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THE EUROPEAN RABBIT
*Oryctolagus cuniculus* L.) AS SEED DISPERSER
OF THE INVASIVE OPIUM POPPY (*Papaver somniferum* L.)
IN ROBINSON CRUSOE ISLAND, CHILE

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ABSTRACT: We investigated whether introduced European rabbit on Robinson Crusoe Island, Chile, has the potential to spread the seeds of the exotic *Papaver somniferum* (opium poppy) via endozoochory. A total of 1320 rabbit droppings were collected during early autumn in the study area and analyzed in laboratory with binocular magnifying glass. Seeds from six different species were found in the droppings: *Papaver somniferum* (Papaveraceae), *Centaurea melitensis* (Asteraceae), *Amaranthus* sp. (Amarantaceae), *Melilotus indicus* (Fabaceae), *Rumex acetosella* (Polygonaceae), and one unidentified species. Poppy seeds were dominant. Most seeds (82%) were destroyed during ingestion, but some of the intact seeds found in pellets remained viable. Germination rate of ingested seeds was similar to control seeds but germination success was lower in the former. Poppy seeds were found in pellets deposited inside poppy patches but also up to 100 m away from patches. In this way, rabbit expands the seed shadow of the plant. Our results suggest that, although poppy lacks morphological adaptations to long distance dispersal, seeds reach favorable places for seedling germination and recruitment via consumption by rabbits, an unspecialized seed disperser. Rabbit activity, together with the effect of other animals and some abiotic factors—wind and rain water, principally—contributes to the spread of poppy with implications for the management of both invasive species in the island.

RESUMEN: El conejo europeo (*Oryctolagus cuniculus* L.) como dispersor de la amapola de opio (*Papaver somniferum* L.) en la isla de Robinson Crusoe, Chile. Se ha investigado si el conejo europeo, introducido en la isla de Robinson Crusoe, Chile, tiene capacidad para dispersar semillas de la amapola del opio (*Papaver somniferum*) vía digestiva. Se recolectaron 1320 fecas a comienzos de otoño en el área de estudio y fueron analizadas en laboratorio con lupa binocular. Se encontraron semillas de seis especies: *Papaver somniferum* (Papaveraceae), *Centaurea melitensis* (Asteraceae), *Amaranthus* sp. (Amarantaceae), *Melilotus indicus* (Fabaceae), *Rumex acetosella* (Polygonaceae) y una no identificada. Las semillas de amapola fueron las más numerosas. La mayoría de las semillas (82%) fueron destruidas durante la ingestión, pero algunas de las que aparecieron intactas en las fecas se mantuvieron viables tras el tránsito por el aparato digestivo. La tasa de germinación de las semillas ingeridas fue similar a la de las semillas control, pero el éxito germinativo fue menor en las primeras. Se encontraron semillas de amapolas en fecas depositadas dentro de las manchas de amapola pero también en fecas depositadas hasta 100 metros de distancia. Por lo tanto, el conejo expande semillas de esta planta. Nuestros resultados sugieren que, a pesar de que la amapola carece de adaptaciones morfológicas específicas para la dispersión a larga distancia, sus semillas pueden alcanzar lugares favorables para la germinación y establecimiento a través del...
INTRODUCTION

The accidental or voluntary introduction of species by humans has removed biogeographic barriers for many organisms which can reach new regions, beyond the limits of their own historical dispersal capabilities (Everett, 2000). Human-facilitated biological invasions are an increasing world-wide environmental concern, as invasive species alter ecosystem processes and cause functional and compositional changes in the biota, becoming a long-term conservation problem when native species are displaced (Ramakrishnan and Vitousek, 1989; Vitousek, 1997). Furthermore, new evidence suggests that the main factors driving global change (i.e., increased atmospheric CO₂ concentration, climate change, habitat fragmentation) are likely to increase the frequency of biological invasions (Dukes and Mooney, 1999). Still, the expansion rate of an introduced plant species is conditioned, among other factors, by its dispersal mechanisms (Rejmanek and Richardson, 1996).

