe section (hereafter Hluhluwe) of the Hluhluwe-
120 iMfolozi Park (28°10' S, 32°00' E), an enclosed c. 90 000-ha mesic savanna in South Africa.
121 Mean annual rainfall ranges between 750 and 950 mm, depending on altitude. Inter-annual
122 variations in monthly rainfall are high during the wet season (CV from 55 to 75 % mm) and
123 even higher during the dry season (CV from 74 to 154 %).

124 The vegetation comprises open grasslands, savannas, broad-leaved thickets and *Acacia*
125 woodlands (see Whateley & Porter (1983) for a detailed description). Grazing lawns occur as
126 small patches (mostly < 8 ha) in a taller bunch-grass matrix and cover less than 10% of the
127 total area of the Park (Archibald *et al.* 2005). Grass species in grazing lawns include, in order
128 of abundance, *Digitaria longiflora*, *Dactyloctenium australe*, *Sporobolus nitens*, *Digitaria*
129 *eylesii* and *Eustachys paspaloides*. Indigenous large grazers include white rhino
130 (*Ceratotherium simum*), African buffalo (*Syncerus caffer*), zebra (*Equus burchelli*), blue
131 wildebeest (*Connochaetes taurinus*), warthog (*Phacochoerus africanus*) and impala
132 (*Aepyceros melampus*). Populations are resident. Herbivore biomass in Hluhluwe (c. 11 000
133 kg live weight km⁻², Ezemvelo KwaZulu-Natal Wildlife data) is high in comparison with
134 other African conservation areas with the same range of rainfall (Fritz & Duncan 1994).
135 White rhinos (c. 480 individuals in 2006) account for around 30% of this biomass and are the
136 main actors of the maintenance of grazing lawns (Waldram *et al.* 2008).

137 We conducted the study in two distinct grazing lawns (Site 1: 2.5 ha; Site 2: 6.6 ha), 7
138 km apart from each other, during both the dry (July - August 2005) and wet (January - March
139 2006) seasons. Daily rainfall data come from four automatic meteorological stations located
140 nearby our study sites.

141

142 **PRIMARY PRODUCTION**

143 We used net biomass accumulation (NBA, $\text{g m}^{-2} \text{d}^{-1}$) instead of NAPP as a measure of
144 primary production. NBA corresponds to NAPP minus the rate of tissue death and provides
145 better estimates of newly produced biomass available to herbivores. We monitored short-term
146 NBA of lawn grass by repeatedly clipping grass inside small exclosures. Four exclosure
147 replicates of 2×2 m were randomly placed in each of the two sites, and six square 0.5-m^2
148 plots were arranged evenly in each of them. Each exclosure had a balanced factorial design
149 with two levels of clipping height (2 and 6 cm) and three levels of clipping frequency
150 (weekly, every 1.5 weeks, and every 3 weeks). Treatments (two clipping heights \times three
151 clipping frequencies) were randomly arranged in each exclosure. This design allowed the
152 simulation of a variety of grazing intensities, as well as monitoring the dynamics of lawn
153 grass production at different time scales (from 1 to 3 weeks). We chose clipping heights of 2
154 and 6 cm to simulate the mean cropping height of white rhino and zebra, respectively. As
155 sward height was extremely short (1-2 cm) and without any growth at the beginning of the
156 dry season, we limited our clipping to the 2 cm clipping treatment thought this season.
157 Clipped samples were oven-dried at 60°C for 8 h to obtain dry mass.

158

159 **STANDING BIOMASS**

160 We divided each site into 12 areas of relatively homogeneous size and vegetation aspect
161 (sward height, presence of bunch grasses or shrubs). During the dry season, three locations
162 were randomly selected in each area and for each sampling event (three by site). Sampling
163 consisted of clipping all standing material within a 60×60 cm quadrat. During the wet
164 season, grazing lawn swards were much more heterogeneous. Thus, we used transects
165 (dimensions 0.1×10 m) rather than quadrats to sample the vegetation during this period. One
166 location was randomly selected inside each area and for each sampling event (three for site 1,

167 two for site 2). Due to safety problems (e.g. presence of lions and elephants), we were not
168 able to complete a third sampling event on site 2 at the end of the study. Transect were chosen
169 along a random direction from the selected location. Because of the change of sampling
170 procedure between the dry and the wet season, we did not try to compare standing biomass
171 between the two seasons. It was clear, however, that standing biomass was higher during the
172 wet than during the dry season. Vegetation samples were sorted by species and tissue type
173 (i.e. green leaves, dead leaves and stems) before they were oven-dried.

