

Effect of native and alien vertebrate frugivores on seed viability and germination patterns of *Rubia fruticosa* (Rubiaceae) in the eastern Canary Islands

M. NOGALES*†, C. NIEVES*, J. C. ILLERA*, D. P. PADILLA* and
A. TRAVESSET‡

*Island Ecology and Evolution Research Group (CSIC-IPNA), CI Astrofísico Francisco Sánchez no. 3, 38206 La Laguna, Tenerife, Canary Islands, Spain; and ‡Institut Mediterrani d'Estudis Avançats (CSIC-UIB), CIMiguel Marqués no. 21, 07190 Esporles, Mallorca, Balearic Islands, Spain

Summary

1. This study shows the first results obtained concerning the relative importance and effect on the seeds of a particular plant species, *Rubia fruticosa* Ait. (Rubiaceae), of passage through the digestive tube of the three main groups of vertebrate seed dispersers: native reptiles and birds, and alien mammals.
2. Native birds and reptiles dispersed a high proportion of undamaged seeds of *R. fruticosa*.
3. In contrast, seeds defecated by the two alien mammals showed significantly greater proportions of damaged seeds. Seed viability was much higher for reptiles and birds than for mammals, which was consistent with germination results.
4. Ingested seeds had a significantly thinner coat than uningested control seeds. Seeds that had passed through native dispersers had a significantly thicker coat than those passed through one of the alien mammals (the squirrel).
5. Considering both quantitative and qualitative components of seed dispersal, we conclude that native reptiles and birds are the most important seed dispersers in this multidisperser system.

Key-words: birds, Canaries, frugivores, mammals, reptiles, *Rubia fruticosa*

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Introduction

Seed dispersal is usually a crucial stage in the life cycle of a plant as it allows offspring to colonize sites, near or far from the parent plant, at the same time that it increases the chance that those seeds will survive and become established adults. In the case of fleshy fruited plants, animals play an important role in determining the success of this critical stage (Levey, Silva & Galetti 2002 and references therein). Most such studies, however, consider only the 'seed-movement' effect, examining the seed shadows produced by frugivores and evaluating the probability of seed (and sometimes also seedling) survival in different microhabitats where those seeds are deposited (Houle 1992, 1998; Herrera *et al.* 1994; Jordano & Herrera 1995; Schupp 1995; Rey & Alcántara 2000; Holl 2002; Traveset *et al.* 2003).

In the case of endozoochory, which is especially frequent in plants bearing fleshy fruits, the other quality

component (besides seed-deposition patterns) of seed dispersal effectiveness (*sensu* Schupp 1993) is that of seed treatment in the disperser's digestive tract – the capacity of seeds to germinate after ingestion by frugivores. This component has generally received less attention, although an increasing number of studies are devoted to this subject (see reviews by Traveset 1998; Traveset & Verdú 2002), which is important for the population dynamics of many plant species and significant for the evolution of plant–frugivore interactions.

For a given plant species, the outcome of seed passage through a digestive tract may depend on the animal species that consumes it. Both morphological traits (e.g. length of digestive tract, presence of a gizzard) and physiological traits (e.g. digestive fluids in the guts) of frugivores affect seed treatment. As the digestive systems of frugivores such as reptiles, birds and mammals differ greatly in both types of trait (Stevens 1988; Robbins 1993; King 1996), we may expect differences in this quality component of seed dispersal, which may counteract other components such as the quality of seed

deposition and the number of seeds dispersed by a given frugivore (quantity component).

The rather scarce information available on the effect of different types (guilds) of frugivores on the seed germination patterns of the same plant species indicates that about half the plant species that have been tested showed very different results (see Tables 2 and 3 in Traveset 1998). According to this review, the most common comparisons have been performed using birds and non-flying mammals; an intermediate number of studies have compared birds and bats; and a smaller number used birds and reptiles. Lieberman & Lieberman (1986) were the first to examine more than two guilds of frugivore (birds, bats and primates), finding consistent results for several plant species and inconsistent results for others. However, no general mechanisms were suggested for such differences.

