Original article

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

Constanza Celedón-Neghme[a,*], Leonardo A. San Martin[c], Pedro F. Victoriano[b], Lohengrin A. Cavieres[a]

[a]ECOBIOSIS, Departamento de Botánica, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción e Instituto de Ecología y Biodiversidad (IEB), Casilla 160C, Concepción, Chile
[b]Departamento de Zoología, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Centro de Investigación en Estudios Patagónicos (CIEP), Concepción, Chile
[c]Facultad de Ciencias Agrarias, Universidad Austral, Isla Teja, Chile

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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

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 m³), 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.

2.4. Germination tests

Both seed treatment groups (controls and lizard-ingested seeds) were stratified at 4 °C in dark, humid conditions for 60 days. Subsequently, all were germinated in Petri dishes at 20 °C in a controlled environment growth chamber. Four replicate petri dishes of each treatment were used, each containing 25 seeds randomly selected. The number of germinated seeds under each treatment was recorded and removed to another marked petri dish once a week, for a total period of 70 days. The criterion used to identify a germinated seed was visible radicle emergence (Baskin and Baskin, 1998). A viability test was performed on those seeds that did not germinate during the observation period using 2,3,5-triphenyl-2H-tetrazolium (TTC: 0.6 w/v in 0.05 M phosphate buffer (pH 7.4); Moore, 1973).

2.5. Seed coat comparisons

Five control seeds and five seeds extracted from feces were metallized in 350 Å thickness gold (S 150 metallizer), and photographed under an Autoscan U-1 scanning electron microscope (ETEC). Another five seeds from each treatment were subjected to kerosene inclusion (see Sakai, 1973), and all seeds from both treatments were cut into 15-μm permanent histological sections. Sections were then stained with safranine-fast green and photographed using a compound optical microscope (Carl Zeiss KF2). To obtain the average mean of the cuticle thickness in the five seeds used in each treatment, we utilized five photographs from each seed in both treatments measuring the cuticle with a rule (mm). The average mean of cuticle of each seed was used for comparisons among digested and control seeds.

2.6. Fecal deposition sites

To assess whether lizard feces are deposited in various microhabitats in proportion to their availability at the study site, the percentage cover of various microhabitats in the study area was recorded. Eight 50×1 m parallel transects were established and 5 microhabitat categories present in the environment were arbitrarily defined: (1) rocks, (2) bare ground with a rock potentially used as perch (<50 cm from a rock), (3) bare ground without a rock (>50 cm from a rock), (4) shrubs, and (5) other (e.g., grass, forbs). Within each transect, the microhabitats of all lizard fecal depositions found were recorded (283 fecal samples).

2.7. Data analyses

Student's t-test was performed to assess differences in germination rate/percentage and the thickness of the cuticles, for seeds from control and lizard-ingested treatments, and data were normalized using an arcsin function in the case of germination (Zar, 1996). Additionally, the germination rate coefficient ($CV = 100 \times \sum N_i / \sum N_i \times T_i$) was calculated for each replicate, and the mean was used to infer differences among treatments, following Scott et al. (1984). In the above expression, N is the number of germinated seeds on day i, and T is the number of days from sowing. A Mann–Whitney U-test (Zar, 1996) was performed to establish if the CV differed between control and lizard-ingested seeds. Finally, we performed a χ^2 test to assess if spatial deposition patterns of feces (percentage of feces deposited at each microhabitat) by *Liolaemus bellii* differs from the availability of the different microhabitats at study site.

3. Results

3.1. Seed germination

Germination rate/percentage of *Berberis empetrifolia* seeds that had passed through the digestive tract of lizards was higher than that of control seeds ($t = -2.828$; d.f. $= 6$; $p = 0.030$). The germination rate coefficient for lizard-ingested *B. empetrifolia* seeds ($CV = 7.33 \pm 0.13$) was superior ($U = 0.00$, $Z = -2.30$, $p < 0.005$) than the control seeds ($CV = 2.35 \pm 0.02$). While lizard-ingested seeds began germinating during the first week, control seeds only started germinating in the sixth week (Fig. 1). The percentage of non-germinated but viable seeds did not differ between treatments ($t = 0.023$; d.f. $= 6$; $p = 0.982$). Lizard-ingested seeds had a viability of $69 \pm 2.95\%$ compared to $69 \pm 6.97\%$ in control seeds, consequently the possibility that non-germinating seeds contained dead embryos could be discarded.