175 GRAZING ACTIVITY

176 We monitored grazing activity of all herbivore species present on the lawns by direct
177 observation during daylight hours (6:00 – 18:00). We conducted observations from hides
178 installed in a tree at the centre of each site. This insured minimal disturbance of the feeding
179 behaviour of observed herbivores. Every 5 min, we counted the number of individuals present
180 for each species, and classified them according by age, sex and activity (young or adult, male
181 or female, grazing or not). Grazing activity ($\text{min kg}^{0.75} \text{ ha}^{-1}$) was calculated as the product of
182 the total time spent grazing by each individual and its metabolic body mass ($\text{BM}^{0.75}$), divided
183 by the area of the site. This was done to allow interspecific and intersite comparisons. We
184 made a distinction in the mean body mass of age–sex classes for white rhinos (adult males:
185 2200 kg, adult females: 1700 kg, young: 400 kg, from Owen-Smith 1988) and warthogs (adult
186 males: 90 kg, adult females: 70 kg, young: 10 kg, from Brooks & MacDonald 1983) only, as
187 these differences were significant for these two species. We used a unique body mass value
188 for other species: zebra, 230 kg; wildebeest, 220 kg; impala, 50 kg (from Brooks &
189 MacDonald 1983).

190 During the dry season, we conducted 12 observation hours a week at each site over
191 seven consecutive weeks. Observations were divided into three sessions of four hours (a

192 morning, a mid-day and an afternoon) conducted at random during the week. During the wet
193 season, grazing activity was much more intense. As a result, we conducted continuous
194 observations (12 hours every day for two or three consecutive weeks). The two sites were
195 observed alternately in the following sequence: site 1 (two weeks), site 2 (two weeks) and site
196 1 (three weeks). We were not able to complete additional observations on site 2 at the end of
197 the study due to safety problems.

199 DATA ANALYSIS

200 The clipping experiment used to monitor NBA had a hierarchical sampling design (exclosures
201 were nested within sites) and temporal pseudo-replication between successive clipping events.
202 We used mixed generalized linear models to test covariates and treatments affecting NBA. As
203 values for NBA were strictly positive with a variance increasing roughly proportionally with
204 the mean, we used a quasi-Poisson distribution in the models, as suggested by Fisher (1949).
205 We used two different models to test effects on NBA under the weekly clipping treatment.
206 The first model used data from the two seasons, with cumulative rainfall over one week
207 (CRain1) and season (Season) as fixed effects. The second model was restricted to data from
208 the wet season. Fixed effects were CRain1, time in days since the beginning of drier
209 conditions, i.e. since the last big rainfall of January (Drier, see Fig. 1b) and clipping height
210 (Ch). We used a third model, restricted to the wet season, to test effects on NBA at a time
211 scale of three weeks. This allowed us to test the effect of clipping frequency (Cf) by pooling
212 over three weeks data from plots with shorter clipping intervals. Fixed effects for this last
213 model were cumulative rainfall over three weeks (CRain3), Ch and Cf. All three models
214 contained two additive terms as random effects. One for the nested hierarchical design with
215 exclosure nested within site, and the other with the number of successive clipping events.
216 Non-significant interactions were systematically removed during the model simplification

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217 procedure. We tested for significant differences in standing biomass by using linear models
218 with log-transformed biomass data. Finally, we used a Spearman rank correlation test to
219 investigate correlations of grazing activity with NBA and standing biomass. All analyses were
220 conducted on R 2.7.0 GUI 1.24 free online software (<http://www.R-project.org>).

Results

PRIMARY PRODUCTION

Net biomass accumulation (NBA) closely matched the rainfall pattern during both the wet and the dry seasons (Figs 1a to 1f). Over the two seasons, the one-week cumulative rainfall positively influenced NBA from the weekly clipping treatment (Table 1, *model 1*, estimate = 0.165 ± 0.016). This relationship had a marked threshold shape (Fig. 2). Weekly NBA remained close to zero for cumulative rainfall lower than 14 mm, whereas it increased linearly for higher rainfall values. Season did not have a significant effect on this relationship (Table 1, *model 1*). During the wet season, the number of days since the beginning of drier conditions (i.e. since the last big rain of January) had an additional negative effect on weekly NBA (Table 1, *model 2*, estimate = -0.056 ± 0.007). On the other hand, clipping height did not have any significant effects (Table 1, *model 2*).

Considering a time scale unit of three weeks, the relationship between NBA (from the three clipping frequencies) and cumulative rainfall was no longer significant (Table 1, *model 3*); neither was clipping height nor clipping frequency (Table 1, *model 3*). The absence of effect of clipping frequency indicates that NBA was a strictly additive process between one and three weeks. A time scale of one week is therefore likely to better capture the effect of a heterogeneous rainfall distribution on NBA.

