Seasonal variation in rumination parameters of free-ranging impalas (*Aepyceros melampus*)

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Abstract. By decreasing particle size of ingested forages, and thereby exposing more surface area to microbial degradation, chewing plays a key role in digestion efficiency in ruminants. However, the investigation of chewing behaviour at a fine scale, and in particular of rumination parameters such as chew number or bolus duration, remains surprisingly largely limited to applied agricultural research. The goal of the present study was to investigate the seasonal effects on rumination parameters in free-ranging impalas (*Aepyceros melampus*), an African ruminant experiencing a strong seasonality in food quality. Male and female impala increased both chew number and bolus duration in the dry season as compared to the rainy season. This is consistent with previous studies on livestock reporting an effect of food quality on rumination parameters, and with previous work on impala reporting an effect of season on food quality. The coefficient of variation in the chew number increased for both sexes between the rainy season and the dry season, consistently with the greater variability in the food items consumed in the dry season as reported by previous studies. Only males had an increased coefficient of variation in bolus duration between the rainy season and the dry season. Because females with young may increase chewing investment as compared to dry females in response to energetic costs of lactation, the heterogeneity in reproductive status among females during the rainy season (i.e. rearing period) may have resulted in heterogeneity in bolus duration, thereby interfering with the effect of the variability in the plants consumed. Rumination is an important process that seems to have been overlooked in field studies. Future studies, based on long-term data sets of marked free-ranging individuals should investigate to which extent parameters as easy to record as chew number or bolus duration could be used by managers to assess factors as food quality and thus, ultimately, population performance in ruminants.

Introduction

Rumination behaviour is classically considered in behavioural ecology studies investigating activity budgets of free-ranging ruminants: a focal individual is « ruminating », as opposed, for instance, to « feeding » or « being vigilant ». « Feeding », or « being vigilant », however, are often further described at a finer scale: information on bite rate or step rate while feeding (Ruckstuhl 1998, Ruckstuhl et al. 2003) or on scan rate or scan frequency while being vigilant (Hunter & Skinner 1998) are widespread in the literature. At the opposite, very few field studies investigated rumination at a finer scale, i.e. at the scale of a bolus (e.g. Ginnett & Demment 1997), and in particular in relation to life history strategies of free ranging animals (e.g. Blanchard 2005). However, by decreasing particle size of ingested forages, and thereby exposing more surface area to microbial degradation (Pond et al. 1984, Pan et al. 2003), chewing plays a key role in digestion efficiency, and in particular during rumination (Trudell-Moore & White 1983, Chai et al. 1984). Accordingly, rumination parameters such as the number of chews per bolus or the bolus duration, have been deeply investigated in agricultural sciences. Numerous studies on livestock reported effects of forage nutritional characteristics on rumination behaviour (Gibb et al. 1999, Tafaj et al. 2005a), and others reported effects of rumination behaviour on digestion efficiency (Domingue et al. 1991). Hence, despite clear evidence for their direct importance in animal feeding biology, the investigation of rumination parameters remains surprisingly largely limited to applied agricultural research (but see Gross et al. 1995, 1996, Ginnett & Demment 1997, Blanchard 2005).