Three different vertebrate classes are involved in most seed-dispersal systems in the world: reptiles, birds and mammals (Stiles 2000). However there are not many seed-dispersal systems in which these three groups participate simultaneously. This is mainly because (1) saurochory is especially an island phenomena (Olesen & Valido 2003; Valido, Nogales & Medina 2003 and references therein); and (2) some active seed-disperser groups in continental ecosystems (such as Macrochiroptera or Carnivora) are frequently absent in islands (Williamson 1983; Gorman 1991; Whittaker 1998).

The Canary Islands are no exception; however, at least 11 wild terrestrial species have been introduced by humans, mostly since the European conquest in the 15th century, and these species have often become feral. Some participate directly in seed-dispersal systems: hedgehogs (*Ateleryx algirus* Lereboullet, Barquín, Nogales & Wildpret 1986); rabbits (*Oryctolagus cuniculus* L., Nogales, Valido & Medina 1995); and feral cats (*Felis catus* L., Nogales, Medina & Valido 1996). In these islands it is possible to find reptiles, birds and mammals coexisting in the same habitats and sharing the same plant resources, for example in the badlands of the northern part of Lanzarote and Fuerteventura, where one of these shared species is *Rubia fruticosa* Ait. (Rubiaceae), an endemic shrub from the central Macaronesian archipelagos of Madeira, Salvages and Canaries.

This system is ideal to compare simultaneously the effects of seed treatment in the guts of the three main different classes of vertebrate (reptiles, birds and mammals) on seed germination of a plant species, something that has not been tested so far. Some patterns that have emerged from recent reviews (Traveset 1998; Traveset & Verdú 2002) suggest that, while birds and bats produce a significant enhancement effect on germination, reptiles and non-flying mammals produce the opposite effect.

Different seed-coat thickness can sometimes account for the different effects of a frugivore on seed germination (Gardener, McIvor & Janzen 1993; Traveset, Riera & Mas 2001). We examined this possibility in all our treatments to see if it could shed light on the mechanisms by which germination of ingested seeds is altered.

Specifically, the objectives of this study were: (1) to study the relative importance of the different primary dispersers (reptiles, birds and mammals) on the *R. fruticosa* seed-dispersal system; (2) to evaluate the damage caused to the seeds consumed by different groups of dispersers; (3) to examine if the different dispersal agents produce a differential effect on seed viability and germination; and (4) to assess if seed-coat thickness is differently affected by the diverse assemblage of dispersers, and if this trait is related to germination success.

Materials and methods

NATURAL HISTORY OF THE SEED-DISPERSAL SYSTEM

Rubia fruticosa is considered an endemic plant that grows in the central Archipelagos of the Macaronesian islands (Madeira, Salvages and Canaries). It is present in all the Canary Islands, and can reach a mean of ≈ 0.49 m² of plant cover and 0.54 m in height ($N = 100$ plants) in the eastern islands of Lanzarote and Fuerteventura. This species produces flowers in late January, and ripe fruits are present in early March in Lanzarote and at the end of this month in Fuerteventura. Fleshy fruits are spherical, translucent berries with an average length of 7.5 mm, a diameter of 5.6 mm, a fresh weight of 0.2 g, a dry weight of 0.037 g, and a water content of 81.5%; they contain a mean number of 1.4 spherical seeds per fruit, and average seed weight is 8.2 mg ($N = 40$ fruits; Nogales, Hernández & Valdés 1999). Seeds from this plant show a relatively high proportion of germination, demonstrating the scarcity of dormancy in this species (Nogales *et al.* 2001).