STANDING BIOMASS

The biomass of green leaves was generally low during the dry season (Figs 1c and 1e). However, it significantly increased at the third sampling event (site 1: $F_{2,73} = 7.77$, $P < 0.001$, contrast: $t = 2.67$, $P = 0.009$; site 2: $F_{2,55} = 15.45$, $P < 0.001$, contrast: $t = 5.17$, $P < 0.001$), after the heavy rains of mid-August. During the wet season, (Figs 1d and 1f) total biomass ($F_{1,54} = 15.24$, $P < 0.001$) and green leaf biomass ($F_{1,54} = 14.15$, $P < 0.001$) were significantly

246 higher on site 2 than on site 1. For site 1, total biomass significantly decreased between the
247 three sampling events ($F_{2,26} = 3.69$, $P = 0.038$), but green leaf biomass remained constant
248 ($F_{2,26} = 1.08$, $P = 0.35$). For site 2, neither total ($F_{1,18} = 0.12$, $P = 0.73$) nor green leaf biomass
249 ($F_{1,18} = 0.18$, $P = 0.68$) significantly changed between the two sampling events.

251 GRAZING ACTIVITY

252 Grazing activity closely matched variations of weekly NBA over time (Fig 1). During the dry
253 season (Fig. 1g), herbivores rarely used grazing lawns prior to the heavy rains of August.
254 After these rains, primary production increased and green leaves re-appeared. As a result,
255 herbivores moved back onto these lawns and total grazing activity reached its highest levels.
256 During the wet season (Fig. 1h), both total grazing activity and weekly NBA declined over
257 time, whereas standing green biomass remained constant.

258 Considering weekly NBA over the week of and before the grazing observations,
259 weekly total grazing activity and NBA were strongly correlated for the 2-cm clipping
260 treatment (Fig. 3a, Table 2). Correlation was not significant for the 6-cm clipping treatment
261 (Table 2), probably because of the low number of replicates. It followed, however, the same
262 trend as the 2-cm clipping treatment (Fig. 3a). Considering each herbivore species
263 independently, the relationship at the 2-cm clipping height was significant for white rhino
264 (see Fig. 3b), wildebeest and warthog, nearly significant for impala and not significant for
265 zebra (Table 2).

266 Total grazing activity over one week was positively correlated to standing green
267 biomass during the dry seasons ($r_s = 0.94$, $P = 0.017$, $N = 6$), but not during the wet season (r_s
268 $= 0.3$, $P = 0.68$, $N = 5$).

Discussion

Many studies have reported that grazing lawns are important areas of highly nutritive food for grazing herbivores (e.g. McNaughton 1984; Person *et al.* 2003; Verweij *et al.* 2006). However, our results show that grazing activity inside lawns is strongly dependent on the short-term rate of primary production of these areas. As a result, the ability of herbivores to use these lawns depends on the sustainability of grass growth. We also found that primary production of grazing lawns had a threshold response to weekly rainfall. This dependence of grazing lawns' primary production on a process as stochastic as short-term rainfall indicates that grazing lawns are, in arid to mesic areas, highly unpredictable resources in time. This makes their exploitation by herbivores unsustainable, particularly for resident populations who cannot migrate to track grass productivity.

DETERMINANTS OF GRAZING ACTIVITY IN LAWNS

Weekly total grazing activity was strongly and positively related to short-term NBA (Fig. 3a). On the other hand, it was poorly related to standing green biomass. Indeed, both NBA and total grazing activity significantly decreased during the wet season, whereas standing green biomass remained constant (Fig. 1). During the dry season, August rainfall resulted in a strong increase of both NBA and total grazing activity. In spite of lower standing green biomass, NBA and grazing activity reached values near the ones observed at the beginning of the wet season (Fig. 1). It is, however, possible that this last pattern was due to the attractiveness of fresh, green leaves being greater during the dry season than during the wet season.

We found a strong positive correlation between grazing activity and standing green biomass during the dry season. This result does not contradict our finding that grazing activity was poorly related to standing green biomass. It only reflects the contrast between conditions

294 in early dry season, when standing green biomass was too low to support grazing activity, and
295 conditions at the end of the dry season, when an increase in standing green biomass allowed
296 grazing activity. As soon as there was enough biomass to support grazing, grazing activity
297 and standing green biomass were no longer related.

298 By adjusting their grazing activity to primary production, large herbivores maintain
299 grazing lawns in a dynamic equilibrium where newly produced biomass is continually
300 consumed, and where standing biomass remains relatively constant. Studies from salt marshes
301 in northern Netherlands (Ydenberg & Prins 1981) reported similar results. On a range of
302 lawns supporting widely different rates of primary production, barnacle geese (*Branta*
303 *leucopsis*) were able to maintain an equal standing biomass by grazing more on sites that were
304 more productive.

305 These findings strongly suggest that the ability of large herbivores to use grazing
306 lawns is driven by short-term primary production rather than standing biomass. The
307 recrudescence of grazing activity after the large rainfall event observed during the dry season
308 confirms that primary production is the determinant of grazing activity, and not grazing
309 activity the determinant of primary production. As a result, environmental conditions
310 affecting the pattern of primary production over time will be the ultimate drivers of the ability
311 of herbivores to use grazing lawns.

