

1 **An experimental demonstration that predation**
2 **influences antelope sex ratios and resource-associated**
3 **mortality**

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5
6 **Christopher A.J. O’Kane** ^{a,1} christopher.okane@zoo.ox.ac.uk

7 **David W. Macdonald** ^a david.macdonald@zoo.ox.ac.uk

8

9 ^a Wildlife Conservation Research Unit, Department of Zoology, University of Oxford,
10 The Recanati-Kaplan Centre, Tubney House, Abingdon Road, Tubney, Oxon OX13 5QL,
11 United Kingdom.

12 ¹Corresponding author: address as at ^a, tel: +44 (0) 1865 393100, fax: +44 (0) 1865
13 393101

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20

21 Summary

22 **1.** Smaller, enclosed reserves lacking large mammalian predators are an increasingly
23 popular commercial model in southern Africa and elsewhere. The presence or absence of
24 predation is likely to have major effects on the population dynamics of sexually
25 dimorphic ungulates, with contradictory implications for multiple-use reserves, and to
26 provide fundamental insights into predator-prey relationships.

27

28 **2.** Over a two and four year period we determined the adult sex ratios and juvenile
29 mortality of two substantial populations of impala *Aepyceros melampus* in South Africa
30 – one in predator-free Ithala Game Reserve (IGR), the other in neighbouring predator-
31 laden Hluhluwe-iMfolozi Park (HiP). Data were collected monthly, over a five day
32 period, by repeated road transects covering a representative sample of the reserves'
33 habitat types. We assessed differences in adult sex ratios by applying Pearson's chi-
34 square test, whilst to explore the relationship between juvenile mortality, the advance of
35 the breeding year, rainfall and the presence or absence of predators, we used a
36 generalized linear model.

37

38 **3.** We found that the impala adult male to adult female ratio was lower in the presence of
39 predation (HiP = 0.43, IGR = 0.69; $\chi^2 = 424.2$, $df = 1$, $P < 0.005$). The generalized linear
40 model revealed that the proportion of breeding herds (defined as herds containing at least
41 one juvenile) formed by juveniles declined, over the breeding year, at a faster rate in the
42 presence of predators.

43

44 **4.** Impala juvenile mortality over the breeding year was not significantly affected by
45 lower rainfall in the absence of predators, but under predation juvenile mortality declined
46 at a faster rate over a drier year compared to years of near average rainfall – a novel
47 finding amongst African antelope.

48

49 **5. *Synthesis and applications.*** We demonstrate that predation skews antelope adult sex
50 ratios towards females, increases juvenile mortality and, a novel finding, influences the
51 interaction between rainfall and juvenile mortality. Such fundamental insights into
52 predator-prey relationships are especially relevant to predator-free reserves, where
53 management and planners should be aware of these influences and, depending on the
54 business model, consider replicating them artificially.

55

56 **Key Words:** Africa, demographics, dimorphic, impala, juvenile mortality, rainfall,
57 savanna, ungulates

58

59 **Introduction**

60

61 Differences in demographics may lead to changes in social interactions (Pace, Pulcini, &
62 Triossi, 2012; Wittemyer, Douglas-Hamilton, & Getz, 2005), have implications for
63 population growth (Fitzgibbon & Lazarus, 1995; P. J. Jarman & Jarman, 1973) and, in
64 the longer term, may affect natural selection (Kasumovic, Bruce, Herberstein, &
65 Andrade, 2009). Such factors may negatively impact biodiversity, tourist revenues, game
66 sales and initiatives to develop conservation partnerships with neighbouring communities
67 based primarily on the harvesting of game. Where differences in demographics are
68 caused by the presence or absence of predation, they also provide fundamental insights
69 into predator-prey relationships (Abrams, 2000; Berryman, 1992; Gervasi et al., 2012),
70 with theoretical implications for productivity of both prey and predator (Abrams, Namba,
71 Mimura, & Roth, 1997; Husek et al., 2013) and possible cascading effects on vegetation
72 (Grabowski, Hughes, & Kimbro, 2008; Maron, 2011).

73 Caughley (1974) observed that age ratios *per se* contain little relevant information
74 and large variations in numbers may go undetected by changes in them. Attwell (1977)
75 described more relevant parameters of population structure, namely the sex ratios of
76 adults, the percentage of juveniles and the juvenile to adult female ratio. A snap shot of
77 demographics is of limited use; reliable information on trends is central to the
78 conservation and management of game populations (Mason, 1990) and to understanding
79 predator-prey dynamics (Bissett, Bernard, & Parker, 2012; Sinclair et al., 2007).
80 Consequently they need to be repeatedly determined over a time frame likely to pick up
81 any such trends.