This plant occupies the lowlands of the Canary Islands and its fruits are eaten by several vertebrates which include lizards (Barquín *et al.* 1986; Valido & Nogales 1994; Valido 1999), birds (Nogales *et al.* 1999; Nogales *et al.* 2001), and introduced mammals (Nogales *et al.* 1995). Native agents of this seed dispersal system in the badlands of Lanzarote and Fuerteventura are *Gallotia atlantica* (Peters & Doria), an endemic Canarian lizard whose adult body size is larger in Lanzarote (6.6–9.0 mm; $N = 33$; *G. a. laurae*) than in Fuerteventura (5.15–5.90 cm; $N = 100$; *G. a. atlantica*) (Castroviejo, Mateo & Collado 1985). Regarding birds, Spectacled and Sardinian Warblers (*Sylvia conspicillata* Temminck and *Sylvia melanocephala* Gmelin) also swallow whole fruits, although the latter species has been recorded only in Lanzarote. The Raven (*Corvus corax* L.) eats a large quantity of fruits during the spring in both badlands, while its consumption by the Yellow-legged Gull (*Larus cachinnans* Pontoppidan) has only been observed in Lanzarote (Nogales *et al.* 2001). Lastly, rabbits (*Oryctolagus cuniculus*; probably introduced during the 15th century) and the Barbary Ground Squirrel (*Atlantoxerus getulus* L.; introduced in the 1960s to 1970s; Machado 1979) also relatively frequently consume fleshy fruits of *R. fruticosa*.

STUDY SITES

The Canarian Archipelago consists of seven primary volcanic islands situated between 27°N–29°N and 13°W–18°W, located less than 100 km off the Atlantic coast of north-west Africa. The present study was carried out in the eastern islands of Fuerteventura (1660 km²) and Lanzarote (846 km²). These are the oldest islands with the ages of main periods of volcanic activity distributed between 22 and 11.8 (Fuerteventura) and 15.5–5.0 (Lanzarote) millions of years before present (Carracedo & Day 2002). These islands are low in altitude, with the highest peak reaching 807 and 671 m for Fuerteventura and Lanzarote, respectively, which reflects intense erosion since the principal shield-building phase of volcanism (Carracedo & Day 2002). The climate is semiarid with dry summers and heavy rains in winter (Marzol-Jaén 1988), but is somewhat influenced by sea spray and the proximity to the African continent. Annual rainfall is scarce in both islands although the Fuerteventura study site supports more annual rain (166.1 ± 96.36 ; $N = 23$ years) than the Lanzarote study site (146.25 ± 18.81 ; $N = 11$ years). There is no specific information available on temperature in the study areas; however, annual mean temperature is around 21 °C, and is probably moderately higher in the study site of Lanzarote (coastal zone, 100 m a.s.l.) than in the Fuerteventura site (inner zone, 220 m a.s.l.) (Fig. 1). The study areas are two lava fields or badlands (locally called ‘malpaís’) which were produced by only one volcanic cone (La Arena) in Fuerteventura, and by a volcanic group (Los Helechos–Montaña Quemada–La Corona) in Lanzarote. Both lava fields belong to the network of Natural Protected Areas of the Canary Islands (Fig. 1). The Fuerteventura study area (named Malpaís de La Arena; 8.71 km²) has been dated as more than 100 000 years old (Meco

et al. 2002), and the Corona volcanic group (named Malpaís de La Corona; 17.97 km²) is estimated to be between 53 000 and 72 000 years old (Carracedo & Day 2002). The vegetation is very similar in both islands, consisting of a sparse xerophytic shrub composed mainly of *Euphorbia regis-jubae* Webb & Berthel *Launaea arborescens* (Batt.) Murb., *Salsola vermiculata* L., *Lycium intricatum* Boiss., *Rubia fruticosa*, *Kleinia neriifolia* Haw. and *Nicotiana glauca* Graham. Species specific to each site included *Asparagus pastorianus* Webb & Berthel. and *Caralluma burchardii* N. E. Br. in Fuerteventura; and *Asparagus nesiotus* Svent., *Asparagus arborescens* Willd. and *Euphorbia balsamifera* Ait. in Lanzarote.