The goal of the present study was to investigate the seasonal effects on rumination parameters in free-ranging impalas (*Aepyceros melampus*), a dimorphic African ruminant experiencing a strong seasonality in climate and food quality. We tested the two following predictions. Forage quality affects rumination parameters (Pérez-Barbería & Gordon 1998). In particular, more fibrous food requires more chewing. Using experimentally controlled diets, several studies on cattle reported a positive influence of fibre content on the chew number and/or on bolus duration (Moon et al. 2004, Tafaj et al. 2005a). Thus, because herbivore diet quality (including those of impalas [Skinner et al. 1983, Meissner et al. 1996]) is lower during the dry season compared to the rainy season, our first prediction was an increase in bolus duration and in the chew number during rumination in the dry season as compared to the rainy season. Impalas are mixed feeders (Hofmann 1989) known to exhibit a great dietary flexibility (Meissner et al. 1996, Sponheimer et al. 2003). In the rainy season, impalas mostly graze, whereas their diet is more balanced between grass and browse in the dry season (Skinner et al. 1983, Klein & Fairall 1986, Meissner et al. 1996, Wronski 2002). Because plant characteristics directly impact on rumination parameters, our second prediction was a decrease in the variability of the chew number and of bolus duration when animals mostly fed on a single type of food, i.e. when grazing during the rainy season. Overall, we thus expected lower average values and lower variability for the chew number and bolus duration in the rainy season as compared to the dry season. If confirmed, these results could promote future applied studies on rumination at a fine scale. A seasonal variation in rumination parameters, by clearly suggesting an effect of food quality, is indeed the first step before investigating to which extent inter-year or inter-population fluctuations of food quality, and thus, ultimately, of population

93 performance, may be assessed by variation in chew number or bolus duration. We also
94 paid particular attention to a potential sex effect on rumination parameters as sexual
95 dimorphism in body size is likely to lead to differences in digestive efficiencies, and
96 thus potentially to compensatory behaviour for the smaller sex (Ruckstuhl & Neuhaus
97 2002), such as increasing mastication investment (even at an intra-specific scale, Gross
98 et al. 1995, 1996, Ginnett & Demment 1997).

Material and methods

Study area and species

Hwange National Park, located on the north-west border of Zimbabwe (19°00'S, 26°30'E), covers an area of *ca.* 15,000 km². Vegetation is typical of southern African dystrophic wooded savannas with patches of grasslands (Rogers 1993). Altitude varies from 800m to 1,100m. The long-term annual rainfall average is 606 mm with most rain falling between November and April. In the Hwange system, young impala are generally born around the end of November or early December. Lactation generally lasts up to early April, when adult males start to exhibit rutting behaviours that last up to early June, with a peak in May. The study was carried out in the Main Camp region of the park, where impala density is ca. 1 ind/km^2 (S. Chamaillé-Jammes, M. Valeix, H. Fritz, M. Bourgarel and S. Le Bel, unpubl. report for the Zimbabwe National Parks and Wildlife Management Authority).

Data Sampling

The data were collected in 2005 during two 10 day periods, one in the rainy (between February 12th and February 22th) and one in the dry (between September 3rd and September 13th) season. Hence, we avoided important changes in forage characteristics within our two observation trials. A single observer (PB) performed all the observations from an open-top car, with 10 x 42 binoculars. We only focused on adults. Impalas were habituated to cars, and easy to observe. Most of the observations took place from 20-50 m. Focal individuals were chosen according to head orientation, since the face had to be clearly visible in order to record jaw movements. Each observation began with the

regurgitation of a bolus chosen randomly, and lasted until the fifth bolus was swallowed. We recorded the amount of time required to process 5 boli using a stopwatch, and the total number of chews performed during the focal (Blanchard 2005). Observations were discarded if the focal individual stopped chewing for at least 5s. We also recorded the sex (males have horns whereas females do not).

Individuals were not captured or marked as part of this study. Therefore, as impalas were not individually recognizable, we may have observed the same animal more than once (although not the same day). We performed a total of 102 observations: 40 and 32 females observed in rainy and dry season respectively (out of respectively 67 and 63 adult females in the studied population), and 16 and 14 males observed in rainy and dry season respectively (out of respectively 25 and 24 adult males). Therefore, by observing about the same proportion of individuals for each sex, we avoided increasing the pseudoreplication problem for one sex in respect to the other.

Data Analysis

We used linear mixed models (Pinheiro & Bates 2000) to investigate the effects of sex and season on both the number of chews requested and the time spent to process 5 boli. When finding a group of individuals ruminating, we often performed several observations within the same group. Therefore, we included “group identity” as a random factor in the analysis in order to control for the non-independence between these observations. To investigate the sources of variation of the number of chews and the total duration of 5 boli, we first tested the effect of the two-way interaction (sex by season) by testing the difference in log-likelihood between the models with and without the interaction. We then removed the non-significant interaction and successively

withdrawed each of the two main factors, testing for their significance by comparing the difference in log-likelihood between the models with and without each of the factors.

