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# Seed dispersal in red deer (*Cervus elaphus* L.) dung and its potential importance for vegetation dynamics in subalpine grasslands

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## Abstract

Free-ranging large herbivores can influence vegetation dynamics through seed dispersal within and among habitats. We investigated the content of germinable seeds in the dung (endozoochory) of red deer (*Cervus elaphus* L.), the most ubiquitous wild ungulate throughout the European Alps, and compared the results with the species composition of the vegetation type in which the dung was dropped. The study was conducted in the subalpine zone of the Swiss National Park and included the three most important vegetation types for red deer: (i) intensively grazed short-grass vegetation, (ii) less intensively grazed tall-grass vegetation, and (iii) adjacent conifer forest understory vegetation. Seeds of 47 species, mostly from small-seeded herbaceous species, were recorded in dung samples with three species accounting for 65% of germinated seeds. Our results confirmed the hypotheses that (H1) small-seeded species were more likely to occur in red deer dung than larger-seeded species, though seed size was unrelated to seed density, (H2) red deer dung contained mostly seeds from short-grass vegetation, with seed species composition in dung collected from any vegetation type being most similar to species composition of relevés from short-grass vegetation, and (H3) seeds were less likely to be dispersed between vegetation types than within vegetation types, with dung dropped in short-grass vegetation having a different species composition and containing over twice as many seeds as dung dropped in the other two vegetation types. These results collectively support the hypothesis that red deer endozoochory contributes to maintaining short-grass vegetation, the favoured grazing sites of hinds in the Swiss National Park, by increasing propagule pressure of seeds from herbaceous forage species adapted to endozoochory relative to other species and especially those from later stages of secondary succession.

## Zusammenfassung

Wilde Huftiere können die Vegetationsdynamik beeinflussen, indem sie Samen innerhalb und zwischen Habitaten verbreiten. Wir untersuchten den Gehalt an keimfähigen Samen (Endozoochorie) im Kot von Rothirschen (*Cervus elaphus* L.), der in den Europäischen Alpen am weitesten verbreiteten Huftierart und verglichen die Resultate mit der Artenzusammensetzung des Vegetationstyps, in welcher der Kot gesammelt wurde. Die Studie wurde in der subalpinen Zone des Schweizerischen Nationalparks durchgeführt und umfasste die drei für Rothirsche wichtigsten Vegetationstypen: (i) intensiv beweidete

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Kurzgrasrasen, (ii) weniger intensiv beweidete Langgrasrasen, und (iii) den Unterwuchs angrenzender Nadelwälder. In den Kotproben wurden Samen von 47 Pflanzenarten gefunden, die meisten von kleinsamigen Krautarten, wobei 65% der gekeimten Samen von nur drei Arten stammten. Die Resultate bestätigten die folgenden Hypothesen: (H1) Kleinsamige Arten kamen mit grösserer Wahrscheinlichkeit in Kotproben vor, obschon die Samendichte im Kot nicht von der Samengrösse abhing. (H2) Rothirschkot enthielt mehrheitlich Samen von Kurzgrasrasenarten, wobei die Artenzusammensetzung der Kotproben von allen drei Vegetationstypen grösste Ähnlichkeit mit Vegetationsaufnahmen aus Kurzgrasrasen aufwies. (H3) Samen wurden häufiger innerhalb desselben Vegetationstyps transportiert als zwischen verschiedenen Vegetationstypen, wobei Kot, der in Kurzgrasrasen gesammelt wurde, eine andere Artenzusammensetzung und eine mehr als doppelt so hohe Samendichte aufwies wie Kot aus Langgrasrasen oder Nadelwäldern. Zusammengenommen unterstützen unsere Resultate die Hypothese, dass endozoochore Samenausbreitung durch den Rothirsch zum Erhalt von Kurzgrasrasen, dem bevorzugten Habitattyp der Hirschkühe im Schweizerischen Nationalpark, beiträgt, indem die relative Häufigkeit keimfähiger Samen von bevorzugten und an Endozoochorie angepassten Pflanzenarten gegenüber anderen Arten, insbesondere Vertretern späterer Stadien der sekundären Sukzession, erhöht wird.