EXPERIMENTAL PROCEDURES

Fieldwork was conducted in the two badlands in order to simultaneously evaluate the robustness of the results obtained and to study the potential differences of these two similar areas from different islands. The study took place during the springs of 2002–04. We collected a total of 200 fruits directly from plants, which served as controls, and also obtained droppings of *Gallotia*, *Sylvia*, *Atlantoxerus* and *Oryctolagus* (about 200 from each species), and a total of 12 pellets from *Corvus*. Due to the difficulty in finding *Larus* pellets in the badland area, we used seeds collected in the nearby islet ‘Roque del Este’, where material comes from this badland (Nogales *et al.* 2001). In both locations, most of the material (except from *Corvus* and *Larus*) was collected from a surface 4000 m² in order to minimize the plant mother’s effect and evaluate the real consequences (viability and germination) of the different gut disperser agents on the seeds. Droppings and pellets were stored independently; seeds were extracted manually and counted. Using a stereomicroscope (10× magnification) we noted the external state of the seeds visually, and classified them in two categories, damaged and undamaged, for the different dispersers or treatments.

Seed viability experiments were carried out for each different treatment ($N = 100$ seeds) using 2,3,5-triphenyl tetrazolium chloride (TTC) (see details in Scharpf 1970) to estimate the possible bias caused by the seed dormancy effect. Seeds were immersed for 24 h in TTC and kept in the dark. Furthermore, we performed a germination experiment in a glasshouse over 6 months (October–March), following the recommendations of Traveset & Verdú (2002). Before planting, 100 seeds of each treatment were measured (diameter) and weighed to study any possible relationship between the metrics and germination performance. We planted (1 October 2002) a total of 200 seeds for most treatments for each island. We sowed each seed independently in a 4 cm² pot ($N = 230$ pots per tray) using a standard substrate (50% turf and 50% culture soil); each seed was buried ≈ 5 mm deep. All pots were watered every 2 days, and germination was monitored daily. The experiment took

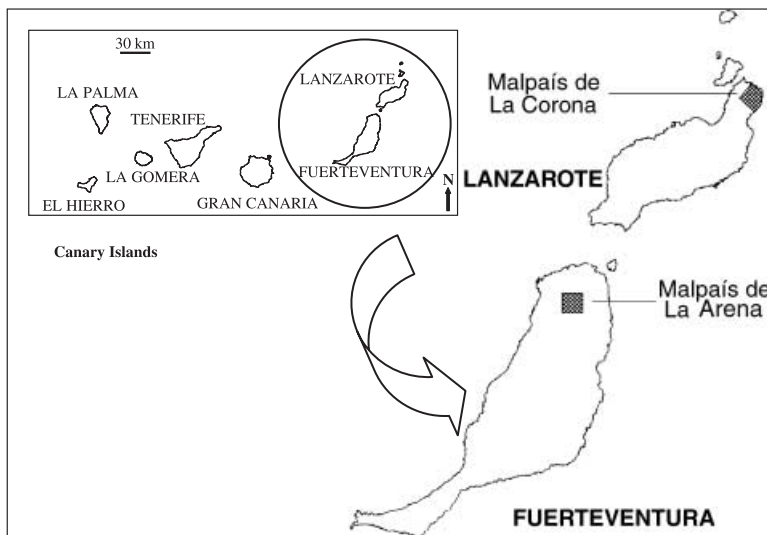


Fig. 1. Map of the Canarian Archipelago showing the situation of the badlands studied (Malpaís de La Corona, Lanzarote; Malpaís de La Arena, Fuerteventura).

Table 1. *Rubia fruticosa* seeds found in droppings and pellets of the different dispersers on Malpaís de La Corona (Lanzarote, L) and Malpaís de La Arena (Fuerteventura, F)