312 DEPENDENCE OF PRIMARY PRODUCTION ON THE PATTERN OF RAINFALL

313 In accordance with the vast majority of studies from grasslands or savanna (e.g. Rosenzweig
314 1968; Sala *et al.* 1988; O'Connor *et al.* 2001), we found a strong relationship between rainfall
315 and primary production. Perhaps more interesting is that this relationship was highly
316 significant at the time scale of one week but not when we looked over three weeks. The
317 threshold response of NBA to weekly rainfall (Fig. 2) can explain this discrepancy. When
318

319 summed over three weeks, rainfalls lower than this threshold (no production) counteract
320 rainfalls higher than the threshold (high production), blurring the relationship.

321 The close synchronization between rainfall and primary production, and the threshold
322 shape of this relationship have important implications. Ultimately, it indicates that grazing
323 lawns are productive areas only when weekly rainfall exceeds the threshold value. Short-term
324 productivity is thus not sustained over time because of high rainfall stochasticity. Using the
325 threshold value, we can predict from historical rainfall data the expected temporal pattern of
326 lawn grass production over the year in Hluhluwe (i.e. when weekly rainfall exceeded 14 mm).
327 In 2002, a particularly dry year, weekly cumulative rainfall exceeded 14 mm for only 71 days,
328 compared to 138 days in 2005, which was an average rainfall year (Fig. 4). We can compare
329 this difference in the number of days of potential lawn grass production (i.e. $\times 2$) to the
330 difference in the annual rainfall between 2002 (480 mm) and in 2005 (763 mm) (i.e. $\times 1.6$).
331 The intra-seasonal distribution of rainfall events may therefore have an effect on primary
332 production as important as the annual amount of precipitation, a result already pointed out in
333 recent studies (Knapp *et al.* 2002; Swemmer *et al.* 2007). Another implication is that during
334 the dry season, a single but sufficient rainfall amount is able to initiate growth in grazing
335 lawns. The resulting green flush of young leaves can be of primary importance for herbivores
336 during this period of limited food quality (Owen-Smith *et al.* 2005; Valeix *et al.* 2008).

337 Surveying primary production at a monthly time scale in the Serengeti, McNaughton
338 (1985) reported that a minimum rainfall of 25 mm month⁻¹ was required for significant
339 productivity of lawn grass areas. He also emphasized that the relevant time scale between the
340 two processes probably ranged from a few days to one week. When we convert our data to a
341 monthly time scale, we find that a minimum rainfall of 26 mm month⁻¹ is needed to reach the
342 weekly threshold of 14 mm week⁻¹ at least once a month. This result closely matches
343 McNaughton's observations. It indicates that the primary production of grazing lawns

344 probably shows the same pattern of response to rainfall in both Hluhluwe and the Serengeti.

345 It is surprising that we did not find any significant effect of clipping frequency or
346 clipping height on the relationship between rainfall and primary production. A large number
347 of previous experiments on lawn grass species in the field (e.g. Hik *et al.* 1991; Green &
348 Detling 2000) or in a greenhouse (e.g. McNaughton *et al.* 1983; Georgiadis *et al.* 1989)
349 reported such effects. This result is probably explained by the predominant effect of rainfall,
350 which overshadowed the effects of the clipping treatments we applied.

351

352 GRAZING LAWNS AND INTENSIVELY MANAGED GRASSLANDS

353 The use of grazing lawns by large herbivores raises the practical question of how sustainable
354 foraging is under repeated grazing? This is a common question in intensively managed
355 grasslands, which has led to the development of a large diversity of grazing systems for farm
356 animals (Parsons 1988; Clark & Kanneganti 1998). ‘Continuous variable stocking’ systems
357 are a form of continuous stocking (see Spedding 1965; Parsons 1984) with a dynamics of
358 grass production and consumption dynamics close to the one we observed in savanna grazing
359 lawns. In grazing lawns, we showed that large herbivores maintained a sward of nearly
360 constant standing biomass by quickly adjusting their grazing activity to the primary
361 production. Similarly, in continuous variable stocking systems, farmers maintain a desired,
362 typically short sward canopy height by frequently and carefully adjusting the stocking density
363 of animals to primary production.

