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Original article

Legitimate seed dispersal by lizards in an alpine habitat: The case of *Berberis empetrifolia* (Berberidaceae) dispersed by *Liolaemus belii* (Tropiduridae)

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ABSTRACT

In this study we determined the effect of seed passage through *Liolaemus bellii* lizard digestive tracts on germination of fleshy-fruited Andean shrub species *Berberis empetrifolia* (Berberidaceae), and evaluated the effect of this passage on seed coat characteristics. In addition, we assessed the spatial patterns of fecal deposition by lizards onto various microhabitats available in the Andean environments of central Chile. The germination rate and the final percentage of lizard-ingested *B. empetrifolia* seeds was greater than control seeds. Comparing photographs and seed coat histological cuts, we suggest that the cutine wax present on seed coats from lizard-ingested seeds was probably removed by abrasion inside the lizards' digestive tract. Sixty-two percent of the lizard's feces was deposited on bare soil near rocks commonly inhabited by lizards. However, this microhabitat represents only 29% of the available ground cover at the study site. By enhancing seed germination and depositing seeds onto potential safe sites for recruitment, the lizard *Liolaemus bellii* is acting, at least qualitatively, as an effective disperser of *Berberis empetrifolia*.

1. Introduction

Endozoochorous seed dispersal is widespread among fleshy-fruited plants (Janzen, 1983), with birds and mammals being the animals most commonly associated with this dispersal mechanism (Traveset, 1998; Jordano, 2000; Stiles, 2000; Traveset and Verdú, 2002). For several fleshy-fruited plants passage of seeds through vertebrate digestive tracts enhances their germination (Jordano, 2000; Traveset and Verdú, 2002). For instance, the passage of seeds through vertebrate digestive tracts can scarify the seed coat, increasing its permeability to water and gases (Barnea et al., 1991; Izhaki and Safriel, 1990; Sahai, 1995; Foster and Delay, 1998; Calviño-Cancela, 2004), hence promoting seed germination. Gut passage also separates seeds from their pulp, enhancing their germination probability, because germination of seeds with intact pulp has

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been reported to be reduced or inhibited (Barnea et al., 1991; Izhaki and Safriel, 1990). Further, the fecal material surrounding seeds after passage through the digestive tract has been shown to enhance nutrient availability for seedling establishment (Traveset and Verdú, 2002).

In addition to these direct effects, frugivores may disperse seeds to different sites depending on their behavior and habitat preference, thereby determining the spatial pattern of seed deposition (Kollman and Pirl, 1995; Calviño-Cancela, 2002). Seed deposition can occur in locations with varied microclimatic conditions and eventually to sites with suitable conditions for germination and seedling establishment (Davidson and Morton, 1981; Howe and Smallwood, 1982; Calviño-Cancela, 2004).

Although it is well known that many birds and mammals serve as seed dispersers of many flowering plants, the role of lizards in this process has traditionally been considered rare or less important (Olesen and Valido, 2003). Lizards are usually ignored as mutualist seed-dispersal agents in the mainstream literature possibly because most of them are regarded as being carnivorous (Cooper and Vitt, 2002). However, many lizards have broad diets, including flowers, fruits, nectar and pollen (Fuentes, 1976; Whitaker, 1987; Cooper and Vitt, 2002; Valido et al., 2003), and some species have been reported to be legitimate seed dispersers (e.g., Traveset, 1995; Varela and Bucher, 2002; Wotton, 2002).

Some studies revealed that the passage of seeds through the digestive tract of lizards accelerates germination and also increases the percentage of seeds germinated (Valido and Nogales, 1994; Willson et al., 1996; de Castro and Galetti, 2004). In addition, some authors suggest that lizards do not randomly deposit seeds in the environment, but rather defecate them in microhabitats suitable for germination (Valido and Nogales, 1994; Varela and Bucher, 2002). For example, in the temperate forest of Chiloé, lizards thermoregulate into forest gaps depositing their feces containing seeds of *Nertera granadensis*, a species that demands light for germination (Willson et al., 1996).