Dispersal of seeds via the digestive tract of herbivores endozoochory has long been known (Ridley, 1930). The coevolutionary implications of endozoochory have been discussed at length but almost exclusively for species with fleshy fruits (Janzen, 1980, 1983; Herrera, 1985, 1995). Species conventionally classified as unspecialized regarding the dispersal mechanism have received less attention, although they may have morphological adaptations for endozoochorous dispersal such as small size and a hard coat (Bruun and Poschlod, 2006). Even in the absence of conspicuous morphological adaptations, endozoochory may become an efficient mechanism for the spread of non-native species into new environments (D’Antonio, 1990).

The role of European rabbit (*Oryctolagus cuniculus*) as seed disperser has been studied from a quantitative perspective mainly in mediterranean continental environments (Soriguer, 1986; D’Antonio, 1990; Zedler and Black, 1992; Muñoz, 1993; Malo and Suarez, 1995; Nogales et al., 1995; Cervan and Pardo, 1997). These works lead to the general conclusion that rabbit acts as a non-specific disperser of dry, small (<1mm) seeds (Malo et al., 1995). Some studies dealt with the influence of rabbit dispersal on the structure and dynamics of these communities (Zedler and Black, 1992; Malo et al., 1995). However, its role as seed disperser in insular ecosystems where it has been introduced remains largely unknown, although it is of prime conservation interest.

The prolonged evolution in isolation in remote oceanic island ecosystems has led to the existence of very singular floras and faunas (Crawford et al., 1987). These fragile ecosystems are particularly vulnerable to biological invasions (Fritts and Rodda, 1998; Bergstrom and Chown, 1999). The aim of this investigation was to assess the importance of rabbit as seed disperser of the exotic opium poppy (*Papaver somniferum*) in Robinson Crusoe Island, off the Chilean coast, where the poppy has been introduced and is currently perceived as a potential soil protector (Cuevas and van Leersum, 2001). Specific goals of the study were to detect and quantify: 1, poppy seeds consumption by rabbit; 2, distance dispersal by rabbit; and 3, seed viability.

MATERIAL AND METHODS

The case of Robinson Crusoe island as a conservation problem

Robinson Crusoe Island contains one of the most interesting island floras on the planet (Stuessy et
This singular flora comprises 131 endemic species (62% of the vascular native flora), 12 endemic genera and 1 endemic family (Marticorena et al., 1998). However, 400 years of human interference including repeated burning, overgrazing and an introduction of animal and plant species have left deep traces in the native plant communities. Nowadays, 212 introduced plant species occupy the island (Marticorena et al., 1998), 73% of the endemic vascular flora has been taken to the verge of extinction, and many native herbs have been replaced by invasive species (Matthei et al., 1993; Stuessy et al., 1998). These factors have great impact at all conservation levels including genetic, populational, specific, and at community levels (Pimm, 1987; Ramakrishnan and Vitousek, 1989).

One of the most important conservation problems in the island is the high density of European rabbit (Oryctolagus cuniculus), with 20-22 rabbits per hectare and a total population of ca. 50,000 individuals (Cuevas and van Leersum, 2001). This small herbivore is responsible for overgrazing of native flora in those habitats where it has been introduced, as is the case in other oceanic islands (Flux and Fullagar, 1992; Towns et al., 1997; Priddel et al., 2000). The rabbit was introduced in Robinson Crusoe in 1935 (Jacksic, 1998) and since then it has occupied the entire area of the island. The rabbit has caused great damage on prairie vegetation raising erosion risk (Cuevas and van Leersum, 2001). Despite its importance as a menace to habitat integrity, information about the biology and ecology of rabbit in the island is still very scarce.

Opium poppy (Papaver somniferum, L.) was introduced in 1980 (pers. obs.) in the aerodrome area as ornamental. Since then it has widely expanded its range over the Western sector of the island, where rabbits occur in higher densities. Although it may protect the soil from erosion, it has the potential to displace native species (Cuevas and van Leersum, 2001).