364 In continuous variable stocking systems, which are mainly used with lactating ewes
365 and dairy cattle, maintaining a short sward canopy height does not constrain herbivores’
366 intake levels to low values. Under continuous grazing, maintaining a short sward reduces the
367 net photosynthetic rate of plants. But because of the rapid tissue turnover in grasses, it also
368 increases the efficiency of forage use by improving the proportion of forage consumed to that

369 which senesces and dies without having been eaten (see Parsons *et al.* 1983). When the
370 balance between net photosynthesis, forage intake and tissues death is optimized, continuous
371 variable stocking systems allow maximizing herbivores' intake levels by unit of grassland
372 area (Ernst *et al.* 1980; Grant *et al.* 1988; Parsons *et al.* 1988; Pulido & Leaver 2003). For
373 example, in temperate areas, when domestic herbivores are grazed on *Lolium perenne* L.
374 swards, such maximum levels of intake are reached for a sward canopy height kept between 3
375 and 6 cm for sheep (Bircham & Hodgson 1983; Grant *et al.* 1983) and between 7 and 9 cm
376 for dairy cattle (Ernst *et al.* 1980). This highlights a key feature of short grasslands in that
377 despite a low standing biomass, herbivores can maintain large levels of intake by using the
378 sward more efficiently. This feature probably explains how grazing lawns support such high
379 levels of intake, as long as rainfall is sufficient.

380 In both continuous variable stocking systems and grazing lawns, continuous grazing
381 does not allow the build up of a consistent standing crop. As a result, instantaneous resource
382 availability depends on the short-term rate of primary production. In natural systems, the
383 diversity of the landscape allows herbivores to use other areas when primary production
384 ceases inside grazing lawns. But in intensively managed grasslands, the risk of pasture
385 shortage constrains farmers to maintain areas devoted to forage conservation (i.e. buffer
386 areas), or to conserve a stock of hay or silage (Mayne *et al.* 2000). The predominance of this
387 farming practice emphasizes the general problem of resource unpredictability in continuously,
388 intensively grazed areas.

389 Despite their dynamics being similar, grazing lawns and continuous variable stocking
390 systems remain fundamentally different in their overall functioning. In intensively managed
391 grasslands, farmers carefully adjust stocking densities as a function of their pasture
392 management planning. As a result, they have control over sward canopy height. In grazing
393 lawns, it is herbivores who adjust their own grazing activity as they are free to move in and

394 out of these areas. Because grazing lawns are highly attractive resources, grazing activity
395 increases in proportion to primary production. As a result, sward height remains short and
396 herbivores have to decrease their consumption rates as soon as production slows down or
397 ceases. Grazing lawn systems do not have the flexibility that farmers have in the range of
398 sward height that can be maintained under intensively managed grassland systems. In some
399 cases, it is possible that sward height of grazing lawns may approach a value that allows
400 maximum levels of intake per unit area similar to that aimed for in intensively managed
401 grasslands. Most of the time, however, sward height in lawns is probably lower than the ones
402 that allow for these maxima.

403 Another important difference between the two systems lies in the nutritional role they
404 play in the individual animals' diet. In intensively managed systems, the grazed forage forms
405 the bulk of the animals diet. To increase the production per animal, or to remedy any
406 deficiencies in nutritional quality or quantity per animal, higher-quality feeds are usually
407 provided in the form of supplements / concentrates. In contrast, although grazing lawns may
408 represent the highest quality part of herbivores diet, the quantity consumed on a daily basis of
409 this material may be limited because of the lawns' low standing biomass. Ultimately, these
410 lawns may play a critical role in the herbivores nutrition. However, the bulk of the animal's
411 diet, particularly over the seasonal time frame, is generally obtained in other, taller grassland
412 or savanna areas that are of lower nutritional value.

413 Continuously stocked grazing systems and grazing lawns are similar with regard to
414 their dynamics, but contrast with regard to their nutritional role in the herbivores' diet. This
415 highlights the artificial nature of intensively managed grazing systems, which is not surprising
416 as artificiality is part of the definition of intensive management (FGTC 1992).

417

418 **Conclusion**

419 By concentrating their grazing activity inside grazing lawns, large herbivores are able to
420 maintain a short-cropped, highly nutritive grass. This can be of high nutritional interest,
421 particularly in environments where the forage resource is often of poor nutritive value. Large
422 herbivores also maintain high levels of intake as short, repeated cropping maximizes the
423 proportion of newly accumulated biomass consumed relative to that which senesces.
424 However, maintaining a short-cropped sward means that instantaneous resource availability is
425 a function of its short-term rate of growth. This is a general limitation on the use of short
426 grass, in grazing lawns, but also in intensively, continuously stocked grazing systems in
427 farms. In mesic to sub-arid environments, short-term primary production of lawn grass is
428 driven by the weekly pattern of rainfall, a highly stochastic process. As a result, resource
429 availability inside grazing lawns is highly unpredictable in time. It is therefore difficult for
430 herbivores, in the elaboration of their foraging strategy, to develop a perfect knowledge of the
431 resource available inside their habitat. Many models in foraging theory assume perfect
432 knowledge of the environment (Stephens & Krebs 1986), but this assumption becomes
433 quickly unreliable with grazing lawns. Grazing lawns are predictable in space, but
434 unpredictable in time, and particularly vulnerable to changes in climatic conditions, such as
435 changes in the frequency and intensity of droughts we face in the present context of climate
436 change.

