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Roan *Hippotragus equinus* population decline in Kruger National Park，South Africa：an alternative complimentary hypothesis*

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Abstract We report on the potential role that ephemeral wetland boundaries played in the population decline of roan antelope *Hippotragus equinus equinus* on the northern plains of Kruger National Park（KNP）between 1979 and the present. Broadly described，drought，associated habitat deterioration and concomitant competition for grazing by generalist herbivores were possible hypotheses explaining the decline of the roan population. We propose that understanding the grazing patch selection of roan and identifying the factors linking ephemeral wetland boundaries and roan population decline reveals an alternative，complimentary hypothesis. The wetland boundary is patchily distributed in space within the northern plains landscape that roan utilize as a mineral rich grazing resource. Most of the artificial water holes placed on the northern plains during the Water for Game management project are situated within or closely adjacent to the wetland boundary attracting increased grazing competition with generalist grazers and predation pressure. Lack of dry season rainfall，coupled with competition for grazing at the ephemeral wetland boundary，and an increase in predation pressure could have provided a trigger for the decline of roan earlier than the general broad scale habitat deterioration of the northern plains landscape［*Acta Zoologica Sinica* 52（2）：406－409，2006］.
Key words Roan，*Hippotragus equinus equinus*，Wetland boundary，Habitat deterioration

南非克留格尔国家公园马羚的种群下降：一个备择假说*

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摘 要 本研究报道了1979年以来南非克留格尔国家公园暂时性沼泽边界对马羚（*Hippotragus equinus equinus*）种群下降的影响。干旱和由此导致的生境退化以及随之产生的食草动物之间的采食竞争是解释马羚种群数量下降的可能假说。我们认为，确定马羚的生境斑块选择并测定影响暂时性沼泽边界变化与马羚种群下降的关联性因子，可解释马羚种群下降的备择假说。在北部平原区，边界呈斑块状分布的沼泽是马羚的高矿质采食源。实施狩猎管理工程期间，人工做成的大多数水道分布于沼泽边界及其附近，造成马羚与其它食草动物的采食竞争和天敌捕食压力的增高。旱季降雨的缺乏，加上沼泽边界区域采食竞争以及天敌捕食压力，是引发马羚在北部平原生境普遍退化之前其种群提前下降的因素［动物学报 52（2）：406－409，2006］。
关键词 马羚 沼泽边界 生境退化

Roan antelope（*Hippotragus equinus* Desmarest）prefer open to lightly wooded areas across central，western，and southern Africa（Wilson and Hirst，1975）. The *H. equinus equinus* subspecies is restricted to the southern portion of the African continent. Kruger National Park（KNP），in north-east South Africa，has a confined roan population occurring on the northern plains（NP）that are considered at their southern most limit of their distribution. Roan antelope are water independent，specialist grazers due to their selectivity of patches at various scales within the landscape（Wilson and Hirst，1975）.

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The roan antelope population on the NP has declined from a population of approximately 350 individuals in 1979, to less than 30 in 2000 (Fig.1). A 4 km^2 enclosure was specifically built on the NP to provide an increased chance of roan breeding success in the hope of repopulating the KNP. By chance, the enclosure surrounded an ephemeral wetland within its borders. This wetland and its associated boundary became the focus of a study investigating roan grazing patch selection in the winter of 2000 (Kröger and Rogers, 2005). Wetlands are the dominant patch type interdigitated within the mopane shrubveld upland matrix on the NP landscape (Harrington et al., 1999). The total area of the plains is 2 800 km^2, of which approximately 18% of the area is an extensive network of relatively wide, shallow, poorly drained ephemeral wetlands. At the time of the study (2000), the roan population on the NP stood at 27 free-ranging individuals. Inside the breeding enclosure, the roan population had increased from an initial population of 7 (1986) to 46 individuals (2001) (De Buys, pers comm.). Breeding success within the enclosure was a result of complete exclusion from other grazers and predators.

