

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

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6 **Christopher A.J. O’Kane** <sup>a,1</sup> christopher.okane@zoo.ox.ac.uk

7 **David W. Macdonald** <sup>a</sup> david.macdonald@zoo.ox.ac.uk

8

9 <sup>a</sup> 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 <sup>1</sup>Corresponding author: address as at <sup>a</sup>, 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.

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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.

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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.

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

58

## **Introduction**

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

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

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

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

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

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

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

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

## **Methods**

### **Study areas**

Both Hluhluwe–iMfolozi Park (900 km<sup>2</sup>) and Ithala Game Reserve (300 km<sup>2</sup>) are situated in KwaZulu–Natal, South Africa (28°00′–28°26′S, 31°43′–32°09′E and 27°30′S, 31°25′E respectively). Both are effectively completely fenced nature reserves, with 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. The vegetation of HiP consists of Zululand lowveld, northern Zululand sourveld and scarp forest, whilst in IGR Zululand lowveld, Zululand bushveld and north-eastern mountain grassland are found (Mucina & Rutherford, 2006). In both reserves impala are found mainly in Zululand lowveld (O'Kane, Duffy, Page, & Macdonald, 2013; O'Kane, Page, & Macdonald, 2014). Structurally, the vegetation in HiP is characterised by fine-leaved *Acacia* savanna with a continuous grass layer and a fairly open tree canopy, whilst in IGR it is a mosaic of grasslands, open savanna dominated by *Acacias* and more or less closed thickets of broad-leaved shrubs and trees. Soils, in both HiP and IGR, are mainly derived from sandstone, shale and dolerite intrusions and are generally eutrophic. In iMfolozi, the section of HiP favoured by impala, long term annual rainfall is 635mm and in IGR 791mm, with rain falling mainly during the warm to hot (18–30°C) summer (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<sup>-2</sup> in HiP and 10 km<sup>-2</sup> 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<sup>-1</sup> 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<sup>-1</sup> 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, 1<sup>st</sup> 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



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

## **Data analysis**

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

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

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

## **Results**

In both reserves we recorded fewer male adult impala than female adult impala. Comparing the combined data from HiP (predators present) with the combined data from IGR (predator free), the adult sex ratio was more biased towards females in the presence of predators (male/female HiP = 0.43, IGR = 0.69;  $\chi^2 = 424.2$ , df = 1,  $P < 0.005$ ). Comparison of all possible pairings of individual year's results from the two reserves revealed the same bias towards females where predators were present (least difference found between HiP Y2 versus IGR Y2: male/female HiP = 0.44, IGR = 0.62;  $\chi^2 = 55.5$ , df = 1,  $P < 0.005$ ).

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

## **Discussion**

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

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

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

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

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

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

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

## Conclusions

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

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

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

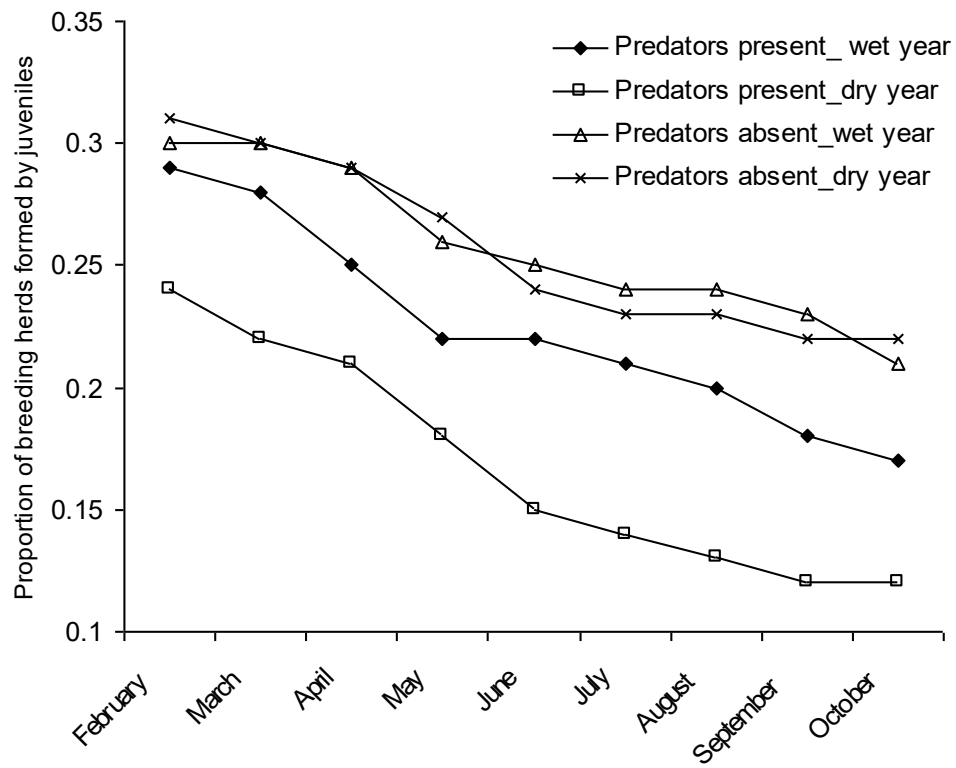
**Table 2.** Output of a generalized linear model of mortality of impala juveniles as the breeding year advances over a dry year, versus a year of normal rainfall, in Hluhluwe-iMfolozi Park. The model (df = 664) has the proportion of breeding herds formed by juveniles (response variable) against the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



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

496 **Figure 1**



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