We compared the variation in rumination parameters using the coefficient of variation (CV), expressed for small samples as CV = (1+1/(4*n))*(standard deviation / mean)*100 (Sokal & Rohlf 1995), with n for the sample size. All statistical analyses used R software (R Development Core Team 2005).

Results

Average values of rumination parameters

Season clearly affected fine scale rumination patterns. From the rainy to the dry season, impalas increased both the number of chews performed per bolus (240.3 versus 268.6 chews for 5 boli in rainy and dry season respectively ; likelihood ratio = 11.5, difference in df = 1, $p < 0.001$; Figure 1) and the duration of a bolus (196.1 and 247.0 s for 5 boli during rainy and dry season respectively ; likelihood ratio = 35.0, difference in df = 1, $p < 0.001$; Figure 2), irrespective of their sex (number of chews for 5 boli : likelihood ratio = 1.9, difference in df = 1, $p = 0.17$ and interaction sex * season : likelihood ratio = 1.6, difference in df = 1, $p = 0.21$; duration of 5 boli : likelihood ratio = 2.1, difference in df = 1, $p = 0.14$ and interaction sex * season : likelihood ratio = 0.72, difference in df = 1, $p = 0.40$).

Variability in rumination parameters

171 The CV in the recorded parameters were affected by sex and season (Table 1). The CV
172 in the number of chews increased in dry season, as predicted by our second prediction,
173 for males (8.2% and 12.1% in rainy and dry season respectively) as for females (9.1%
174 and 14.5% in rainy and dry season respectively). However, sex impacted on the effect
175 of season on the CV of boli duration, with an increase in dry season for males (11.5% as
176 compared to 7.1% in rainy season), but not for females (12.4% as compared to 12.2% in
177 rainy season).
178
179 **Discussion**
180
181 Whereas behaviours such as foraging or vigilance are extensively investigated in free
182 ranging ruminants both at the scale of the time budget and at a finer scale (e.g. records
183 of bite rate or scan rate), rumination at fine scale (i.e. at the bolus scale) remains largely
184 overlooked in literature, despite its particular importance for ruminant feeding ecology.
185 Here, we focused on seasonal variation of rumination patterns in free ranging impalas.
186 Our data suggest that sex and season impacted on chew number and bolus duration.
187 Clearly, male and female impala increased both parameters while ruminating in the dry
188 season as compared to the rainy season, consistently with our first prediction based on
189 previous studies reporting a negative effect of food quality on the average values of
190 these rumination parameters (Moon et al. 2004, Tafaj et al. 2005a), and a diet of better
191 quality in rainy season compared to dry season for impalas (Skinner et al. 1983,
192 Meissner et al. 1996). Sex did not influence average values of chew number or bolus
193 duration. Sexual differences in body size are likely to lead to differences in feeding
194 behaviour, including rumination parameters (Gross et al. 1995, 1996, Ginnett &