82 Polygynous mating systems involve competition between males, leading to the
83 evolution of sexual dimorphism through sexual selection (Darwin, 1871). Variation in
84 mammalian adult sex ratios is striking both intra- and inter-specifically; Darwin
85 suggested that causes of variation might include competition between males for females
86 and predation, and recognized that the degree of competition might be related to the
87 extent of sexual dimorphism. In African antelope species Jarman (1974) proposed a
88 series of relationships between habitat use, food dispersion and social behaviour, and
89 hypothesised a series of evolutionary steps (Perez-Barberia, Gordon, & Pagel, 2002)
90 leading to sexual dimorphism in body size through sexual selection. Although a
91 straightforward link between sexual dimorphism and mortality has been widely
92 discussed/presumed (Alexander, Hoogland, Howard, Noonan, & Sherman, 1979;
93 Andersson, 1994; Clutton-Brock, Albon, & Harvey, 1980; Weckerly, 1998), studies
94 where the effects of common ancestry have been removed by computing phylogenetically
95 independent contrasts failed to detect this link (Berger & Gompper, 1999; Toigo &
96 Gaillard, 2003). It seems, rather, that species' life-history traits predispose sexes to
97 differential mortality and that these characteristics are shaped, at a proximate level, by
98 environmental conditions including predation.

99 *Impala Aepyceros melampus* Lichtenstein, a sexually dimorphic and ubiquitous
100 antelope of the southern African region (Smithers, 1983), are heavily predated. Adult
101 male impala are preferentially selected by predators in general (Hirst, 1969), and by lion
102 in particular (Funston, Mills, & Biggs, 2001; Mitchell, Shenton, & Uys, 1965; Pienaar,
103 1969). Additionally, vigilance behaviour in impala has been shown to be markedly
104 increased in the presences of predators (Hunter & Skinner, 1998; Periquet et al., 2012),

105 whilst herbivore populations not exposed to high predation pressure over as few as
106 several generations appear to lose some of their antipredator behaviour (Blumstein, 2002;
107 but see Dalerum & Belton, 2015). Reduced time spent in vigilance in the absence of
108 predators probably translates into energy saving and, as herd size and vigilance behaviour
109 show a negative correlation in impala (Hunter & Skinner, 1998), this is likely to
110 disproportionately benefit males as bachelor groups are smaller than breeding groups.

111 Standing crop biomass and production by large mammalian herbivores in African
112 savannas show a high degree of correlation with mean annual precipitation, particularly
113 where mean annual precipitation is less than 700mm (Coe, Cumming, & Phillipson,
114 1976; East, 1984). It has been demonstrated in African ungulates that predator prey
115 choice may change in response to rainfall, via a presumed link between ungulates'
116 condition and their susceptibility to predation (Mills, Biggs, & Whyte, 1995; Owen-
117 Smith & Mills, 2006).

118 Hluhluwe-iMfolozi Park (HiP) and Ithala Game Reserve (IGR), South Africa, are
119 two fenced game reserves composed of similar habitat types separated by less than 100
120 km. However, whilst HiP (created 1895) has always contained a full suite of large
121 mammalian predators, IGR has been virtually predator free since its creation in 1972. In
122 both reserves impala are the prevalent antelope and their demographics are readily
123 determined and monitored by repeated road transects. Over a period of two and four
124 years we recorded and compared the age and sex structure of impala in the two reserves,
125 to assess the influence predation may have on impala demographics. We hypothesised
126 that the presence or absence of predation will influence 1) impala adult sex ratios, 2)

127 impala juvenile mortality, and 3) the interaction between impala juvenile mortality and
128 rainfall.