437

438

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577 **Tables**

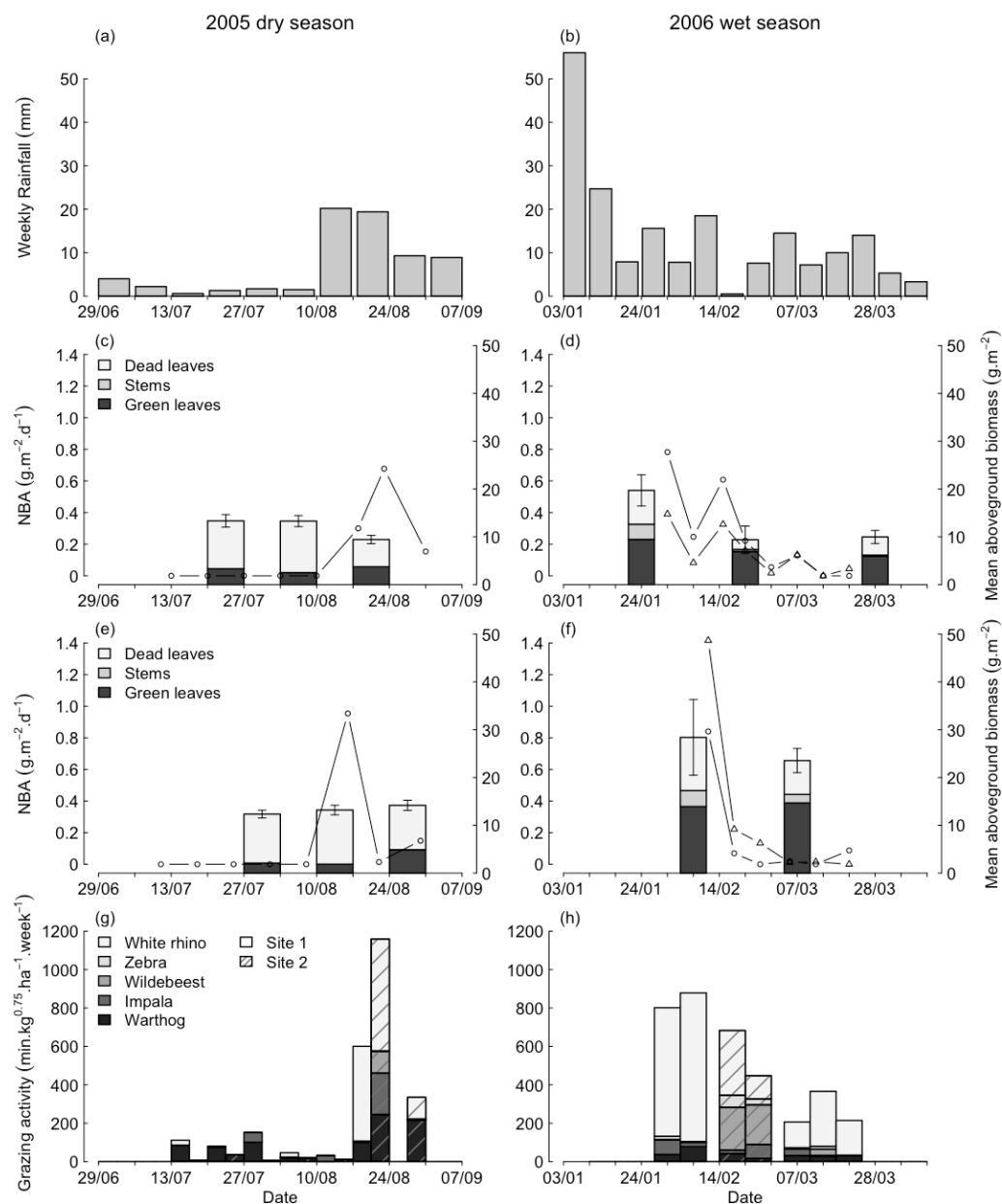
578 **Table 1.** Analysis of variance from mixed generalized linear models for effects of
 579 environmental conditions and treatments on net biomass accumulation. Covariates (fixed
 580 effects) – *CRain1*: cumulative rainfall over one week, *CRain3*: cumulative rainfall over three
 581 weeks, *Drier*: number of days since the beginning of drier conditions (i.e. since the last big
 582 rain of January). Factors (fixed effects) – *Season*: studying period (wet or dry season), *Ch*:
 583 clipping height (2 or 6 cm), *Cf*: clipping frequency (weekly, every one week and half, and
 584 every three weeks)