195 Demment 1997). However, the sexual dimorphism displayed by our studied animals
196 (about 20%, M. Bourgarel & H. Fritz, unpubl. data) was probably too small compared
197 to those reported by previous studies (about 135% for Nubian Ibex, Gross et al. 1995) to
198 easily detect potential sexual differences in rumination patterns. The CV in the number
199 of chews increased for both sexes between the rainy season and the dry season, whereas
200 only males increased CV in bolus duration. Once again, it is broadly consistent with our
201 prediction that the greater variability in the food items consumed in the dry season
202 (Skinner et al. 1983, Meissner et al. 1996, Wronski 2002) should lead to an increase in
203 the variability in the chew number and in bolus duration from the rainy season to the
204 dry season.
205
206 Average values of rumination parameters
207
208 Rumination parameters reflect the physical and chemical characteristics of previously
209 ingested forages (Pérez-Barbería & Gordon 1998). In particular, more fibrous forages
210 require higher chewing effort. In an indoor trial conducted with red deer (*Cervus*
211 *elaphus*) fed either fresh perennial ryegrass (*Lolium perenne*) or chicory (*Chicorium*
212 *intybus*), Hoskin et al. (1995) reported higher chewing effort, including chew number,
213 for deer fed with the more fibrous ryegrass. Moon et al. (2004) reported longer bolus
214 duration in dairy cows fed with experimental diets increasing in fiber concentration.
215 Here, we report that both bolus duration and chew number increased in the dry season
216 as compared to the rainy season, irrespective of the sex of the animals. Impalas are
217 mixed feeders (Hofmann 1989), moving to more woody browse in the dry season, when
218 grass quality becomes too low (Klein & Fairall 1986, Meissner et al. 1996, Wronski

2002). Therefore, the decrease in the quality of the forages ingested by impala during the dry season (Skinner et al. 1983, Meissner et al. 1996) probably results in the longer bolus duration and in the increase in the chew number we report as compared to the rainy season.

Food quality, and in particular fiber content, has also been reported to affect the total time devoted to rumination (Moon et al. 2004), and intake rate may impact on rumination parameters (Bae et al. 1979, Tafaj et al. 2005b). Further studies performed at both fine and large scales for a single population, could improve the understanding of the relationships between food quality, food quantity, time budget and rumination parameters. Further, because many of the indices used by managers to assess nutritional status of free-ranging populations require the capture or the killing of the animal and /or are expensive or irrelevant (Blanchard et al. 2003), future studies should investigate the reliability of rumination parameters in assessing the variability of food quality for a given species according to season, year for a given season, or locality / population.

Variability in rumination parameters

We report that season broadly impacted on the variability in rumination parameters, probably explained by a broader range of food items selected in the dry season as compared to the rainy season, as suggested by previous studies (Skinner et al. 1983, Meissner et al. 1996, Wronski 2002). This explanation is also consistent with personal observations in the study area: impalas were mostly seen grazing during the wet season, whereas they relied on more various sources of food in the dry season, including browse and *Acacia* pods but also dried grass, which may form the bulk of their rumen fill. The

243 increase in the variability in the food items consumed during the dry season therefore
244 probably explains the increase in the variability in the chew number reported for both
245 sexes, with more chews being performed when ingesting lower quality items (i.e. lower
246 than the average forage quality, already lower than mean forage quality in rainy season).
247 The CV in bolus duration was lower in the rainy season as compared to the dry
248 season for males, as predicted by our second prediction, but the CV in females bolus
249 duration was not affected by season. Females showed about the same variability in both
250 seasons, with more variability than males in the rainy season. Differences in the
251 reproductive statuses of females may explain this result. Some of the females observed
252 during the rainy season (i.e. the rearing period) were probably lactating while other
253 were probably not (48 juveniles were present in the study area over a total of 67 adult
254 females in the rainy season), whereas all young were weaned in the dry season so that
255 all adult females had similar status. This heterogeneity in reproductive statuses in the
256 rainy season may have been translated into a heterogeneity in bolus duration. Blanchard
257 (2005), focusing on the rearing period, investigated variation in rumination parameters
258 as a function of presence / absence of lamb in bighorn sheep ewes (*Ovis canadensis*),
259 and suggested that lactating females increased chewing effort, in response to an
260 increased energetic demand and risk of predation, as compared to yeld females. In order
261 to avoid foraging longer than yeld females to meet the energetic costs of lactation, and
262 thus to enjoy the benefit of group foraging (Kie 1999, Sevi et al. 1999) through
263 synchronization of activities (Ruckstuhl 1998), lactating females may compensate for an
264 increase intake rate by increasing chewing effort during rumination (Blanchard 2005).
265 In the present study, lactating females may decrease bolus duration as compared to yeld
266 females, in order to process more boli during the same amount of time spent ruminating.