Physical features of the study area

Robinson Crusoe island is located in the Pacific Ocean, some 670 km West off the Chilean coast (Juan Fernández archipelago – Chile; 78° 51’ W, 33° 45’ S). This small island (47.9 km²) of volcanic origin (4.5 million years) presents a very rough topography with less than 3% of the surface below 15% inclination. Maximum altitude is 915 m a.s.l. at El Yunque. The island has been protected as a National Park since 1935, and it was declared World Biosphere Reserve by the UNESCO in 1977. Local human population is 500, all in San Juan Bautista village. Climate is Mediterranean with intense oceanic influence; mean annual temperature is 15.4 °C and total precipitation is 890 mm. However, the extremely rough topography generates strong microclimatic differences in short distance (Cereceda et al., 1994). As a consequence, two main environments can be distinguished in the island. The relatively mesic NE zone, with highest altitudes and woody vegetation, and the SW zone (our study area), a semi-arid biome where vegetation today consists mainly of a impoverished grassland of introduced weeds including Erodium cicutarium, Hordeum murinum, Acena argentea, Anthoxanthum odoratum, Centaurea melitensis and Conium maculatum (for more information on exotic vegetation see Matthei et al., 1993). Native species such as Dendroseris pruinata, D. marginata and Wahlenbergia berteroii have almost disappeared (Stuessy et al., 1998). In this zone, soils are highly eroded as a consequence of topography and overgrazing by cattle and rabbits. Overall, about 40% of the island is affected by severe or extremely severe erosion (Cuevas and van Leersum, 2001).

Rabbits and livestock

Livestock population greatly exceeds carrying capacity of the island and concentrates in the SW area, where rabbit densities are also highest (Saíz, 1999). Rabbits eat seedlings of native and invasive species and erode the hillsides with their extensive warrens (Acevedo, 1990). These factors, combined with other natural erosion factors such as precipitation, strong wind, steep slopes, and soils with low water retention capacity, have led to the gradual impoverishment of soils, one of the most important conservation problems nowadays (Cuevas and van Leersum, 2001).

Opium poppy (Papaver somniferum L.)

One of the most recently introduced weeds in the island is the opium poppy. Papaver species are considered highly invasive weeds, characteristic of disturbed habitats, roadsides and cultivate land (Hanf, 1983). Papaver somniferum is an annual herb, toxic or narcotic that contains more than 25 alkaloids which make the poppy unpalatable for most herbivores (Mattson, 1980). The fruit is a capsule in the end of a long (ca. 1 m) stalk, and houses many small seeds (0.5 mm approx.) with no evident morphological adaptation for dispersal. Seeds fall just below the plant from dehisced capsules and become dormant, showing a long drawn out sequence of seedling emergence. As a conse-
sequence, the plant shows a contagious distribution in patches of variable size (Hanf, 1983).

**Sampling design and data collection**

Feces were collected in autumn 2001 just before the rainy season. Two sampling procedures were carried out in order to (a) quantify and compare the presence of seeds in rabbit feces collected inside and outside poppy patches, and (b) evaluate the dispersal distance of seeds in feces.

a. **Fecal sampling stations** (n = 10) were selected in the study area. Each station consisted of an isolated poppy patch surrounded by grassland. Feces (50 approximately) were collected randomly both inside and outside patches, 25 m away in the direction of the slope, which was considered the most probably dispersal direction. In addition, a soil sample of 50 cm³ (see below) was taken inside and outside patches close to the fecal collection spot. Poppies were also collected directly from plants as controls for germination experiments. Additional separate stations (n = 4) were sampled in the same way in order to detect seeds of other weed species (Acaena argentea, Conium maculatum, Silybum marianum and Centaurea melitensis) in rabbit feces. Results from these last stations were not included in poppy analysis but used in determining the general spectrum of seeds found in rabbit feces (Table 1).

b. **Distance transects** (n = 4). In each of four of the poppy sampling stations a distance sampling transect was conducted. Rabbit feces (ca. 50) were collected in the border of the patch and outside every 25 m along a transect up to 100 m away in the direction of the slope. A soil sample (50 cm³; see below) was also taken at each distance. In all cases, samples were labeled, preserved dried in paper bags and individually analyzed in laboratory.

