Ecological and biogeographical implications of Yellow-Legged Gulls (*Larus cachinnans* Pallas) as seed dispersers of *Rubia fruticosa* Ait. (Rubiaceae) in the Canary Islands

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Abstract

Aim Few data sets exist on the role of gulls as seed dispersal agents. Our purpose is to quantify the number of seeds dispersed, to assess damage to the seeds regurgitated and those expelled via cloaca, to check for possible differences in seed viability and germination rates, to study the seed retention time, and to evaluate gulls as adequate dispersal agents throughout the Canary Islands and for the colonization of this archipelago by this plant species (or its ancestor), from Africa.

Location This study was developed in ‘Los Islotes’, a small archipelago located off the northern part of Lanzarote Island (Canaries).

Methods We counted the number of seeds in each pellet and dropping collected and we measured and weighed them. Seed viability and germination from the three treatments (plants, pellets and droppings) were studied. Gut pass time (GPT) was assessed in two gulls by using glass beads (similar in size with *Rubia fruticosa* Ait. seeds). We employed a combination of univariate and bivariate statistical tests to analyse the data.

Results From 81 pellets and 84 droppings, we extracted a total of 60,679 seeds (48,460 and 12,219, respectively). Data obtained in the GPT experiments show that a similar number of seeds are defecated and regurgitated. No externally damaged seed was observed and the majority were viable, giving more than 95% in all treatments (seeds from plants, droppings and pellets). Most seeds on these treatments showed germination rates of over 80%, verifying the importance of the gulls as legitimate dispersers of this Macaronesian endemic plant species. Taking into account that the gulls’ flight cruise speed is about 31–40 km h⁻¹ and mean GPT of these birds is between 9.51 and 16.92 h, they could cover a distance between 295 and 677 km before expelling the seeds. This distance is well within the range of colonization of the different islands of the Canaries and the neighbouring archipelagos of Salvages and Madeira from the north-west of Africa, where the ancestor of this plant may have originated.

Main conclusions The results support the idea that gulls could have been one of the main agents responsible for the movement of *R. fruticosa* seeds among the islands of the Canaries and for the colonization of the Macaronesian archipelagos from Africa. Furthermore, this study suggests that gulls are generalist feeding seabirds with high capacity for seed transport and high long-distance power displacements, could have played a more important role than that currently recognized by most authors, in the colonization of oceanic islands by some plants whose genetic origins were located at long-distances.

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Keywords

Larus cachinnans, *Rubia fruticosa*, seed dispersal, seed viability and germination, colonization of islands, Canary Islands.

INTRODUCTION

The diet of the Yellow-Legged Gull (*Larus cachinnans* Pallas) and related gulls has been considered as widely omnivorous in the Palearctic region (Cramp & Simmons, 1983; Götmark, 1984). Most studies carried out on its diet have reported the important presence of fish (Andersson, 1970; Witt *et al.*, 1981; Hillström *et al.*, 1994) and marine invertebrates (Spaans, 1971; Sueur, 1990; Munilla, 1997). Furthermore, they show a great capacity to obtain food derived from human activities (Furness & Monaghan, 1987), including very often both anthropogenic rubbish (Monaghan, 1977; Verbeek, 1977; Mudge & Ferns, 1982) and fishery waste (Furness *et al.*, 1992; Oro *et al.*, 1995). Some analyses have been made on the diet in the Macaronesian islands, with the importance of Myctophiformes fish noted in the Azores (Hamer *et al.*, 1989), seabirds (mainly small petrels) in Salvages (Mougin & Stahl, 1981) and in some colonies in the Canaries, the food spectrum is rather varied, as occurs in Timanfaya National Park-Lanzarote (Concepción, 1992) and at Alegranza (Jorge *et al.*, 2000).

Although most of the gull's diet is based on fish, marine invertebrates and rubbish, some studies have reported important quantities of vegetable material in the pellets of this species and related gulls (Gillham, 1952; Harris, 1965; Andersson, 1970; Nogales *et al.*, 1995a). However, the presence of fruits in the diet of gulls is quite scarce in most of their geographical range (Cramp & Simmons, 1983). Only some authors have reported the role of gulls as dispersers of wild seeds (Ridley, 1930; Gillham, 1952; Morton & Hogg, 1989; Cortés, 1994; and references therein). Most of these studies are largely based on descriptive information and mention the presence of a number of different seed plant species in gulls' pellets, but the authors have been reluctant to interpret this biological phenomenon in the context of plant-animal interaction. Furthermore, most studies carried out on seed dispersal systems have been developed with small or medium-sized birds (see reviews of Moermond & Denslow, 1985; Snow & Snow, 1988; Jordano, 1992; Herrera, 1995; and references therein) and some of them have focussed on generalist bird species of large size that show a great capacity of seed transport and a high long-distance power displacement (e.g. Morton & Hogg, 1989; Nogales *et al.*, 1999).

