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## A test of the key resource hypothesis in the Richtersveld, South Africa

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**Key words:** key resource model, herbivory, density-dependence, Succulent Karoo biome

**Introduction** The key resource model predicts that herbivore numbers in seasonally-variable grazing systems are determined by access to a critical subset of forage resources, and that herbivore population dynamics are essentially uncoupled from resources accessible during the growing season (Illius & O'Connor 2000). This contrasts with the view that nonequilibrium dynamics are ubiquitous in variable environments, with weak or no coupling between herbivore and resource dynamics (Ellis & Swift 1988). We tested predictions of the key resource model in the Richtersveld National Park (RNP), South Africa, where herders move their herds in response to local resource availability (Hendricks et al. 2005). Herd dynamics, local densities and habitat use were examined to test whether herbivores are: (1) limited by density-dependent competition for the dry season forage resource; and (2) coupled to their forage resource in the dry season, but not in the wet season.

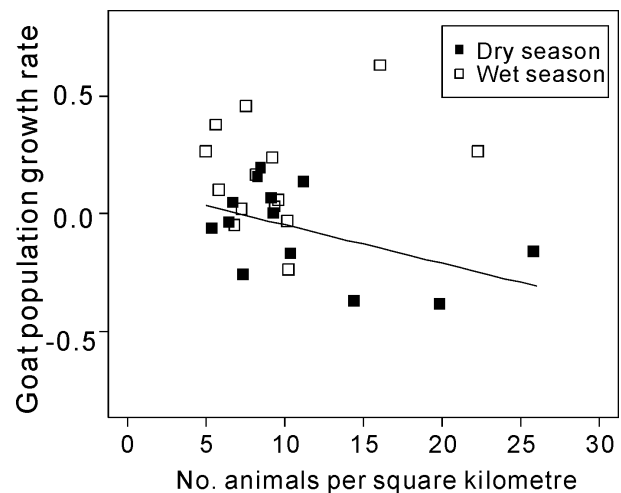
**Materials and methods** Regular censuses of the mixed goat and sheep herds in the RNP were initiated in July 1995. These were used to determine goat population growth rate, calculated as  $\ln(N_{t+1}/N_t)$ , during the period November 1999–October 2001, for which weekly records of herd positions were also kept. Local animal densities were calculated for 15 regions within which the daily foraging paths from individual stockposts were likely to overlap. These regions were classified into three habitat types: riparian, plains and mountains. The climate is arid and erratic, but three-month summed rainfall over the study period were twice as high on average for a wet season month ( $20.4 \pm 22.9$  mm; April–October) as for a dry season month ( $11.7 \pm 19.2$  mm; October–April). The effects of season and local animal density on goat population growth rates were examined, as were seasonal habitat preferences.

**Results and discussion** Goat herd growth rate and local animal density were not correlated in the wet season (Figure 1;  $n=14$ ,  $R^2=0.05$ ,  $p=0.419$ ), but were negatively correlated in the dry season ( $n=13$ ,  $R^2=0.25$ ,  $p=0.085$ ). Mean goat population growth was positive in the wet season [ $0.165 \pm 0.23$  (s.e.)] and negative in the dry season ( $-0.062 \pm 0.18$ ). During the wet season, animal numbers were split fairly evenly between riparian (55%) and non-riparian (45%; plains=35%, mountains=10%) habitats. However, the riparian zone was preferred (79%) to non-riparian habitats (21%; plains=17%, mountains=3%) in the dry season.

**Conclusions** The density-dependent decline of herd growth rate in the dry season suggests resource limitation at this time. This is not apparent in the wet season. Hendricks et al. (2005) and our discussions with the herders indicate that movements away from the riparian zone are in order to access the flush of annual forage species on the plains after rain events. In contrast, movements back to the riparian zone are due to the need for daily access to drinking water, rather than forage resource limitation. The riparian zone thus appears to form a key resource in the RNP, and there is some degree of support for the first two predictions of the key resource model: (1) density-dependent limitation may occur in the dry season, likely due to coupling with the forage resource, while (2) the population appears to be relatively uncoupled from the wet season resource.

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**Figure 1** Goat population growth rate versus local animal density for the dry and wet season. The solid line represents the best fit for the dry season ( $y = -0.016x + 0.116$ ,  $R^2 = 0.25$ ,  $p = 0.085$ ).