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An experimental demonstration that predation influences antelope sex ratios and resource-associated mortality

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Abstract

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

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

We found that the impala adult male to adult female ratio was significantly lower in the presence of predation (HiP = 0.43, IGR = 0.69). The generalized linear model revealed that the overall proportion of juveniles in breeding herds (defined as herds containing at least one juvenile) declined, over the breeding year, at a faster rate in the presence of predators.

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

Such fundamental insights into predator–prey relationships are especially relevant to predator-free reserves, where management and planners should be aware of these influences and, depending on the business model, consider replicating them artificially.

Zusammenfassung

Kleinere, eingezäunte Reservate ohne große Raubtiere werden als kommerzielles Modell immer beliebter in Südafrika und anderswo. Vorhandensein und Fehlen von Prädation haben wahrscheinlich erhebliche Auswirkungen auf die Populationsdynamik sexualdimorpher Ungulaten (mit widersprüchlichen Auswirkungen für Mehrzweckreservate) und ermöglichen grundsätzliche Erkenntnisse zu Räuber-Beute-Beziehungen. Über eine zwei- bzw. vierjährige Periode bestimmten wir das

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Geschlechterverhältnis der Adulten und die Mortalität der Juvenilen von zwei großen, südafrikanischen Impala-Subpopulationen (*Aepyceros melampus*), die eine im räuberfreien Ithala Wildreservat (IGR), die andere im benachbarten Hluhluwe-iMfolozi Park (HiP), wo auch Großraubtiere vorkommen. Die Daten wurden monatlich erhoben, über fünf Tage und mit wiederholten Straßentransekten, die eine repräsentative Stichprobe der Habitattypen in den Reservaten abdeckten. Wir bestimmten Unterschiede im Geschlechterverhältnis mit Hilfe von Pearsons Chi^2-Test und untersuchten die Beziehung zwischen Jungtiermortalität, Fortschreiten des Zuchtjahres, Niederschlag und An- bzw. Abwesenheit der Räuber mit einem generalisierten linearen Modell. Wir fanden, dass das Verhältnis von adulten männlichen zu weiblichen Impalas bei Prädation signifikant geringer war: (HiP = 0.43; IGR = 0.69). Das GLM zeigte, dass der Individuenanteil der Jungtiere in Fortpflanzungsherden (=Herden mit mindestens einem Jungtier) im Jahresverlauf bei Anwesenheit von Großräubern schneller abnahm. Die Sterblichkeit der Jungtiere wurde bei Abwesenheit der Räuber von den Niederschlagsmengen nicht signifikant beeinflusst, dagegen nahm unter Räuberdruck die Sterblichkeit der Jungtiere in einem trockenen Jahr schneller ab als in Jahren mit durchschnittlichen Regenmengen. Derartige Erkenntnisse zu Räuber-Beute-Beziehungen sind besonders wichtig für räuberfreie Reservate, in denen Manager und Planer sich dieser Zusammenhänge bewusst sein sollten und erwägen sollten, sie -je nach Geschäftsmodell- künstlich zu replizieren.

Keywords: Africa; Demographics; Dimorphic; Impala; Juvenile mortality; Rainfall; Savanna; Ungulates

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; 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 (Gervasi et al., 2012; Abrams, 2000; Berryman, 1992), with theoretical implications for productivity of both prey and predator (Husek et al., 2013; Abrams, Namba, Mimura, & Roth, 1997) and possible cascading effects on vegetation (Maron, 2011; Grabowski, Hughes, & Kimbro, 2008).

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 (Weckerly, 1998; Andersson, 1994; Clutton-Brock, Albon, & Harvey, 1980; Alexander, Hoogland, Howard, Noonan, & Sherman, 1979), studies where the effects of common ancestry have been removed by computing phylogenetically independent contrasts failed to detect this link (Toigo & Gaillard, 2003; Berger & Gompper, 1999). 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 predated. Adult male impala are preferentially selected by predators in general (Hirst, 1969), and by lion in particular (Funston, Mills, & Biggs, 2001; Pienaar, 1969; Mitchell, Shenton, & Uys, 1965). Additionally, vigilance behaviour in impala has been shown to be markedly increased in the presences of predators (Periquet et al., 2012; Hunter & Skinner, 1998), whilst herbivore populations not exposed to high predation pressure over as few as several generations appear to lose some of their antipredator behaviour (but see Dalerum & Belton, 2015; Blumstein, 2002). Reduced time spent in vigilance in the absence of predators probably translates into energy