**Fecal analysis**

A subsample (n = 30) of randomly chosen feces from those collected at each point from both sampling regimes (a and b above) were individually searched for poppy seeds using a binocular magnifying glass. Previous estimates showed that the volume 30 feces occupy once grounded is ca. 50 cm³; this made a baseline comparison for soil samples. Poppies are easily detected due to their dark colour, small size and reticulated surface. They were counted and measured to the nearest 0.01 mm. Three seed categories were distinguished: (i) whole, not damaged after gut passage; (ii) unviable, totally or partially digested; (iii) fragments of seeds destroyed during the process. In this latter case, the following ratio was fixed a priori for seed quantification: 3 fragments = 1 seed ingested. Seeds from species other than poppy found in feces were preserved and, if they could not be identified directly, they were sown and growth until seedling was identified.

**Germination experiments**

A germination test of three treatments, namely control from plants, seeds from soil bank, and undamaged seeds from feces, was carried out with n = 135 for each treatment. Seeds were planted individually in sown-trays with sterile substratum (pine bark) and maintained under controlled conditions (22ºC and ambient light) until no further germination was detected in controls (35 days). Before sowing, seeds were measured individually. Germination experiments with other species found in feces were also conducted in the same manner.

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>Size</th>
<th>Percentage germinated</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>In feces</td>
<td>In soil</td>
<td>In feces</td>
</tr>
<tr>
<td>Papaver somniferum</td>
<td>582</td>
<td>0.79 ± 0.76</td>
<td>6</td>
</tr>
<tr>
<td>Centaurea melitensis</td>
<td>41</td>
<td>2.23 ± 0.61</td>
<td>32</td>
</tr>
<tr>
<td>Amaranthus sp.</td>
<td>15</td>
<td>0.90 ± 0.31</td>
<td>25</td>
</tr>
<tr>
<td>Melilotus indicus</td>
<td>23</td>
<td>1.44 ± 0.25</td>
<td>15</td>
</tr>
<tr>
<td>Rumex acetosella</td>
<td>20</td>
<td>0.62 ± 0.08</td>
<td>10</td>
</tr>
<tr>
<td>Undetermined</td>
<td>15</td>
<td>1.2 ± 0.35</td>
<td>-</td>
</tr>
</tbody>
</table>

* p < 0.05; ** p < 0.01.

Differences in frequencies of germinated seeds (feces vs. soil) were tested by Chi-square test.
Statistical analyses

Normality of data was tested with Kolmogorov-Smirnov and Lilliefors methods. Chi-square test was used to check differences in expected frequencies of seeds found in feces (with Yates correction for continuity) and frequencies of germinated seeds. Parametric t-tests were used for comparison of seed sizes. ANOVA was used to check differences among sizes of plant and soil seeds and whole seeds from feces and, when significant, a posteriori Tukey test was employed for two by two comparisons of means (Sokal and Rohlf, 1981). Germination cumulative distributions of the different treatments were analyzed with non-parametric Kolmogorov-Smirnov test. All analyses were performed using STATISTICA v. 4.5 (Stat Soft, 1995).

RESULTS

A total of 1320 feces were analyzed from both sampling schemes; 1080 of them were collected in poppy sampling stations, 39% inside patches and 61% outside. All whole seeds (n = 696) belonged to five invasive weeds plus one unidentified species (Table 1). *Papaver somniferum* seeds were dominant (84%) and only this species is considered in further analyses.

Poppy seed dispersal

Poppy seeds were present in 44% (n = 473) of feces. A similar proportion of positive feces were collected inside patches (49%) and outside patches (51%). From these positive feces, 231 (49%) were collected inside patches and 242 (51%) outside.