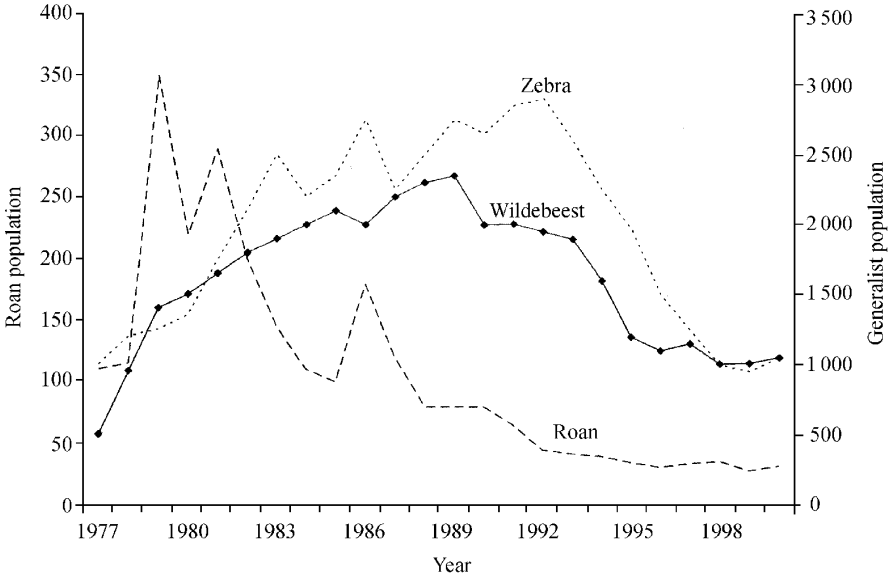

Fig.1 Roan population decline over time on the northern plains of Kruger National Park and the subsequent increase in zebra and wildebeest densities as a result of available perennial water sources

Roan population dynamics, conservation, and in particular the declining population was and still is a highly debated issue in KNP (Wilson and Hirst, 1975; Joubert*; Heitkonig and Owen-Smith, 1998; Harrington et al., 1999; McLoughlin and Owen-Smith, 2003; Kröger and Rogers, 2005). Five possible hypotheses of roan decline have been asserted: a) habitat deterioration of the NP landscape as a result of drought; b) influx of generalist grazers increasing grazing competition; c) an increase in predator numbers, particularly lions, following the buildup of generalist numbers; d) localized anthrax outbreaks; e) and stress associated with anthrax immunization.

The first hypothesized cause was a general habitat deterioration of the NP landscape following the '82 – '83 and '91 – '92 droughts. These droughts primarily resulted in a reduction in grassland condition (Harrington et al., 1999), and a lack of dry season rainfall (Ogutu and Owen-Smith, 2003). Dry season rainfall extends the availability of grass sward green leaf, an essential nutritious forage through unfavorable periods of time (Mduma et al., 1999). The reduced grassland condition placed pressure on selective grazers in finding adequate nutrition. It is highly likely that these droughts had a significant indirect effect on the roan population; however, we hypothesize that droughts had a greater effect on certain patch types within the landscape that were being utilized by roan as essential dietary resources.

Hypothesis two was formulated around the excessive water on the northern plains available to grazers. The NP are seasonally ephemeral systems and did not, prior to 1960, contain any perennial water sources. During the second half of the 20th century the Water for Game project increased the availability of perennial water on the NP by providing artificial permanently installed water holes (29 windmills and

* Joubert SCJ, 1976. The population ecology of the roan antelope *Hippotragus equinus equinus* (Desmarest, 1804) in the Kruger National Park. D.Sc Thesis, University of Pretoria, Pretoria, South Africa.

3 dams). The provision of these water holes permitted water dependent grazers such as zebra and wildebeest to increase population numbers five fold on the NP where historically their distribution was seasonally episodic (Harrington et al., 1999) (Fig.1). This build up in abundance of herbivore numbers and increase in residence time on the plains were postulated to have intensified competition with rare antelope, such as roan, for grazing habitat on the NP and a subsequent overgrazing of habitat patches (Harrington et al., 1999). Further, a lack of dry season rainfall and a lack of greenness within the upland grass sward within the winter would attract grazers (roan and other generalists) to favorable locations in the landscape (Owen-Smith et al., 2005). The spatial heterogeneity of the NP suggests that certain patch types would be favored for their nutritive qualities, retention of green leaf through the winter and close proximities to water sources, and thus could be potentially overgrazed before others.