This would mean that lactating females increase rumination speed, as reported for bighorn sheep (Blanchard 2005).

Future studies should investigate the impact of reproductive status on foraging behaviour on marked female impalas, as this interpretation remains speculative. Also, if lactating females ruminate faster than yeld females (Blanchard 2005), the CV in rumination speed among females during the rearing period should crudely scale with the ratio of lactating female to yeld female, i.e. the young:female ratio, an index often used by managers to infer ungulates population dynamics (Bonenfant et al. 2005).

Rumination, and in particular at a fine scale, seems to have often been overlooked in field studies. More studies are thus required to improve our understanding of the relationship between rumination behaviour at both large and fine scales (Ginnett & Demment 1997), food characteristics and population dynamics. Because ungulate population dynamics is strongly influenced by changes in density and climatic conditions (Saether 1997, Gaillard et al. 1998), mostly through their effect on food availability and quality, a proxy of nutritional status would be useful for managers interested in wildlife demography (Blanchard et al. 2003). Future studies, based on long-term data sets of marked free-ranging individuals should investigate to which extent measures as easy to record as chew number or bolus duration could be used to assess factors as important as resources properties and thus, ultimately, population performance in ruminants.

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References

Bae, D. H., Welch, J. G. & Smith, A. M. 1979: Forage intake and rumination by sheep. - Journal of Animal Science 49: 1292-1299.

Blanchard, P. 2005: On lactation and rumination in bighorn ewes (*Ovis canadensis*). - Journal of Zoology 265: 107-112.

Blanchard, P., Festa-Bianchet, M., Gaillard, J.-M. & Jorgenson, J. T. 2003: A test of long-term fecal nitrogen monitoring to evaluate nutritional status in bighorn sheep. - Journal of Wildlife Management 67: 477-484.

Bonenfant, C., Gaillard, J.-M., Klein, F. & Hamann, J.-L. 2005: Can we use the young : female ratio to infer ungulate population dynamics? An empirical test using red deer *Cervus elaphus* as a model. - Journal of Applied Ecology 42: 361-370.

Chai, K., Kennedy, P. M. & Milligan, L. P. 1984: Reduction in particle size during rumination in cattle. - Canadian Journal of Animal Science 64: 339-340.

Domingue, B. M. F., Dellow, D. W. & Barry, T. N. 1991: The efficiency of chewing during eating and ruminating in goats and sheep. - British Journal of Nutrition 65: 355-363.

Gaillard, J.-M., Festa-Bianchet, M. & Yoccoz, N. G. 1998: Population dynamics of large herbivores - variable recruitment with constant adult survival. - Trends in Ecology & Evolution 13: 58-63.

Gibb, M. J., Huckle, C. A., Nuthall, R. & Rook, A. J. 1999: The effect of physiological state (lactating or dry) and sward surface height on grazing behaviour and intake by dairy cows. - Applied Animal Behaviour Science 63: 269-287.

318 Ginnett, T.F. & Demment, M.W. 1997: Sex differences in giraffe foraging behavior at
319 two spatial scales. - Oecologia 110: 291-300.
320 Gross, J. E., Demment, M. W., Alkon, P. U. & Kotzman, M. 1995: Feeding and
321 chewing behaviours of Nubian ibex - compensation for sex-related differences in
322 body size. - Functional Ecology 9: 385-393.
323 Gross, J. E., Alkon, P. U. & Demment, M. W. 1996: Nutritional ecology of dimorphic
324 herbivores - digestion and passage rates in Nubian ibex. - Oecologia 107: 170-
325 178.
326 Hofmann, R. R. 1989: Evolutionary steps of ecophysiological adaptation and
327 diversification of ruminants: a comparative view of their digestive system. -
328 Oecologia 78: 443-457.
329 Hoskin, S. O., Stafford, K. J. & Barry, T. N. 1995: Digestion, rumen fermentation and
330 chewing behaviour of red deer fed fresh chicory and perennial ryegrass. - Journal
331 of Agricultural Science 124: 289-295.
332 Hunter, L. T. B. & Skinner, J. D. 1998: Vigilance behaviour in african ungulates: the
333 role of predation pressure. - Behaviour 135: 195-211.
334 Kie, J. G. 1999: Optimal foraging and risk of predation: effects on behavior and social
335 structure in ungulates. - Journal of Mammalogy 80: 1114-1129.
336 Klein, D. R. & Fairall, N. 1986: Comparative foraging behaviour and associated
337 energetics of impala and blesbok. - Journal of Applied Ecology 23: 489-502.
338 Meissner, H. H., Pieterse, E. & Potgieter, J. H. J. 1996: Seasonal food selection and
339 intake by male impala *Aepyceros melampus* in two habitats. - South African
340 Journal of Wildlife Research 26: 56-63.