On the assumption of a 3:1 ratio of fragment:whole seed, a total of 3168 seeds were removed from feces. The majority of seeds (82%) were physically destroyed by ingestion while 18% were whole, probably viable seeds ($\chi^2 = 1267$; d.f. = 1; $p<0.001$). Total number of whole seeds in feces collected in the center of patches (n = 241) was significantly higher than in feces collected 25 m away from patches (n = 105; 300 feces analyzed in each location; $\chi^2 = 52.67$; d.f. = 1; $p < 0.01$). The mean ($\pm$ SD; range) number of whole seeds found in positive droppings was 2.33 ($\pm$ 2.35; 1-15) inside patches and 2.05 ($\pm$ 1.55; 1-8) outside.

Distance dispersal

The limited dispersal capability of poppy seeds is reflected by the fact that, for both a and b sampling designs (see Methods), only 10 seeds were found in soil samples 25 m away from poppy patches while a much higher number (651 seeds) was found in samples collected inside patches. A total of 582 whole seeds were found in rabbit feces analyzed. Therefore, seeds were significantly more numerous in soil samples than in feces ($\chi^2 = 4.48$; d.f. = 1; $p < 0.05$), likely reflecting a cumulative history of deposition. However, the presence of an important number of seeds in feces outside patches is again verified. Feces collected inside patches contained a total of 338 whole poppy seeds, while as many as 244 seeds came from feces outside patches, even 100 m away from the patches (Table 2).

Germination and viability of poppy seeds

Differences in mean size across the three types of seeds used in germination experiments (i.e. control seeds from plants and soil samples and whole seeds from feces) were significant.

<table>
<thead>
<tr>
<th>Origin</th>
<th>Distance</th>
<th>Center</th>
<th>Border</th>
<th>25 m</th>
<th>50 m</th>
<th>75 m</th>
<th>100 m</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feces</td>
<td></td>
<td>110</td>
<td>105</td>
<td>45</td>
<td>40</td>
<td>37</td>
<td>35</td>
</tr>
<tr>
<td>Soil</td>
<td></td>
<td>305</td>
<td>105</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Table 2

Pooled number of *P. somniferum* whole seeds found in rabbit feces and in soil samples at varying distances away the center of poppy patches (n= 4 transects).
A posteriori Tukey Tests showed that differences were due to the smaller size of whole seeds in feces with respect to both controls (soil and plant) seeds, while no differences were observed between both controls. Seeds from all three treatments exhibited, in general, low germination percentages (6% in whole seeds in feces, 16% in seeds from the soil bank, and 0.75% in seeds from plant controls) but these differences were significant across treatments ($\chi^2 = 22.19$; d.f. = 2; $p < 0.01$). When comparing germination frequencies between seeds from feces and pooled control seeds, differences were also significant ($\chi^2_{\text{df (YATES)}} = 5.63; p < 0.05$). No differences were found in the size of whole seeds found in feces that germinated ($0.841 \pm 0.064$ mm; $n = 8$) and germinated control seeds ($0.849 \pm 0.054$ mm; $n = 23$) ($t = 0.18$; n.s.).

Germination started very soon for soil control seeds and very late for the single plant seed that germinated; 63% of seeds from soil that germinated, did so in the first 10 days. No differences were observed in the germination rate of whole seeds from feces and soil controls (Kolmogorov-Smirnov test; $D = 0.11$; $p = 0.2$). The same was true for whole seeds versus plant seeds ($D = 0.059$; $p = 0.7$). Only differences between soil and plant seeds germination rate was significantly different ($D = 0.165$; $p = 0.05$; Fig. 1).

**DISCUSSION**

Our results demonstrated the potential for endozoochorous seed dispersal of the exotic opium poppy by European rabbit in Robinson Crusoe Island. Previous works have shown that rabbits select specific parts of plants for consumption (Catling and Newsome, 1992; Martin et al., 2003) even consuming plants with a high content of salt (Dawson and Ellis, 1979) or important physical and chemical defenses (Pakeman et al., 1998). Ingestion by rabbits of capsules still on the plants is difficult as stalks grow over one meter above the ground. Seed ingestion is accidental (Janzen, 1984) and occurs when rabbits eat poppy capsules dropped on the ground, which had lost most of their seeds by dehiscence (pers. obs.).