3.2. Seed coat comparisons

Under the scanning electron microscope, the seed coat surfaces of seeds extracted from feces had deteriorated compared to control seeds (Fig. 2). The removal of the most external layer of the seed coat (the cuticle) was seen in lizard-ingested seeds (Fig. 2A–C), while a continuous surface is visible in control seeds (Fig. 2D–F). The cells that make up the most external cellular layer of the seed coat are clearly observable in lizard-ingested seeds (Fig. 2A). Further, cuticle and palisade sclerenchyma thinning was evident in the coat of lizard-ingested seeds (0.86 ± 0.07 mm) (Fig. 3A and B) but
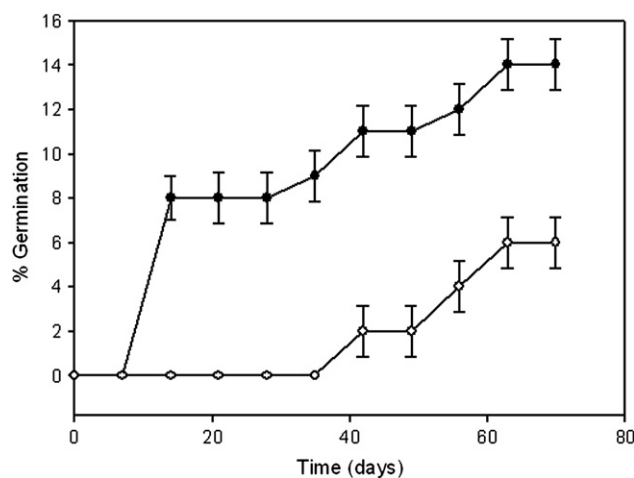