341 Moon, Y. H., Lee, S. C. & Lee, S. S. 2004: Effects of neutral detergent fiber
342 concentration and particle size of the diet on chewing activities of dairy cows. -
343 Asian-Australasian Journal of Animal Sciences 17: 1535-1540.
344 Pan, J., Koike, S., Suzuki, T., Ueda, K., Kobayashi, Y., Tanaka, K. & Okubo, M. 2003:
345 Effect of mastication on degradation of orchardgrass hay stem by rumen
346 microbes: fibrolytic enzyme activities and microbial attachment. - Animal Feed
347 Science and Technology 106: 69-79.
348 Pérez-Barbería, F. J. & Gordon, I. J. 1998: Factors affecting food comminution during
349 chewing in ruminants : a review. - Biological Journal of the Linnean Society 63:
350 233-256.
351 Pinheiro, J. C. & Bates, D. M. 2000: Mixed-effects models in S and S-PLUS. Springer-
352 Verlag. New York. 528 pp.
353 Pond, K. R., Ellis, W. C. & Akin, D. E. 1984: Ingestive mastication and fragmentation
354 of forages. - Journal of Animal Science 58: 1567-1574.
355 R Development Core Team. 2005: R: A language and environment for statistical
356 computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-
357 900051-07-0. URL http://www.R-project.org.
358 Rogers, C. M. L. 1993: A woody vegetation survey of Hwange National Park. Report
359 for the Department of National Parks and Wildlife Management.
360 Ruckstuhl, K. E. 1998: Foraging behaviour and sexual segregation in bighorn sheep. -
361 Animal Behaviour 56: 99-106.
362 Ruckstuhl, K.E. & Neuhaus, P. 2002: Sexual segregation in ungulates: a comparative
363 test of three hypotheses. - Biological Reviews 77: 77-96.

364 Ruckstuhl, K. E., Festa-Bianchet, M. & Jorgenson, J. T. 2003: Bite rates in rocky
365 mountain bighorn sheep (*Ovis canadensis*): effects of season, age, sex and
366 reproductive status. - Behavioral Ecology and Sociobiology 54: 167-173.
367 Saether, B.-E. 1997: Environmetal stochasticity and population dynamics of large
368 herbivores - a search for mechanisms. - Trends in Ecology & Evolution 12: 143-
369 149.
370 Sevi, A., Casamassima, D. & Muscio, A. 1999: Group size effects on grazing behaviour
371 and efficiency in sheep. - Journal of Range Management 52: 327-331.
372 Skinner, J. D., Monro, R. H. & Zimmermann, I. 1983: Comparative food intake and
373 growth of cattle and impala on mixed tree savanna. - South African Journal of
374 Wildlife Research 14: 1-9.
375 Sokal, R. R. & Rohlf, F. J. 1995: Biometry: the principles and practice of statistics in
376 biological research. 3rd edition. W. H. Freeman and Co. New York. 887 pp.
377 Sponheimer, M., Grant, C. C., de Ruiter, D., Lee-Thorp, J., Codron, D. & Codron, J.
378 2003: Diets of impala from Kruger National Park: evidence from stable carbon
379 isotopes. - Koedoe 46: 101-106.
380 Tafaj, M., Kolaneci, V., Junck, B., Maulbetsch, A., Steingass, H. & Drochner, W.
381 2005a: Influence of fiber content and concentrate level on chewing activity,
382 ruminal digestion, digesta passage rate and nutrient digestibility in dairy cows in
383 late lactation. - Asian-Australasian Journal of Animal Sciences 18: 1116-1124.
384 Tafaj, M., Maulbetsch, A., Zebeli, Q., Steingass, H. & Drochner, W. 2005b: Effects of
385 physically effective fibre concentration of diets consisting of hay and slowly
386 degradable concentrate on chewing activity in mid lactation dairy cows under
387 constant intake level. - Archives of Animal Nutrition 59: 313-324.