129

130

131 **Methods**

132

133 **Study areas**

134 Both Hluhluwe–iMfolozi Park (900 km²) and Ithala Game Reserve (300 km²) are situated
135 in KwaZulu–Natal, South Africa (28°00′–28°26′S, 31°43′–32°09′E and 27°30′S,
136 31°25′E respectively). Both are effectively completely fenced nature reserves, with
137 altitude ranging from 450 m to 60 m a.s.l. in HiP and from 1550 m to 350 m a.s.l. in IGR.
138 The vegetation of HiP consists of Zululand lowveld, northern Zululand sourveld and
139 scarp forest, whilst in IGR Zululand lowveld, Zululand bushveld and north-eastern
140 mountain grassland are found (Mucina & Rutherford, 2006). In both reserves impala are
141 found mainly in Zululand lowveld (O’Kane, Duffy, Page, & Macdonald, 2013; O’Kane,
142 Page, & Macdonald, 2014). Structurally, the vegetation in HiP is characterised by fine-
143 leaved *Acacia* savanna with a continuous grass layer and a fairly open tree canopy, whilst
144 in IGR it is a mosaic of grasslands, open savanna dominated by *Acacias* and more or less
145 closed thickets of broad-leaved shrubs and trees. Soils, in both HiP and IGR, are mainly
146 derived from sandstone, shale and dolerite intrusions and are generally eutrophic. In
147 iMfolozi, the section of HiP favoured by impala, long term annual rainfall is 635mm and
148 in IGR 791mm, with rain falling mainly during the warm to hot (18-30°C) summer
149 (October to March). The second year of study in both reserves was a particularly dry year

150 (HiP: Y1 713mm, Y2 481mm; IGR: Year1 681mm, Y2 427mm, Y3 534mm, Y4
151 561mm).

152 Both reserves carry a full suite of megaherbivores (elephant, rhino and giraffe)
153 and mesoherbivores (impala, kudu, nyala, wildebeest, zebra) typical of the region, with
154 impala at a density of 26.1 km⁻² in HiP and 10 km⁻² in IGR (K.Z.N.Wildlife, 2008).
155 Although there are rare sightings of leopard, IGR is not stocked with the major predators
156 (lion, hyaena, cheetah, leopard and wild dogs) that exist in considerable numbers in HiP,
157 especially in the regions of iMfolozi favoured by impala.

158

159 **Data collection**

160 Data were collected in HiP over two years and in IGR over four years. In each reserve we
161 drove at 20 km h⁻¹ on the same fixed route through a representative sample of the
162 different vegetation types, using the reserve's road network, for 5 d mo⁻¹ throughout the
163 year. Once within a classifiable distance with an unobstructed view of the individual or
164 herd of impala, the total number of animals (IGR = 8,054; HiP = 24,576), their age and
165 sex were determined. Impala are seasonal breeders and, as previously observed (Brooks,
166 1985), usually give birth at Ithala and HiP over a few weeks in November and December.
167 Therefore, for convenience, 1st November was taken as the start of the breeding season,
168 so that during that month animals will be newborn (juveniles), 12 months (yearlings) or
169 24 months and above (adults). Due to the difficulty in differentiating yearling and adult
170 impala females, all analysis on adults incorporates both yearling and adult in the same
171 category. Whilst impala males bear horns, impala females do not. Due to the increasing
172 difficulty (except at close range) in the second half of the breeding year in distinguishing

173 female impala juveniles from female yearlings or adults, as of 1st May all females were
174 counted together. In southern Africa juvenile impala of both sexes remain within their
175 natal herd throughout the first year of life (P. J. Jarman & Jarman, 1973; Murray, 1982).
176 Therefore, for the period 1st May to 31st October the number of juvenile females was
177 taken to be the same as the number of (easily distinguishable, horned) juvenile males, as
178 it seems reasonable to assume there is no difference in their mortality while both sexes
179 remain within the herd. The precise criteria for age and sex classification are as per
180 Brooks (1985).

181

182 **Data analysis**

183 Using a database we determined the total number of adult male versus female impala
184 over a complete breeding year (1st November to 31st October). To assess whether there
185 was a difference in impala adult sex ratios (male/female) in HiP (predators present)
186 versus those in IGR (predators absent), we applied Pearson's chi-square test with Yates'
187 continuity correction (Crawley, 2005) to the contingency table. We tested for significance
188 of difference between the combined four year data set from IGR and the combined two
189 year data set from HiP, and between all possible combinations of comparing an
190 individual year's adult sex ratios in one reserve with those from the other reserve.

191 As virtually all impala juveniles remain, in both reserves, within their natal
192 breeding herd, we assessed juvenile mortality in terms of the monthly decline in the
193 proportion of breeding herds that juveniles form per month (i.e. total number of impala
194 juveniles in breeding herds per month/total number of all impala in breeding herds per
195 month). This proportion peaks in February and declines as the breeding year advances.