Dispersers	Island	Seed number per droppings or pellets (mean ± SD)	Percentage frequency in pellets or droppings	Number of pellets or droppings analysed	Percentage undamaged seeds	Total seeds found
<i>Gallotia</i>	L	8.50 ± 4.62	90.5	200	99.2	1 269
	F	7.00 ± 3.02	77.5	200	97.8	696
<i>Sylvia</i>	L	–	–	112	99.2	489
	F	–	–	268	99.6	446
<i>Corvus</i>	F	236.33 ± 82.96	100	12	100	2 836
<i>Larus</i>	L	598.00 ± 285.10	100	81	100	48 460
<i>Atlantoxerus</i>	F	1.00 ± 3.64	62.5	200	64.6	554
<i>Oryctolagus</i>	L	5.50 ± 3.37	94.5	200	37.7	938
	F	3.00 ± 3.47	51.5	200	4.8	440

place at Tagoro (Tenerife Island; 300 m a.s.l.) where the night–day period was similar to that found in the study areas. Germination was defined as the emergence of any seedling part from the soil surface. Although the experiment was followed daily, we used the accumulation of seed emergence every 5 days to calculate speed of germination. Seed-coat thickness was measured for five seeds ($N = 5$ measures per seed) from each treatment and control for each island, by means of a dissecting microscope connected to a computer using IMAGE PRO-PLUS ver. 4.5.1.2.2.

Results

SEED-DISPERSAL SYSTEM

Rubia fruticosa seeds were found in the highest frequency in pellets from the two long-distance dispersers (capable of flying some kilometres), ravens and gulls (Table 1), which clearly show a larger capacity for seed transport. The endemic lizard *G. atlantica* was next in importance in the number of seeds dispersed, and significantly more so in Lanzarote than in Fuerteventura (Mann–Whitney test, $Z = 6.67$, $P < 0.001$). Seeds defecated by warblers (*Sylvia*) appeared rather scattered, and the usual number of seeds recorded in each scat was two to three. Lastly, if the *Sylvia* droppings are excluded, the smallest quantity of seeds per dropping corresponded to the two alien mammal species, being significantly higher in the case of rabbits than in the desert squirrels in Fuerteventura ($Z = 1.97$, $P = 0.049$). Rabbit droppings contained more seeds in Lanzarote than in Fuerteventura ($Z = 9.26$, $P < 0.001$), and appeared more frequently (likelihood ratio test, $G_1 = 104.33$, $P < 0.001$).

SEEDS STATE AND VIABILITY

External visible damage to *R. fruticosa* control seeds was very low, and the proportion of undamaged (intact) seeds ingested by either reptiles or birds was quite high—over 97% (Table 1). However the percentage of intact seeds was clearly lower for mammals: 64.6% for

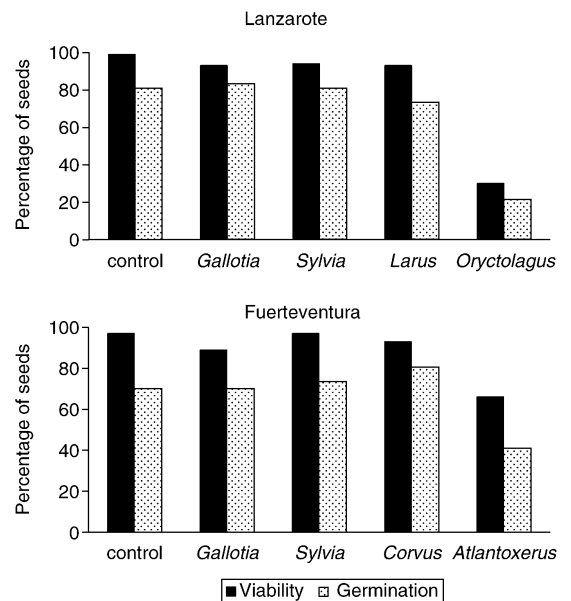


Fig. 2. Seed viability and germination of the different treatments of *Rubia fruticosa*.

Atlantoxerus, and 37.7 and 4.8% for *Oryctolagus* in Lanzarote and Fuerteventura, respectively ($G_1 = 8741.87$, $P < 0.001$). Differences between the two mammal species were very significant ($G_1 = 231.59$, $P < 0.001$) as well as differences between islands for the *Oryctolagus* treatment ($G_1 = 201.15$, $P < 0.001$).