<i>Source of variation</i>	<i>d.f.</i>	<i>Deviance</i>	χ^2	<i>P</i>
Model 1: two seasons, weekly clipping treatment only				
<i>CRain1</i>	1	30.53	20.08	< 0.001
<i>Season</i>	1	0.01	0.01	0.92
Model 2: wet seasons, weekly clipping treatment only				
<i>CRain1</i>	1	14.79	7.07	0.008
<i>Drier</i>	1	9.56	11.13	< 0.001
<i>Ch</i>	1	0.01	0.01	0.93
Model 3: wet seasons, all three clipping treatments				
<i>CRain3</i>	1	0.70	0.62	0.43
<i>Ch</i>	1	0.71	0.74	0.39
<i>Cf</i>	2	0.07	0.07	0.96

585
 586
 587 **Table 2.** Spearman rank correlation test between grazing activity over one week and weekly
 588 net biomass accumulation over the week of and before the grazing observations. Clipping
 589 height is the clipping treatment used for the measurements of net biomass accumulation

<i>Herbivore species</i>	<i>Clipping height (cm)</i>	<i>N</i>	<i>Total observed grazing time (min)</i>	<i>r_s</i>	<i>P</i>
<i>All</i>	2	17	15 565	0.86	< 0.001
<i>All</i>	6	6	15 565	0.77	0.10
<i>White rhino</i>	2	17	4 015	0.89	< 0.001
<i>Wildebeest</i>	2	17	1 655	0.71	0.001
<i>Warthog</i>	2	17	6 135	0.54	0.024
<i>Impala</i>	2	17	2 710	0.46	0.057
<i>Zebra</i>	2	17	1 050	0.37	0.147

592 **Figures**



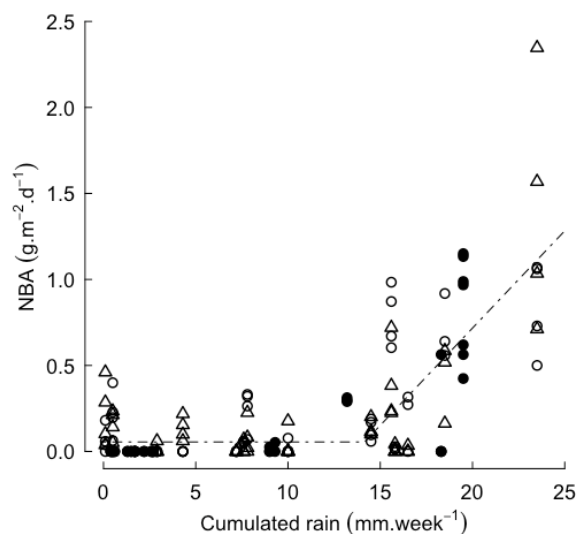
593
 594 **Fig. 1.** Dynamics of monitored grazing lawns during the 2005 dry season (left column) and
 595 the 2006 wet season (right column). X-axis ticks correspond to one week. **a-b:** weekly rainfall
 596 (mm). **c-f:** Solid lines: net biomass accumulation (NBA, $\text{g m}^{-2} \text{d}^{-1}$) from clipping experiment
 597 (\circ clipping height = 2 cm, \triangle clipping height = 6 cm). Only weekly clipping frequency is
 598 presented. Histogram bars: mean standing biomass (g m^{-2} , \pm SE of total biomass). **c** and **d** are
 599 results for Site 1, **e** and **f** for Site 2. **g-h:** total grazing activity during day hours over one week
 600 in minutes spend grazing \times kg of metabolic body mass ($\text{BM}^{0.75}$) by ha for each observed

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601 species.

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603



604

605 **Fig. 2.** Relationship between lawn grass net biomass accumulation (NBA, $\text{g m}^{-2} \text{d}^{-1}$) at the
 606 weekly clipping frequency and cumulative rainfall (mm week^{-1}) over the seven days
 607 preceding the clipping event. ● dry season, 2-cm clipping treatment; ○ wet season, 2-cm
 608 clipping treatment; △ wet season, 6-cm clipping treatment. Dashed line is the linear threshold
 609 function minimizing deviance of fitted values: $\text{NBA} = 0.055$ for cumulative rainfall < 14.14
 610 mm week^{-1} , and $\text{NBA} = 0.11 X - 1.54$ for cumulative rainfall $> 14.14 \text{ mm week}^{-1}$.