196 To explore the relationship between juvenile mortality, the advance of the breeding year
197 and the presence or absence of predators, we used a generalized linear model having the
198 proportion of breeding herds formed by juveniles per month as the response variable
199 (thus requiring a Binomial family with a logit link), with number of months passed from
200 the February peak (continuous), HiP or IGR (categorical) and interactions as explanatory
201 variables (Crawley, 2005). Again, data were analysed both using the combined data sets
202 from each reserve and using individual year's data, with the latter allowing exploration of
203 any possible link between juvenile mortality, yearly rainfall and the presence or absence
204 of predators. All statistical procedures were carried out in S-PLUS (Mathsoft 1999.
205 Lucent Technologies, Inc., Murray Hill, USA).

206

207

208 **Results**

209

210 In both reserves we recorded fewer male adult impala than female adult impala.

211 Comparing the combined data from HiP (predators present) with the combined data from

212 IGR (predator free), the adult sex ratio was more biased towards females in the presence

213 of predators (male/female HiP = 0.43, IGR = 0.69; $\chi^2 = 424.2$, $df = 1$, $P < 0.005$).

214 Comparison of all possible pairings of individual year's results from the two reserves

215 revealed the same bias towards females where predators were present (least difference

216 found between HiP Y2 versus IGR Y2: male/female HiP = 0.44, IGR = 0.62; $\chi^2 = 55.5$, df

217 = 1, $P < 0.005$).

218 The percentage individuals in impala breeding herds that were juveniles showed a
219 peak (February) to trough (October) of 26% to 16% in HiP (Y 1: 29% to 17%, Y 2: 24%
220 to 12%) and 30% to 22% in IGR (Y 1: 30% to 21%, Y 2: 32% to 22%, Y3: 29% to 22%,
221 Y 4: 30% to 21%). The generalized linear model showed a strong correlation between the
222 monthly decline in the proportion of breeding herds formed by juveniles and the number
223 of months passed from the February peak; this was the case with both the combined data
224 and individual year's data in both reserves. The slope of this correlation was greater
225 where predators were present (HiP) compared to where predators were absent (IGR)
226 (Table 1). The y intercept of the regression for IGR was higher than that for HiP. Whilst
227 there was no difference between the unusually dry year (Y 2) and the other three years
228 where there were no predators (IGR), the slope of this correlation was greater over the
229 unusually dry year (Y 2), compared to the year of more normal rainfall, where predators
230 were present (HiP) (Table 2 and Figure 1).

231

232

233 **Discussion**

234

235 Our results strongly suggest that predators influence the sex ratio of adult impala,
236 reducing the proportion of adult males in the population. Results from other southern
237 African sites suggest that lions preferentially kill male impala (lion absent: adult male to
238 female ratio 0.57 (Dasmann & Mossman, 1962), 0.56 (Brooks, 1975); lion present: 0.44
239 (Dasmann & Mossman, 1962), 0.41 (Anderson, 1967)), whilst cheetah preferentially kill
240 female impala (Brooks, 1975; Pienaar, 1969). It seems likely that the comparatively

241 smaller and more delicate cheetah's strategy is to avoid potential injury from the male's
242 substantial horns, whilst the larger, pride hunting lion, un-intimidated by the male's
243 horns, selects the larger prey (60 kg vs. 45 kg (Estes, 1997)). Our findings suggest that
244 where a full suite of predators exists, the overall effect is a reduction in the male to
245 female impala ratio. Levels of vigilance are also probably relevant to variations in sex
246 ratios. Territorial males, solitary or preoccupied with the females in their territory, are
247 likely to be more susceptible to predation, as are groups of bachelor males where the
248 combined vigilance of the group is likely to be less than that of the substantially larger
249 breeding groups, in which all female impala reside (see Hunter & Skinner, 1998).
250 Additionally, as discussed in the introduction, the reduced vigilance requirement in the
251 absence of predators is likely to disproportionately benefit the energy budget of impala
252 males, in the smaller bachelor groups, compared to females.