Seed viability was consistently high in the plant populations of both islands (Lanzarote, 99%; Fuerteventura, 97%) ($G_1 = 1.06$, $P > 0.05$; Fig. 2). This parameter was also found to be high ($\geq 93\%$ for Lanzarote; $\geq 89\%$ for Fuerteventura) in those seeds passed through guts of native dispersers (reptiles and birds) – these two groups presented no significant differences ($P > 0.05$). In contrast, seed viability was found to decrease in seeds ingested by the introduced mammals (*Atlantoxerus*, 66%; *Oryctolagus*, 30%; $P < 0.001$ for all comparisons with respect to other dispersers and control seeds); differences between these two mammals were highly significant ($G_1 = 26.55$, $P < 0.001$). When comparing the same treatment between islands, statistical

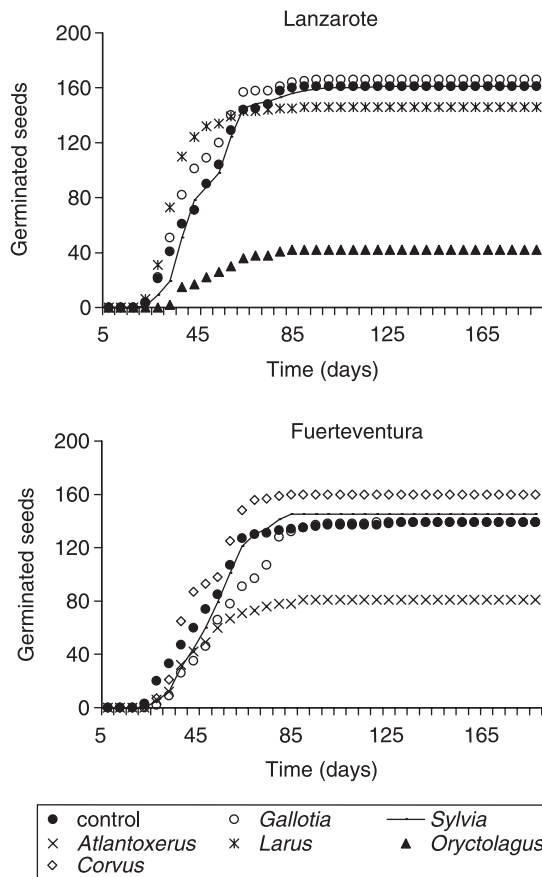


Fig. 3. Seed germination of *Rubia fruticosa* in the different treatments (seed dispersers) and controls (uninged seeds).

differences were not appreciated (control seeds, *Gallotia* seeds and *Sylvia* seeds; $P > 0.05$).

GERMINATION

Germination results coming from the different dispersers followed a trend similar to those obtained in the viability experiments (Fig. 2). Therefore native dispersers (reptiles and birds) did not affect the general pattern of germination of uninged control seeds ($P > 0.05$). The alien mammals, in contrast, had a

significantly negative effect on seed germination compared with controls and native dispersers. When we compared the three common treatments (*Rubia*, *Gallotia* and *Sylvia*) between islands, differences in germination in the two former treatments were higher in Lanzarote than in Fuerteventura ($G_1 = 6.49$, $P < 0.01$ and $G_1 = 10.17$, $P < 0.001$, respectively) (Fig. 2).

The speed at which seeds germinated did not differ greatly among treatments within each island (Fig. 3). However, a similar pattern was found in the two islands. Seeds from long-distance dispersal agents (*Corvus* and *Larus*) were fastest to germinate followed by those coming from short-distance dispersers and the controls and, lastly, by seeds from the two mammal species. In this regard, seeds from Rabbits (Lanzarote) germinate significantly later than those from the rest of the treatments (Kolmogorov–Smirnov test, $P < 0.001$). Although native dispersers did not differ significantly from controls, the two mammals did reduce the proportion at which seeds germinated, and more so for *Oryctolagus* (Lanzarote) that *Atlantoxerus* (Fuerteventura) ($Z = 3.30$; $P < 0.001$). When comparing the three common treatments (*Rubia*, *Gallotia* and *Sylvia*) between islands, seeds from *Gallotia* (Lanzarote) germinated earlier than those from Fuerteventura ($Z = 1.32$, $P < 0.05$).