***Keywords:*** Endozoochory; European Alps; Free-ranging herbivores; Grazed ecosystems; Selective habitat use

## Introduction

Large herbivores are generally recognized as one of the main driving forces behind vegetation dynamics of grazed ecosystems (e.g. Gill & Beardall 2001; Erschbamer, Virtanen & Nagy 2003; Mouissie, Apol, van Diggelen & Heil 2008). It has been suggested that the activities of free-ranging ungulates lead to maintaining the vegetation of their favoured grazing sites (McNaughton 1984; Vera 2000). However, empirical evidence for this hypothesis is largely lacking. Comprehensive data on seed dispersal by wild ungulates in unmanaged ecosystems may provide evidence for such effects of large herbivores.

Wild ungulates are potentially important long-distance dispersers of seeds (Janzen 1984). Seeds of many species can be dispersed in dung (endozoochory), especially those from herbaceous species with small, hard seeds (Yamashiro & Yamashiro 2006; Rosas, Engle, Shaw & Palmer 2008; Pakeman & Small 2009) that lack obvious morphological adaptation to a specific dispersal vector (Gill & Beardall 2001; Eycott, Watkinson, Hemami & Dolman 2007). Endozoochory and epizoochory have been identified as evolutionary adaptations that facilitate both the dispersal of plant species and the reseeding of areas under intense herbivory (Howe & Smallwood 1982). Preferred forage species often locate their reproductive organs and numerous seeds among or above green leaves (Janzen 1984; Hülber, Ertl, Gottfried, Reiter & Grabherr 2005), increasing the chance of seeds being eaten inadvertently with other plant parts (Shiponeni & Milton 2006), and their small seeds are more likely to pass the herbivore's digestive tract undamaged (Gill & Beardall 2001; Pakeman & Small 2009; Kuiters & Huiskes 2010). Several studies have investigated seed dispersal in wild ungulate dung (e.g. Welch 1985; Heinken, Hanspach, Raudnitschka & Schaumann 2002; Myers, Vellend, Gardescu & Marks 2004; Oheimb, Schmidt, Kriebitzsch & Ellenberg 2005; Brodie, Helmy, Brockelman & Maron 2009), but these have rarely considered the spatial variation in the return of seeds across a range of different vegetation types (but see Malo, Jiménez & Suárez 2000; Yamashiro & Yamashiro 2006). Most wild ungulates range widely and move regularly between different habitats for foraging (Georgii & Schröder 1983; Gill & Beardall 2001), and the seed content of dung therefore reflects their foraging behaviour and the composition of the plant communities where they feed (Malo & Suarez 1995; Hülber et al. 2005). Since seeds normally remain in the digestive tract for several hours (Oheimb et al. 2005; Bruun, Lundgren & Philipp 2008), they may be dispersed among other habitats within the animal's range (Heinken et al. 2002; Myers et al. 2004; Cosyns, Claerbout, Lamoot & Hoffmann 2005; Rosas et al. 2008).

Wild ungulates are selective in their use of habitat (Meyer & Filli 2006; Mouissie et al. 2008), and in some sexually dimorphic ungulate species, patterns of habitat selection also differ between the sexes (Clutton-Brock, Guinness & Albon 1982; Georgii & Schröder 1983; Conradt, Clutton-Brock & Thomson 1999). In red deer (*Cervus elaphus* L.), the most ubiquitous wild ungulate throughout the European Alps (Erschbamer et al. 2003), hinds prefer highly digestible, nutrient-rich plant material because they have high energy requirements for pregnancy and lactation (Clutton-Brock et al. 1982; Conradt et al. 1999), whereas stags, with their higher forage requirement due to larger body size, prefer to graze vegetation with high forage biomass (Georgii & Schröder 1983). The potential importance of habitat selection for seed dispersal via wild ungulate dung (endozoochorous seed dispersal) has rarely been considered (Malo et al. 2000; Shiponeni & Milton 2006; Rosas et al. 2008). Red deer have been shown to disperse seeds of several species in their dung (e.g. Welch 1985; Malo & Suarez 1995; Malo et al. 2000; Oheimb et al. 2005; Eycott et al. 2007), potentially affecting the dynamics and structure of the vegetation to a considerable degree. For instance, red deer might maintain vegetation in their favoured grazing sites by promoting some species, e.g. by dispersing their seeds to available germination sites, while constraining others, e.g. by destroying