253 The mortality suffered by impala juveniles throughout the year in the absence of
254 predation was, presumably, consequent on disease, injury and declining resource
255 availability following reduced rainfall over the dry season. The lack of a statistically
256 significant increase in the rate of this mortality in response to the unusually dry year in
257 predator-free IGR, is probably due to the mixed-feeding ability of impala. The effect of
258 one year's lower rainfall on the browse would be limited compared to its effect on grass
259 growth (Owen-Smith & Mills, 2006) and, although impala prefer grass, they are adept at
260 switching between browse and grass (Smithers, 1983). Indeed, given the extreme length
261 of time impala, almost unique amongst the original African antelope, have had to adapt to
262 their environment (Matthee & Davis, 2001; Mooring, 1999; Vrba, 1983), it is not
263 surprising that they balance their grass versus browse intake to an optimal extent

264 (Meissner, Pieterse, & Potgieter, 1996). That a full suite of predators increased the
265 mortality rate of impala juveniles was unsurprising, but the demonstration of a
266 statistically significant interaction between lower rainfall and increased juvenile mortality
267 only in the presence of predators (HiP) is, as far as we are aware, a novel finding in
268 African antelope. Owen-Smith & Mills (2008) describe how over periods of low rainfall
269 Kruger lions switched their prey choice to include African buffalo. Our finding may be
270 consequent on similar prey switching (Dell'Arte, Laaksonen, Norrdahl, & Korpimäki,
271 2007; Patterson, Benjamin, & Messier, 1998) by smaller predators (e.g. jackals, martial
272 eagles, baboons) to include weakened impala juveniles, or may simply be due to the usual
273 suite of predators of juvenile impala achieving a higher capture rate of their weakened
274 prey. Impala mothers calve away from the herd, with fawns remaining concealed and
275 separate from the herd for a couple of days (M. V. Jarman, 1979). The cryptic predation
276 of these vulnerable juveniles is probably the explanation of the lower proportion juveniles
277 form of the breeding herds in HiP at the February peak (y intercept in glm, Table 1) of
278 the breeding year, rather than any consideration of resource limitation (see below).

279 Our findings should, however, be treated with caution as we have only shown
280 correlations between our results and the presence or absence of predation. Impala exist at
281 a considerably higher density in HiP (26.1 km⁻²) compared to IGR (10 km⁻²). The higher
282 density in HiP might be expected to translate into increased resource competition,
283 disproportionately increasing juvenile mortality and possibly influencing adult sex ratios
284 (Toigo & Gaillard, 2003). However in neither reserve are impala populations in decline,
285 arguing against marked resource limitation. Additionally in IGR we recorded atypical
286 seasonal habitat use by impala, which appears to be due to inter-specific competition for

287 grass with pure grazers which are at high densities (wildebeest, 6 km⁻²; zebra, 5.6 km⁻²
288 (C. A. J. O'Kane et al., 2014)) in that reserve but not in HiP (wildebeest, 1.1 km⁻²; zebra,
289 1.6 km⁻² (K.Z.N.Wildlife, 2008)). Thus any evidence of resource competition appears to
290 lie in IGR – yet this is the reserve in which we found lower rates of juvenile mortality,
291 arguing against resource competition as an alternative explanation of our findings. The
292 presence or absence of predators is the most likely, or parsimonious, explanation of our
293 findings. A mooted introduction of cheetah into IGR in the future will provide a natural
294 experiment, especially since cheetah do well in the absence of other predators
295 (Laurenson, 1995).

296 Smaller reserves lacking detectable predation are an increasingly popular
297 commercial model in southern Africa. If unusual adult sex ratios in mesoherbivores are to
298 be avoided, management needs to replicate the sex biased selection of predators, aiming
299 to achieve adult sex ratios observed in comparable locations with a full suite of predators.
300 It should be noted that removing equal numbers of both sexes, a standard procedure in
301 many predator-free reserves, will disproportionately reduce the minority sex. The
302 statistically significant influence that predators have on mesoherbivore productivity
303 necessitates careful consideration of introducing predators into reserves where
304 mesoherbivores, via photographic tourism and/or meat sales, are a central aspect of the
305 business model.

306

307 Conclusions

308 Our results strongly suggest that a full suite of predators biases impala adult sex ratios
309 towards females, increases impala juvenile mortality over the breeding year and exposes

310 impala juveniles to increased mortality over periods of unusually low rainfall. It seems
311 probable that other, heavily predated mesoherbivores may experience similar influences,
312 although these are likely to be modified by differing life-history traits (e.g. degree of
313 dimorphism, social structure, whether mixed feeder, obligate browser or grazer). These
314 influences of predation need to be considered, and where appropriate replicated, when
315 managing current reserves or constructing business models for planned reserves.