Subsequently, an over-abundant generalist grazer population and the added effect of augmented water availability in the area resulted in a concomitant increase in the lion predator population which affected roan and other rare antelope species. Although data were weak, casual observations in ranger logs suggested that there was an increase in predator numbers in the roan's range (Harrington et al., 1999), postulating a third hypothetical cause. An increase in roan numbers in a provided enclosure from 7 individuals to over 46 animals in the absence of predation provides further evidence for the importance of predation (McLoughlin and Owen-Smith, 2003). The fact that roan juveniles lie up in the tall grass swards of ephemeral wetlands, adjacent to the boundary and artificial waterpoints, would increase the likelihood of encounters with predators and decrease roan juvenile survivorship (Joubert, 1976).

Possible causes d) and e) are not supported by any sound scientific data and are mentioned in brief. Localized anthrax outbreaks were suggested as a possible cause for the mortalities of some roan, though it is very unlikely that it occurred in enough magnitude to cause the observed decline. Lastly, stress associated with anthrax immunization through the usage of the bio-bullet method might have had some effect on roan decline; however, most of the roan were not immunized between 1992 – 1996.

Harrington et al. (1999) concluded that a combination of general habitat deterioration, overgrazing due to drought, as well as competition for limited resources from increased herbivore numbers were the main factors contributing to the decline of the roan antelope population in KNP. However, these conclusions were drawn irrespective of landscape scale or hierarchy, and fall into past foraging studies where scales of landscapes are implicitly ignored or assumed (Wallis deVries and Laca, 1999). Subsequently through model simulation the direct consequences of drought combined with habitat deterioration were inadequate to explain the roan decline (McLoughlin and Owen-Smith, 2003). However, the degree to which habitat deterioration affected roan could have been higher if roan were concentrating their foraging, in the dry season, on an essential dietary resource at fine spatial scale within the landscape, such as the wetland boundary. Our alternative yet complimentary hypothesis is that roan would first experience the effects of habitat deterioration and competition at the wetland boundary and then successive deterioration of other patch types on the northern plains. This suggests that fine scale habitat deterioration would exert a more substantial impact on the survival rate of roan (McLoughlin and Owen-Smith, 2003).

In KNP, well documented observations show that roan preferentially grazed and rested in the ephemeral wetland boundary and wetland, especially in the winter (Joubert, 1976; Kröger and Rogers, 2005). Mono-specific stands of *Sporobolus ioclados* (Trin.) Nees and bare patches of saline soils dominate the wetland boundary. High concentrations of nitrogen and sodium within *S. ioclados* in winter attract roan and other grazers providing an essential nutrient rich forage (Kröger and Rogers, 2005). Importantly, many of the artificial water holes on the NP were located within, or adjacent to, a wetland boundary because of easy access to groundwater at this point in the landscape. Roan and generalist grazers focused grazing efforts at a fine scale within the NP landscape because of perennial water sources, the vegetative nutritive qualities of the wetland boundary, and the retention of dry season greenness within the wetland boundary as a result of the close proximity of the water table and drainage depressions.

The heterogeneous patterns and nature of landscapes provides a patchy distribution of resources in space and time (Pickett and Cadenasso, 1995). Examination of the NP ephemeral wetlands and more specifically the associated wetland boundary highlights how patchily distributed this resource is within the landscape. It is highly likely that a combination of factors played a role in the decline of roan on the NP landscape of KNP. Selective patch grazing by roan antelope (Wilson and Hirst, 1975; Kröger and Rogers, 2005), fine scale habitat deterioration and competition for wetland boundary resources by generalist grazers, an increased predation pressure (McLoughlin and Owen-Smith, 2003), and range shifts due to climatic variation (Ogutu and Owen-Smith, 2003) pose limitations on roan antelope's

health and survival in an enclosed reserve such as KNP. The scale at which these factors, observations, and important interactions take place in the landscape is vital to understanding their role in the population dynamics of roan and other ungulate species.

Future studies on roan should take a scaled approach when examining roan population dynamics. Similarly, managers should recognize that factors affecting roan and probably other rare antelope species at the limits of their range can be located at specific scales in the landscape and management practices should be re-examined with this in mind.

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