Fig. 1 – Germination percentage (±2 standard errors) of *Berberis empetrifolia* seeds that had passed through the digestive tract of *L. bellii* lizards (black circles) and that were directly collected from the plant (control seeds, open circles).
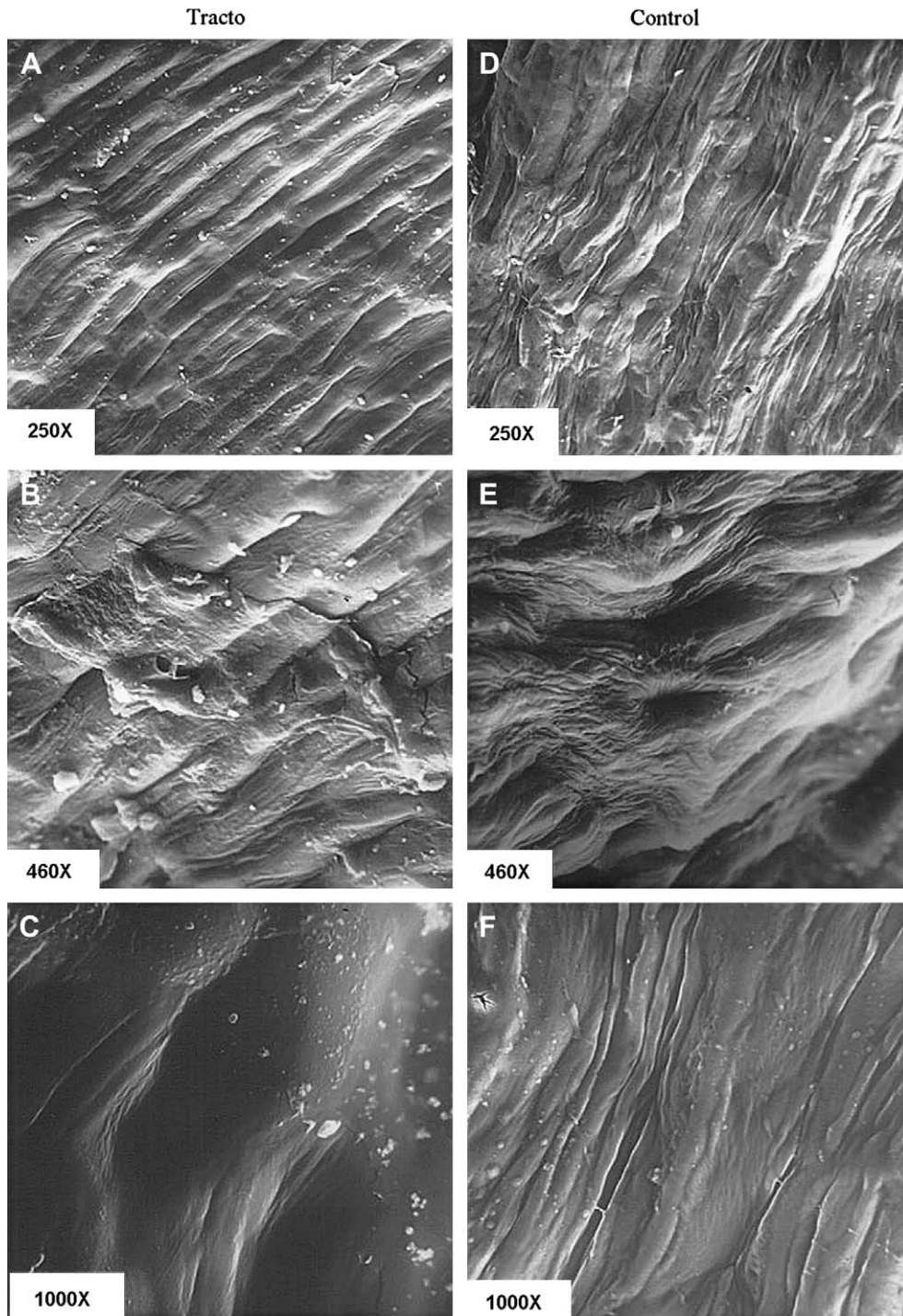
Tracto   Control

Fig. 2 – Micrographs (scanning electron microscope) of the seed coat from B. empetrifolia that were ingested by the lizard (A–C) and those of controls (D–F).

not in the control (1.72 ± 0.03) (Fig. 3C and D) under the permanent histological cuts (t = −4.905; d.f. = 8; p = 0.001).

3.3. Fecal deposition sites

Lizards did not deposit feces in the various microhabitats in proportion to their availability at the study site ($\chi^2 = 114$;