When evaluating the effectiveness of a seed disperser, several quantitative and qualitative factors ought to be considered: (i) the amount of seeds ingested, (ii) the effect of manipulation and gut passage in their viability, and (iii) the adequacy of the seed shadow they produce (McKey, 1980). In the case of the poppy, a high proportion of seeds are destroyed chemi-
POPPY SEED DISPERSAL BY RABBIT IN A CHILEAN ISLAND

POPPY SEED DISPERSAL BY RABBIT IN A CHILEAN ISLAND

ically and mechanically (82%). Nevertheless, 18% of seeds survive gut passage, which can be considered a rather good survival rate for a generalist herbivore (Schupp, 1993; Mouissie et al., 2005). Actually, the abundance of rabbits may compensate for individual seed loses. In addition, an important number of seeds are deposited outside poppy patches in rabbit droppings, which modifies the size and spatial pattern of the seed shadow without dispersers. In this way, seeds are widely spread on the landscape and some of them have the chance to reach adequate places for establishing a new poppy patch (“dispersal bridgeheads” sensu Cerván and Pardo, 1997).

Seed dispersal distance is a function of: (i) the seed retention time, quite short in rabbits due to their small body size (Staniforth and Caves, 1977), and (ii) the movements of the dispersal agent. Seeds have been detected in feces up to 100 meters away from poppy patches but even longer displacements are expected since in Robinson Crusoe Island rabbit movements are not affected by predators (Sáiz and Ojeda, 1988). As a consequence, fecal deposition is unrestricted. We have verified elsewhere that other non-native vertebrate species such as cattle and pigeons are also contributing to this dispersion (Fernández and Sáiz, 2002).

Undamaged poppy seeds in feces are significantly smaller than controls; this is probably because when rabbits eat fallen capsules on the ground only the smallest seeds remain inside the capsule (pers. obs.). Nevertheless, some of those seeds are viable after gut passage and no differences in size are detected between germinated fecal and control seeds.

Our results show low percentages of germination in general, which affords evidence of a “low-investment” reproductive strategy of the plant (McKey, 1980). Our results also indicate that entire seeds from feces germinated at the same rate than control seeds from soil, but in lower percentage. Low germination success in the plant control suggest the need of a scarification or a dormancy process. Thus, the dispersal effect of rabbits derives from accidental consumption of seeds trapped in poppy capsules, followed by deposition and subsequent incorporation of some seeds to the seed bank away from parent plants. Thus, gut passage seems to cause partial scarification completed in the soil (see Taylor, 1981). Feces may constitute temporary refuges for seeds, avoiding early germination or destruction by pathogens or predators (Schupp, 1988). Also, the small number of seeds in each dropping indirectly aids seedling establishment because in this way seeds avoid early competitive interactions with other seedlings (Janzen, 1983).

We contend that, altogether, these processes contribute to the success of the opium poppy as an invading species on a limited individual basis, but have the potential to be greatly amplified due to rabbit abundance.

In summary, interaction between these two introduced species confirms that precise co-evolutionary adjustment between plant and dispersers is not necessary for successful dispersal under certain conditions (Herrera, 1985). An unspecialized species as opium poppy may take advantage of a generalist herbivore like the rabbit for seed dispersal. From the conservation point of view, this interaction is having an important effect on the current distribution of this aggressive weed in the island. Its rapid expansion, to which the rabbit contributes, creates a conservation dilemma: the trade off between the potential benefit of the poppy as a soil protection, and the damage it causes displacing native flora (Cuevas and van Leersum, 2001). We suggest that any strategy to control non-native plants in the island must involve an understanding of the mechanisms of dispersal and the management of animals acting as generalized dispersers (Constible et al., 2005).

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