SEED TRAITS, COAT THICKNESS AND GERMINATION RELATIONSHIPS

Seed size (diameter) was slightly larger in Fuerteventura (2.30 ± 0.22 mm, $N = 100$ seeds) than in Lanzarote (2.21 ± 0.26 mm, $N = 100$) (Kruskal–Wallis test, $Z = -2.46$, $P = 0.014$). Likewise, seed weight was also heavier in Fuerteventura (0.0061 ± 0.0016 g, $N = 100$) than in Lanzarote (0.0051 ± 0.0016 , $N = 100$) (t -test, $t_{198} = -4.53$, $P < 0.001$), probably due to the strong relationship between these two parameters in both islands (Pearson's correlation coefficient, $r_p = 0.91$ and $r_p = 0.87$ for Lanzarote and Fuerteventura, respectively, $N = 100$, $P < 0.001$). Seed size and weight did not influence seed germination in any treatment (all $P > 0.05$).

Control seeds showed a significantly thicker seed coat than those ingested by the different dispersers, including lizards, birds and mammals, both in Lanzarote (ANCOVA, $F_{4,19} = 12.75$, $P < 0.001$) and Fuerteventura ($F_{4,19} = 17.10$, $P < 0.001$; Table 2). In Lanzarote, no significant differences in seed-coat thickness were noted among lizards, birds and rabbits. In Fuerteventura, in contrast, seeds ingested by squirrels presented a significantly thinner coat than those ingested by either lizards or birds.

Table 2. Seed-coat thickness of *Rubia fruticosa* in the different treatments from the two badland areas of Lanzarote and Fuerteventura

	Lanzarote		Fuerteventura	
	Seed coat (μm) (mean \pm SD)	Percentage reduction (cf. control)	Seed coat (μm) (mean \pm SD)	Percentage reduction (cf. control)
Control	86.15 \pm 8.65	—	89.56 \pm 10.43	—
<i>Gallotia</i>	52.90 \pm 4.59	38.6	72.61 \pm 8.59	18.9
<i>Sylvia</i>	46.12 \pm 4.24	46.5	66.52 \pm 7.98	25.7
<i>Corvus</i>	—	—	69.92 \pm 8.49	21.9
<i>Larus</i>	44.67 \pm 5.74	48.1	—	—
<i>Atlantoxerus</i>	—	—	57.72 \pm 7.10	35.6
<i>Oryctolagus</i>	45.87 \pm 7.54	46.8	—	—

Discussion

MOVEMENT OF SEEDS BY DIFFERENT DISPERSERS

The largest amount of seeds found in the two long-distance dispersers are clearly related to the high potential

for seed transport of these larger birds (ravens and gulls) compared with the other dispersers of *R. fruticosa* seeds. Both ravens and gulls probably play an important role in the seed-dispersal process of this plant at long distance, both within the islands (Nogales *et al.* 1999) and between them (Nogales *et al.* 2001).

Regarding lizards, a different subspecies of *G. atlantica* exists in each island, being of a larger size in Lanzarote than in Fuerteventura (Castroviejo *et al.* 1985), which explains the slightly higher quantity of seeds moved by the former. The same pattern based on differences in body size is observed in the case of the two alien mammals. Rabbits, larger in size than squirrels, also move greater quantities of seeds.

SEED TREATMENT IN DIFFERENT DISPERSERS' GUTS

External damage of *R. fruticosa* seeds was negligible in the case of reptiles and birds, but was clearly greater in the two mammal species. Both dispersers, reptile and bird, are native to the Canary Islands, and thus have probably evolved in contact with the plant over time. In contrast, the two mammals were introduced by humans relatively recently. Our results showed that seeds ingested by native animals are more viable, and germinate in greater proportions, than those consumed by the alien species in both islands. This represents one more example of the negative consequences that alien (particularly invasive) species can have on native mutualisms, especially in islands (Traveset & Santamaría 2004).