d.f. = 16; $p < 0.001$). Sixty-two percent of all lizard feces collected was deposited on bare ground with a rock that can be potentially used as a perch (<50 cm from a rock). Actually, this type of microhabitat represents only 29% of the ground cover at the study site (Fig. 4). Twenty percent of the 283 pellets collected to evaluate the fecal deposition pattern had on average 3 ± 2 seeds.
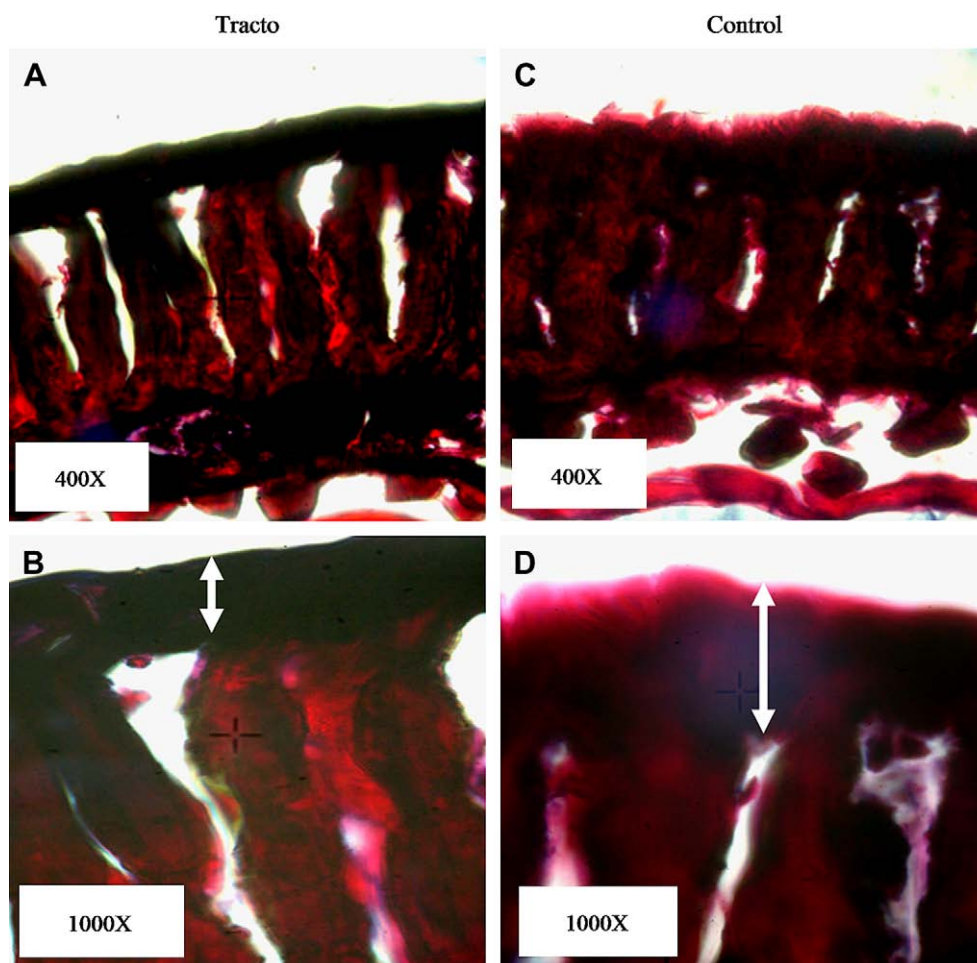
Tracto   Control

Fig. 3 – Permanent histological cuts showing cuticle and palisade sclerenchyma thinning in lizard-ingested seeds (A,B) and control seeds (C,D).

4. Discussion

The effect produced on seeds by passage through vertebrate guts varies among plant species (Lieberman and Lieberman, 1986). In the case of reptiles, some authors have found that ingestion by lizards does not influence, or negatively affects the final percentage seed germination of some plant species (Traveset, 1990; Valido and Nogales, 1994; Willson et al., 1996; Castilla, 2000; Varela and Bucher, 2002). However, in other plant species, especially those possessing drupe- or berry-type fleshy fruits, higher percentages of germination for lizard-ingested seeds have been reported regularly (Valido and Nogales, 1994; Willson et al., 1996; de Castro and Galetti, 2004). Our results showed that the germination rates and final germination percentages of seeds of the alpine fleshy-fruited shrub *Berberis empetrifolia* that are ingested by *Liolaemus belii* lizard species were significantly greater compared to non-ingested control seeds.

The significant enhancement of both variables is probably due to the modification of the seed coat in the digestive tract of the lizard as can be observed in the histological cuts (Figs. 2 and 3). Castilla (2000) suggests that the passage through

a lizard gut has an abrasive effect on seed coat, which may stimulate germination by increasing seed coat permeability to water and gases (Sahai, 1995). The evident thinning of the seed coat observed in the ingested seeds is probably due to cutin and lignin removal from the cuticle by the enzymatic and chemical environment of the ecthothermal digestive tract (Rick and Bowman, 1961). Nevertheless, it should be noted that the rate of germination reached for both treatments was rather low. A reasonable explanation for this is the efficiency of seed-coat degradation after passing through the lizard's digestive tract. Despite the degradation observed on those seeds collected from lizard's feces, this degradation was not complete (Figs. 2 and 3). Thus, restrictions on the passage of oxygen and water to the embryo due to the presence of the cuticle could explain the overall low germination rates found.