611

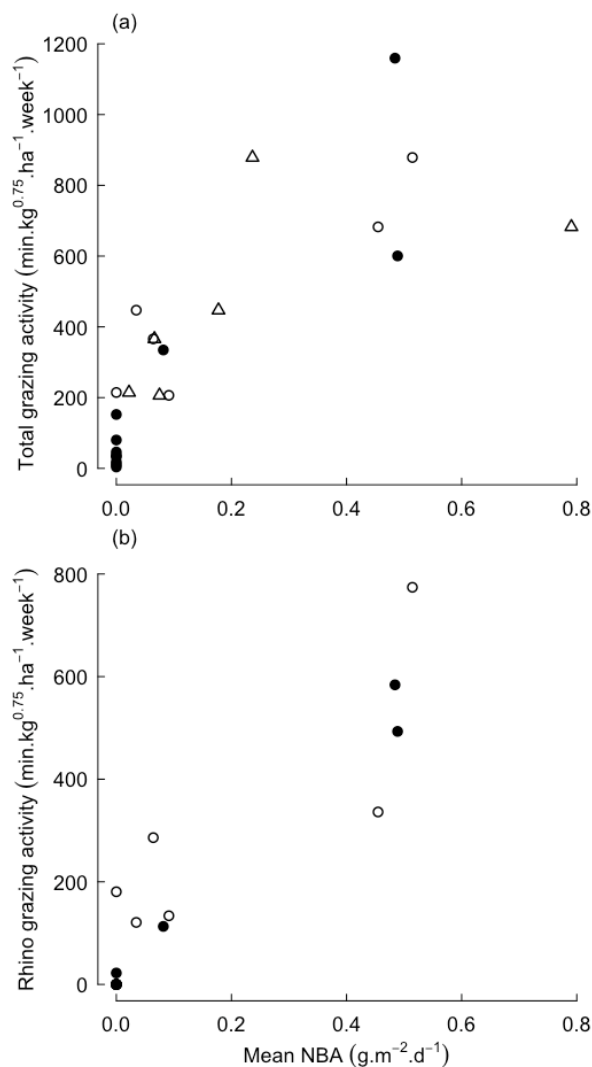


Fig. 3. Relationship between grazing activity over one week in minutes spent grazing \times kg of metabolic body mass ($BM^{0.75}$) by ha, and mean net biomass accumulation (NBA, $g\ m^{-2}\ d^{-1}$) of lawn grass from the weekly clipping treatment over the week of and before the grazing activity observations. **a)** Total grazing activity for all species, **b)** grazing activity for white rhino only. ● dry season, 2-cm clipping treatment; ○ wet season, 2-cm clipping treatment; △ wet season, 6-cm clipping treatment.

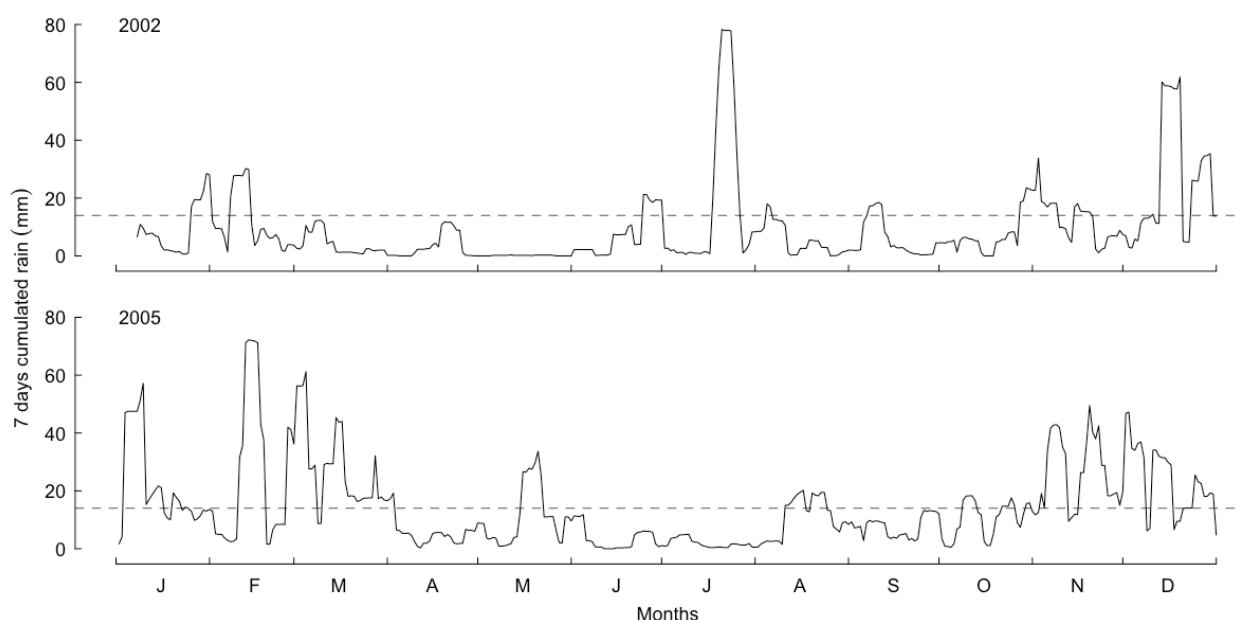


Fig. 4. Daily variation of cumulative rainfall (mm) over seven preceding days in Hluhluwe during two contrasted years (an exceptionally dry year: 2002, and an average rainfall year: 2005). Dashed line represents the threshold of weekly cumulative rainfall (14 mm) allowing a significant primary production of grazing lawns. A total of 71 and 138 days exceeded this threshold for 2002 and 2005 respectively.