388 Trudell-Moore, J. & White, R. G. 1983: Physical breakdown of food during eating and
389 rumination in reindeer. - Acta Zoologica Fennica 175: 47-49.
390 Wronski, T. 2002: Feeding ecology and foraging behaviour of impala *Aepyceros*
391 *melampus* in Lake Mburo National Park, Uganda. - African Journal of Ecology
392 40: 205-211.

393 **Table 1.** Coefficients of variation (CV) in the number of chews and the time required to
394 process 5 boli according to sex and season in impalas, Hwange National Park.
395

	Parameters	CV for rainy season	CV for dry season
Males	Number of chews / 5 boli	0.082	0.121
	Duration of 5 boli (s)	0.070	0.115
Females	Number of chews / 5 boli	0.091	0.145
	Duration of 5 boli (s)	0.122	0.124

Figures legend

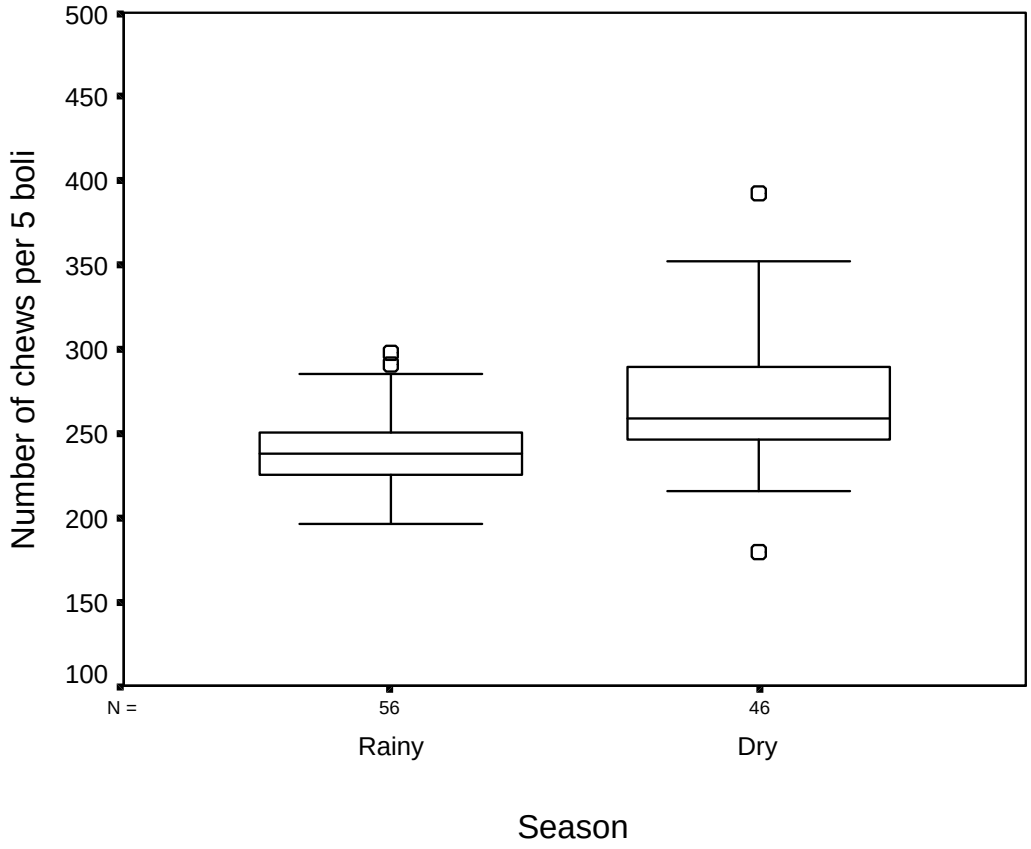