On the other hand, the fecal material surrounding the seeds after passage through the digestive tract has been shown to enhance nutrient availability favoring germination and seedling establishment (Jobidon, 1993; Traveset and Verdú, 2002). But the responses can vary depending on the species and other studies have demonstrated that seed germination is negatively affected due to the soil acidification
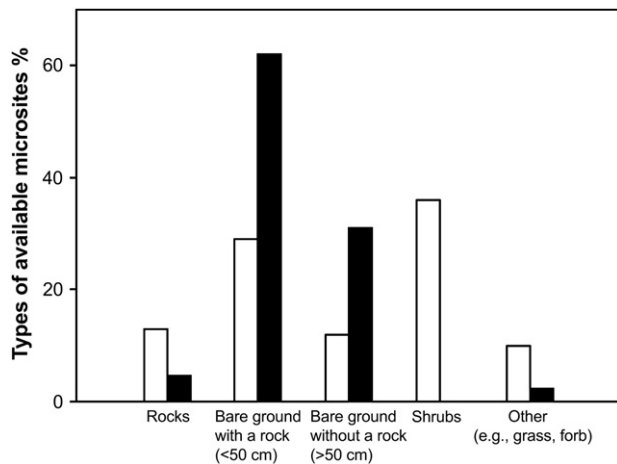
Fig. 4 – Percentage cover of various microhabitats at a high-altitude ecosystem in the Andes Mountains of central Chile (white bars) and proportions of defecated seeds deposited onto these various microhabitats (black bars).

(e.g., Roem et al., 2002). Nevertheless, further studies are needed to clarify this issue; in our experiment we removed the fecal material surrounding the seeds to avoid the influence of nutrient on seed germination, thus assessing only the effect of the digestive tract on germination.

Alpine habitats are characterized by the short period suitable for seed germination and seedling recruitment (Körner, 2003). Thus, the enhancement of germination rates could be favorable for plants which grow in sites with limited growing seasons (Baskin and Baskin, 1998). At the study site, the growing season is from mid-October to mid-May, but considering that the fruiting period of *B. empetrifolia* occurs between January and February the seeds have very a short time to germinate and become a seedling. Additionally, in alpine areas with a Mediterranean-climate, the water shortages that prevail at the end of the growing season are an important limiting factor on seed germination and seedling recruitment (Ehleringer and Miller, 1975; Rada et al., 1999). Consequently, passage through a lizard's digestive tract could be hypothesized to give ingested seeds important ecological advantages if they consistently germinate and become established before those that are not ingested. Seedlings emerging earlier can produce a well developed root system that can reach deeper moist soil layers, and hence would not be limited by the water scarcity produced at the end of the growth season. Future field germination research with seeds of *B. empetrifolia* should shed more light on these potential advantages of lizard-ingested seeds.

Another putative advantage of this process is that lizards deposit their feces into microsites that can favor seed germination and seedling establishment (Willson et al., 1996; Varela and Bucher, 2002). In our case the majority (62%) of feces were deposited on bare ground located <50 cm from a rock commonly used as a perch (Muñoz and Arroyo, 2004), although this microhabitat represented only 29% of the available microhabitat at the study site. This type of microhabitat could be very favorable for *Berberis empetrifolia* seedling establishment

because the soil below rocks maintains higher moisture than surrounding bare ground, and dew accumulation is commonly observed next to rocks, thus further improving the moisture conditions in the absence of precipitation (Jumpponen et al., 1999). In this system, this plant species grows in patches of the same shrub or associated with rocks (Celedón-Neghme, personal observation).

We conclude that, in the Andes Mountains of central Chile, passage through the digestive tract of lizards favors the germination process of seeds of the fleshy-fruited shrub species, *Berberis empetrifolia*, potentially contributing towards its reproductive success. 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*.

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