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Original article

Unpreferred plants affect patch choice and spatial distribution of European brown hares

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ABSTRACT

Many herbivore species prefer to forage on patches of intermediate biomass. Plant quality and forage efficiency are predicted to decrease with increasing plant standing crop which explains the lower preference of the herbivore. However, often is ignored that on the long-term, plant species composition is predicted to change with increasing plant standing crop. The amount of low-quality, unpreferred food plants increases with increasing plant standing crop. In the present study the effects of unpreferred plants on patch choice and distribution of European brown hare in a salt-marsh system were studied. In one experiment, unpreferred plants were removed from plots. In the second experiment, plots were planted with different densities of an unpreferred artificial plant. Removal of unpreferred plants increased hare-grazing pressure more than fivefold compared to unmanipulated plots. Planting of unpreferred plants reduced hare-grazing pressure, with a significant reduction of grazing already occurring at low unpreferred plant density. Spatial distribution of hares within this salt-marsh system was related to spatial arrangement of unpreferred plants. Hare-grazing intensity decreased strongly with increasing abundance of unpreferred plants despite a high abundance of principal food plants. The results of this study indicate that plant species replacement is an important factor determining patch choice and spatial distribution of hares next to changing plant quality. Increasing abundance of unpreferred plant species can strengthen the decreasing patch quality with increasing standing crop and can decrease grazing intensity when preferred food plants are still abundantly present.

1. Introduction

Many species of herbivores prefer to forage on patches of intermediate plant standing crop (Langvatn and Hanley, 1993; Wallis DeVries and Daleboudt, 1994; Wilmshurst et al., 1995). On the one hand this is the result of a decreasing plant quality, as food for herbivores, with increasing plant standing crop. An increasing standing crop may coincide with increasing canopy height and increasing amounts of standing dead plant biomass (Van de Koppel et al., 1996). Both factors result in a higher proportion of fibre and a lower C/N ratio of the forage, and subsequent lower forage quality (Wilmshurst et al., 1995; Bos et al., 2004). On the other hand, foraging efficiency of the herbivore can decrease with increasing plant standing crop. Due to increased search rate and handling time, food intake rate can decrease at high plant standing crop (Van der Wal et al., 1998).

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However, many studies ignore that next to a decreasing plant quality, in the long-term, plant species composition is predicted to change with increasing plant standing crop (Tilman, 1990). At sites of low biomass, plants will mainly compete for nutrients, whereas, competition for light dominates at sites of high biomass. Based on these changing resources, a shift in plant species is predicted from good nutrient-competitors at low biomass towards good light competitors at sites of high biomass (Tilman, 1990). These patterns of plant species replacement are predicted to further strengthen the decreasing food quality with increasing biomass. Good light-competing species are in general characterised by a tall and erect growth form, high stem/leaf ratio and high fibre or lignin content of tissues to support an erect growth form (Tilman, 1990). These features increase the competitive ability of the plant species but also decrease food quality for the herbivore (Huisman et al., 1999). The effects of a changing plant species composition on patch choice of herbivores have received little attention.

Vegetation succession on temperate European back-barrier salt marshes occurs along a productivity gradient (Van de Koppel et al., 1996; Olff et al., 1997). Grazing intensity of natural herbivores at salt marshes (geese, hares and rabbits) shows an optimum during salt-marsh vegetation succession with the highest densities occurring at sites of intermediate plant standing crop. The decreasing numbers of herbivores have been explained by a decreasing foraging efficiency with increasing plant standing crop (Van de Koppel et al., 1996). However, with increasing plant standing crop, the vegetation is composed of an increasing proportion of tall-growing plant species which are unpreferred by the herbivores (Van der Wal et al., 2000a; Kuijper et al., 2008). In the present study, we studied how the presence of unpreferred plant species influences patch choice and large-scale spatial distribution of an intermediate-sized herbivore, European brown hare *Lepus europaeus*, in a temperate salt-marsh system.