Figure 1

Number of chews performed to process 5 boli according to the season for impalas observed in Hwange National Park. The line across the grey box indicates the median. The box represents the interquartile range that contains the 50% of values. The whiskers are lines that extend from the box to the highest and lowest values, excluding outliers. Outliers (values between 1.5 and 3 box lengths from the upper or lower edge of the box) are represented by open circles.

Figure 2

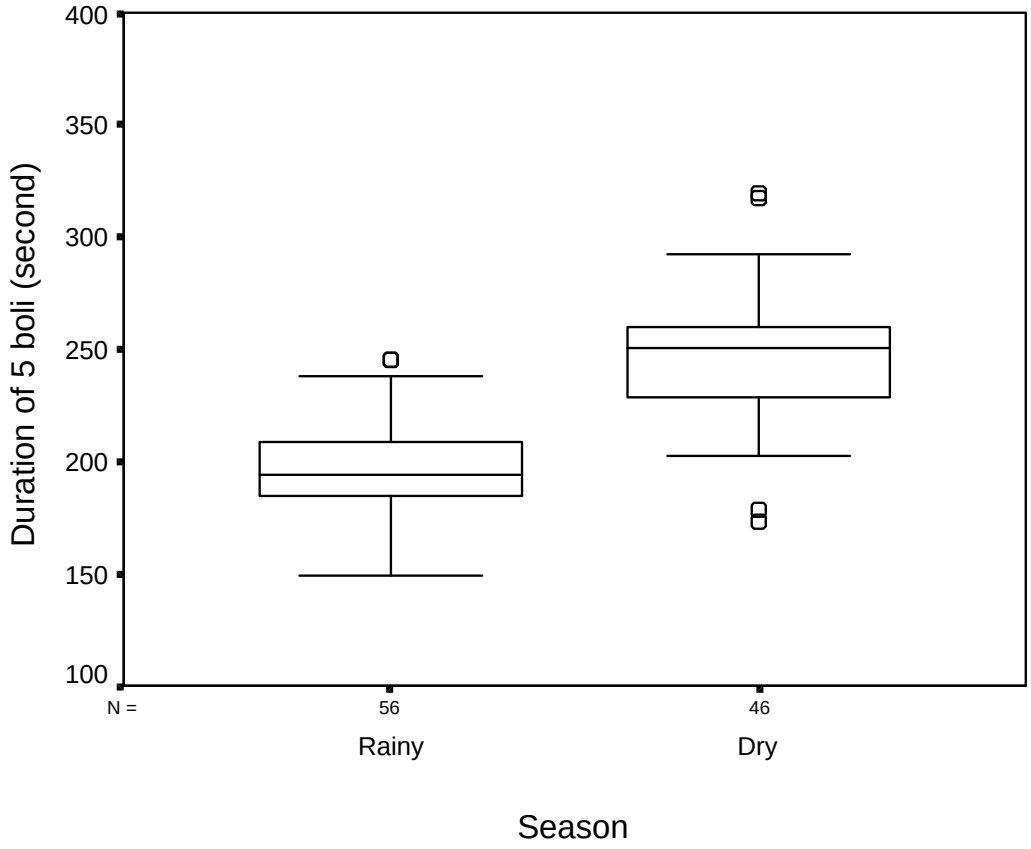
Duration (second) of five boli according to the season for impalas observed in Hwange National Park. See Figure 1 legend for graph displays explanations.

409 **Figure 1**



410

411 **Figure 2**



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