Regarding the speed of germination, and despite the similarities of general patterns in the two badlands, it is interesting to note the existence of some asynchronies in the phenology of seed germination in the two islands. Seeds dispersed by lizards in Lanzarote germinate earlier than those of Fuerteventura. Although climatic differences are not so great between the two study areas, seeds germinated earlier in the drier habitat of the Lanzarote coastal zone. Some authors have already reported that seed germination processes in arid ecosystems appear to be closely related to rainfall patterns (Izhaki & Safriel 1990; Baskin & Baskin 2001; Nogales *et al.* 2002). According to Izhaki & Safriel (1990), early germination is important in geographic zones where rain is unpredictable and where it increases the probability of successful seedling recruitment over a longer period.

SEED SIZE, COAT THICKNESS AND GERMINATION

Seed size and seed retention time in frugivores' guts can be important factors for some species in determining their germination success (Traveset 1998). In our case, however, differences in viability and germination among treatments and islands were certainly not due to differences in seed size. With regard to retention time, seeds remain for longer inside the gut of mammals

than for birds and reptiles, which appears to influence seed germination.

Seed-coat thickness was found to decrease consistently after passing through the animals' digestive tracts, in both islands, and regardless of the type of disperser. A previous study reported that 'soft' legume seeds were more likely to become fragmented and die than 'hard' seeds in the digestive tract of cattle (Gardener *et al.* 1993). On Fuerteventura, the thinnest seed coat corresponds to seeds ingested by squirrels which, in turn, are the less viable or worst to germinate. However, on Lanzarote seeds ingested by rabbits showed the lowest levels of germination, but their coat thickness did not differ from the rest of dispersers. Clearly seed-coat scarification is not the only mechanism that produces changes in germination patterns. In this respect, other factors related to seed dormancy effects should probably be considered (Baskin & Baskin 2001).

The rather scarce data, compared with other frugivore groups, on the effect of reptiles on germination patterns showed that reptiles tend to inhibit germination, decreasing either seed germinability, germination velocity, or both (Traveset 1998; Valido 1999; Traveset & Verdú 2002; Liu, Platt & Borg 2004). In a study on a related species (*Rubia peregrina* L.), lacertid lizards were found to accelerate seed germination compared with controls in field experiments, but to have no effect in garden conditions, and inconsistent results were also found for birds (Rodríguez-Pérez, Riera & Traveset 2005).

The neutral effect of seed treatment in birds' digestive tracts on *R. fruticosa* has also been observed in other populations of the western Canary Islands (Nogales *et al.* 1999). However, those western populations showed a lower germinability for both bird-ingested seeds and controls. Such a neutral effect has been also found in other studies examining the effect of avian dispersers on seed germination of *Rubia* species, for example in *R. peregrina* tested with warblers and blackbirds (Traveset *et al.* 2001); and in *Rubia tenuifolia* tested with blackbirds, bulbuls and some warbler species (Izhaki & Safriel 1990; Barnea, Yom-Tov & Friedman 1991).

FINAL ECOLOGICAL CONSIDERATIONS

The two badlands studied are quite rocky, and native dispersers guarantee that seeds arrive at the diverse types of microhabitat. This seed-shadow pattern is probably more favourable than the clumping seed distribution produced by the two introduced mammals (latrines located in plains in the case of rabbits, and on the top of stony hills for squirrels). This characteristic seed-clumping distribution produced by mammals (Howe 1986; White & Stiles 1990) has been shown to have important negative implications for seed survival, germination and seedling competition in a number of species (Jordano 1992). In our system, however, the presence of these two alien mammals is unlikely to interfere in the fitness of *R. fruticosa*, at least in the two

areas studied, given that (1) the plant is mainly dispersed by native frugivores, reptiles and birds which are rather abundant; and (2) it shows high levels of seed production, viability and germination.

We conclude that both reptiles and birds are the most effective seed dispersers in this multidisperser system. We believe our results can be extrapolated to other species in the Canary Islands, and probably to other insular ecosystems as well, where the plant is widespread, abundant, has a high level of seed production, and is dispersed by a wide array of frugivore species.

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