2. Material and methods

2.1. Study site

This study was conducted in the salt marsh of the island of Schiermonnikoog, in the Dutch Wadden Sea (53 30′N, 6 10′E). The entire salt-marsh system (circa 700 ha) is inhabited by 300–600 European brown hares, *L. europaeus* (Van Wieren et al., 2006). Rabbits (*Oryctolagus cunniculus*) are present in low numbers in the salt marsh and mainly inhabit dune areas (Kuijper and Bakker, 2005). Next to these lagomorphs, large numbers of migrating Brent geese (*Branta bernicla*) and Barnacle geese (*Branta leucopsis*) visit the salt marshes mainly as spring staging site (Stahl et al., 2002). Brown hare, rabbit and the two goose species, do not have carnivores in this system as they are absent from this island (Kuijper and Bakker, 2005).

Due to the eastward expansion of this island, a series of salt marshes at different developmental stages can be found adjacent to each other. A well-developed chronosequence is found from east to west across the island (Olff et al., 1997). Clay layer thickness and hence nitrogen content of the soil increases with marsh age (Olff et al., 1997; Van Wijnen and Bakker, 2000). As a consequence the chronosequence represents a natural productivity gradient (Van de Koppel et al., 1996). Total standing crop of the vegetation increases towards the more productive end of the gradient. The increasing standing crop is associated with increasing vegetation height and proportion of standing dead plant biomass (Van de Koppel et al., 1996). As a consequence, potential food availability is negatively related to food quality as both vegetation height and proportion of standing dead decrease forage quality. Each elevation class in this salt marsh shows a distinctive pattern of plant species replacement along the productivity gradient (Olff et al., 1997). At high marsh elevation, early successional stages are dominated by the small-statured grass *Festuca rubra*. This is a highly preferred food plant for hares and predominates its summer diet (Kuijper et al., 2008). Two plant species invade this *F. rubra*-dominated vegetation with increasing soil productivity. Firstly, the herb *Seriphidium maritimum* (plant nomenclature follows Van der Meijden (1996), old name *Artemisia maritima*) reaches a peak in abundance at intermediate productivity. Secondly, the tall-growing grass *Elytrigia atherica* (old name *Elymus athericus*) dominates the productive, late successional stages (Olff et al., 1997; Van Wijnen and Bakker, 2000). The grass *Elytrigia* can grow up to 1 m high and can overgrow most other salt-marsh plants. The high investment in structural tissue (fibres) makes it an unattractive food plant and it is negatively selected by hares (Kuijper et al., 2008). *Seriphidium* is a herb, up to 50 cm high, with strong smelling leaves which indicate the presence of secondary plant compounds, which may act as herbivore defence. The plant is virtually absent in the summer diet of hares (Kuijper et al., 2008), whereas stems of this plant are consumed in winter (Van der Wal et al., 2000b). Hence, with increasing productivity of the salt marsh, the abundance of unpreferred food plants is increasing in vegetation consisting of the preferred forage species and eventually replaces the principal food plant of hares at the most productive successional stages.

2.2. Experimental manipulation of vegetation

Two experiments were carried out in which plots consisting of natural vegetation were manipulated and the effect on patch choice of hares was studied. Both experiments were located at a salt marsh of approximately 25 years old which harboured peak density of hares observed at this island. Within this area two sites were selected, at a distance of circa 200 m from each other, which were dominated (>80% visual cover) by the principal food plant of hares, *F. rubra*. One of the sites had a low hare-grazing intensity (based on dropping counts) and a high cover of the unpreferred plant *S. maritimum* (30–40% cover), whereas the other had a high hare-grazing intensity and a low cover of unpreferred plants (<5% visual cover). At the first site, in July 2000 plots were created from which the unpreferred plants were removed, whereas at the second site, in May 2000 plots were created on which different densities of unpreferred plants were planted. Taking into account the observed home range size of hares on this island of 28.7 ha (Kunst et al., 2001), the experimental sites were within the home range of an individual hare. However, hares have overlapping home ranges (Kunst et al., 2001) and the area