Lizard frugivory has been reported in a variety of environments, such as Mediterranean-type climate ecosystems (e.g., Traveset, 1995) and temperate rain forests (e.g., Willson et al., 1996). However, in high-elevation habitats where abiotic plant dispersal is widespread (Marchand and Roach, 1980; Cavieres et al., 1999), and with only a few species possessing morphological traits adapted to animal dispersal (Müller-Schneider, 1986, cited in Hülber et al., 2005), consumption of fleshy-fruits by lizards has been reported (e.g., Donoso-Barros, 1966; Fuentes, 1976). In the central Chilean Andes, the shrub *Berberis empetrifolia* (Berberidaceae) is the only species reported to possess fleshy fruits and the fleshy fruits are ingested as part of the omnivorous diet of the lizard, *Liolaemus bellii* (Donoso-Barros, 1966; Muñoz, 2003). The seeds of this shrub were the only ones found in lizard feces among remains of insects such as dipterans and coleopterans.

In the present study, we address the following questions: (1) What are the effects of the passage of *Berberis empetrifolia* seeds through the digestive tract of the lizard, *Liolaemus bellii*, on germination capabilities and seed coat thickness?, and (2) Is seed deposition via fecal material congruent with the proportional availability of microhabitats in the environment inhabited by this lizard species?

2. Materials and methods

2.1. Study area

Research was conducted on an 18-ha site at 2600 m altitude in the lower alpine belt, Valle Nevado area (33°21′S, 70°16′W), Andes of central Chile, ca. 50 km east of Santiago. Climate is alpine with Mediterranean influence, with a mean annual precipitation at 2400 m of 431 mm, falling predominantly as snow during the winter months from June to August.

The growing season (corresponding to the snow-free period) at this altitude commonly extends from mid-October to mid-May (Arroyo et al., 1981). The study site is south-facing, with gentle ($<15°$) slopes. At this elevation, vegetation is dominated by low stature (<45 cm) spiny shrubs of *Berberis empetrifolia*, *Chuquiraga oppositifolia* and *Anarthrophyllum cumingii* (Cavieres et al., 2000). Herbaceous species, such as *Acaena pinnatifida*, *Phacelia secunda*, *Stachys philippiana*, and various species of *Adesmia* and *Senecio*, are also abundant. Rocks of varying size (0.001–2.5 m^3), with an estimated cover of 15%, are interspersed among the shrubs (see also Muñoz and Arroyo, 2004).

The study area is characterized by a high density of large (10–12 cm snout–vent length) territorial lizards belonging to the species *Liolaemus leopardinus* and *L. bellii* (Tropiduridae), with $>95\%$ of all individuals belonging to the latter species. Lizards use rocks as permanent territories throughout the spring–autumn snow-free period (Muñoz and Arroyo, 2004).

2.2. Focal plant and lizard species

In Chile, the shrub *Berberis empetrifolia* (Lam.) (Berberidaceae) grows in the Coastal and Andes Mountain ranges from Coquimbo (30°S) to Tierra del Fuego (55°S) (Landrum, 1999). Its fruits are dark purple sub-globular berries, 4–7 mm in diameter, containing between 3 and 7 seeds, each measuring approximately 3–4 mm (Landrum, 1999). Peak flowering of this shrub is between November and December, with fruiting occurring between January and February (Arroyo et al., 1981).

The lizard *Liolaemus bellii* (Squamata: Tropiduridae) is distributed in the Andes of central Chile (33°S) between 2500 and 3500 m a.s.l., and is a saxicolous omnivore with ovoviviparous reproduction (Donoso-Barros, 1966).

2.3. Collection of Berberis empetrifolia seeds

To obtain the seeds that had passed through lizard digestive tracts we collected 580 samples of *L. bellii* feces from the study area in February 2004. A total of 232 seeds were extracted from these feces in the laboratory, and seeds of *Berberis empetrifolia* were identified through comparisons with seeds obtained from fruit collected directly from the plants. Additionally, 300 fruits were collected from 40 *B. empetrifolia* bushes present in the study site. The pericarp was removed from each fruit in the laboratory, and the extracted seeds were used as controls in the experiments described below.