316

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324

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473 **Table 1.** Output of a generalized linear model of mortality of impala juveniles as the
 474 breeding year advances in Hluhluwe-iMfolozi Park (HiP) versus in Ithala Game Reserve
 475 (IGR). The model (df = 1392) has the proportion of breeding herds formed by juveniles
 476 (response variable) against the number of months passed from the February peak
 477 (continuous explanatory variable), Reserve (HiP or IGR; categorical explanatory
 478 variable) and interactions.

	Estimate	SE	z value	P value
(Intercept)	-1.01	0.049	-20.55	< 0.001
Months since peak	-0.082	0.0094	-8.74	< 0.001
Reserve IGR	0.23	0.069	3.35	< 0.001
Months since peak: reserve IGR	0.022	0.013	2.16	0.034

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481 **Table 2.** Output of a generalized linear model of mortality of impala juveniles as the
 482 breeding year advances over a dry year, versus a year of normal rainfall, in Hluhluwe-
 483 iMfolozi Park. The model (df = 664) has the proportion of breeding herds formed by
 484 juveniles (response variable) against the number of months passed from the February
 485 peak (continuous explanatory variable), normal or dry year (categorical explanatory
 486 variable) and interactions.

	Estimate	SE	z value	P value
(Intercept)	-0.85	0.069	-12.17	< 0.001
Months since peak	-0.087	0.012	-7.22	< 0.001
Dry year	-0.14	0.1	-1.43	0.15
Months since peak: dry year	-0.053	0.02	-2.61	0.009

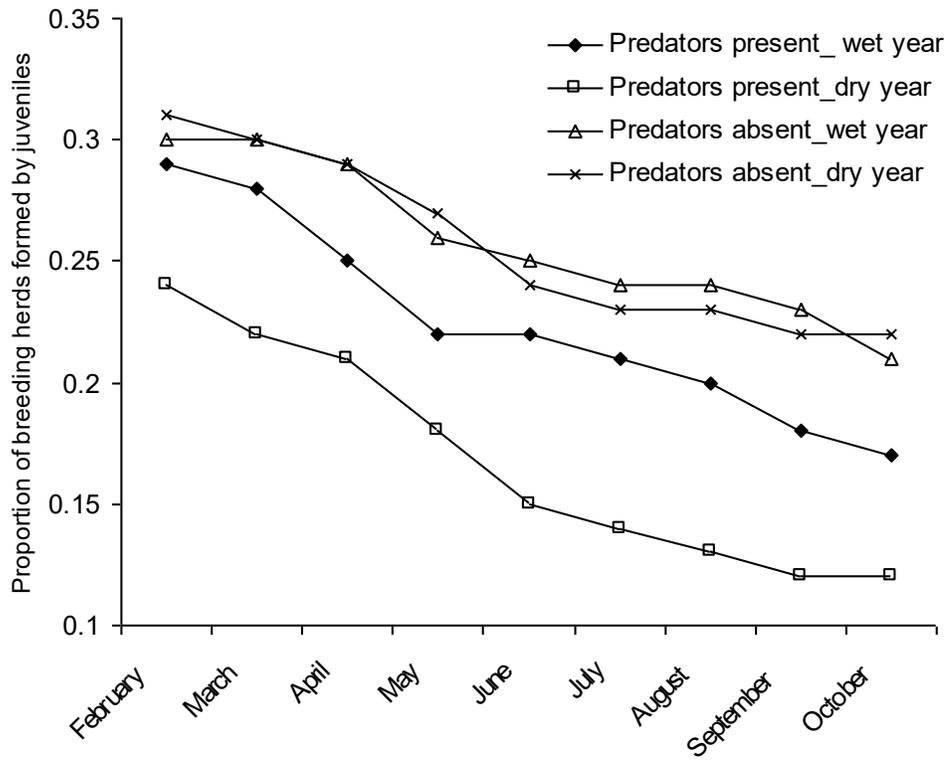
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489 **Figure 1.** The proportion of impala breeding herds formed by juvenile impala as the
490 breeding year advances in Hluhluwe-iMfolozi Park (predators present) and Ithala Game
491 Reserve (predators absent), South Africa. Attention is drawn to the significant (see text)
492 interactive effect between predation pressure and rainfall on the change over the breeding
493 year in juvenile proportion.

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496 **Figure 1**



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