Biogeographers have engaged in an ongoing controversy about how plants colonize oceanic islands. Suggested means of dispersal include ancient land bridges, sea currents, jet streams, seed water flotation, rafting, air flotation, or transport by vertebrates, mainly birds (e.g. Ridley, 1930;

van Steenis, 1962; Carlquist, 1965, 1967; Whittaker, 1998; Shilton *et al.*, 1999). Various authors have supported the intervention of birds as dispersers of several plant species, and these vertebrates possess the suitable characteristics (Carlquist, 1965, 1974; Proctor, 1968; Porter, 1976; Valdebenito *et al.*, 1990; Whittaker & Jones, 1994). However, this process is very difficult to evidence; and faced with this difficulty, and in order to gain insight on this matter, many researchers have presented several arguments in the attempt to demonstrate how birds must have participated in the movement of seeds. These arguments often are based on indirect evidence such as the design of the fruits (Carlquist, 1965, 1967; Porter, 1976; among others) or the hierarchical ecological links of plants with animals (Bush & Whittaker, 1991).

In this contribution, we explore the plausibility of Yellow-Legged Gulls acting as legitimate seed dispersers of the Macaronesian endemic plant (*Rubia fruticosa* Ait., Rubiaceae) across the islands of a small archipelago, known as 'Los Islotes' or 'Archipiélago Chinijo' (thereafter Los Islotes), located in the north-eastern part of the Canaries near to Lanzarote Island (Fig. 1). This archipelago offers a microcosm of how seed dispersal takes place. This model could be applied at a larger scale over a longer time-span. In this paper, we address five main targets: (1) to study the importance of the Yellow-Legged Gull as seed dispersal agent of *R. fruticosa*, (2) to assess the damage to the seeds regurgitated and those expelled via cloaca, (3) to check for possible differences in seed viability and germination rates exposed to different dispersal treatments (directly collected from plants, gull pellets and gull droppings), (4) to study the seed retention time inside the gut of the gulls, (5) to evaluate the likelihood that historically this gull was an adequate dispersal agent throughout the Canary Islands and for the colonization of this archipelago, by this plant species (or its ancestor), from the African continent.

STUDY AREA

The Canarian archipelago (27°37'–29°25' N and 13°20'–29°25' W) is of volcanic origin and is located off the Atlantic coast of north-west Africa, from which it is approximately 100 km at the closest point (Fuerteventura). This study was conducted in a small archipelago located off the northern part of Lanzarote Island (Los Islotes), which is composed of five islets: La Graciosa (27.4 km²), Alegranza (10.2 km²), Montaña Clara (1.3 km²), Roque del Este (0.064 km²) and Roque del Oeste (0.016 km²) (Fig. 1). Miocene volcanic activity started around 15 Ma in Lanzarote, forming a succession of basaltic lavas and pyroclastic flows; this period

Figure 1 Map of the Canary Islands and situation of Los Islotes.

includes five separate volcanic edifices that form the islets of Los Islotes (Coello *et al.*, 1992). The eastern Canary Islands (Fuerteventura, Lanzarote and surrounding islets) were joined during the glacial periods on several occasions, the most recent being 18,000 and 12,000 years ago (García-Talavera, 1997). As occurs in the rest of the lowlands of the Canary Islands, the temperature in Los Islotes ranges around 21 °C and rainfall does not surpass 200 mm year⁻¹. The vegetation is made up of a sparse xerophytic shrubland. These islands harbour some of the main colonies of seabirds and raptors of the Canaries and represent one of the best places for observing the passage of migratory birds, with more than 60 species having been recorded on Alegranza alone (Martín & Nogales, 1993). All the islands are uninhabited except La Graciosa where approximately 650 people live (most of them employed in fishing). This archipelago together with 'Riscos de Famara' has been designated as a natural park.

The main part of this study was carried out in Roque del Este, the eastern-most component of the archipelago located at 10.9 km off Lanzarote. It consists of a small volcanic cone whose maximum altitude is 84 m a.s.l. (El Campanario) and is badly eroded, in part because it was the target of military manoeuvres by the armies of several countries until the 1970s when an expedition from the Universidad de La Laguna and ICONA prompted the end of these destructive practices. The vegetation is composed of 11 plant species: *Zygophyllum fontanesii* Webb et Berth. (Zygophyllaceae),

Mesembryanthemum crystallinum L. and *M. nodiflorum* L. (Aizoaceae), *Salsola oppositifolia* Desf., *Chenopodium murale* L., *Patellifolia patellaris* (Moq.) S., F.-L. et W., *Suaeda vera* Forssk. ex J. F. Gmel. and *Chenoleoides tomentosa* (Lowe) Botsch. (Chenopodiaceae), *Sonchus bourgeauii* Sch. Bip. (Compositae), *Lycium intricatum* Boiss (Solanaceae) and *R. fruticosa*.

NATURAL HISTORY OF THE SYSTEM

Rubia fruticosa is an endemic plant of some Macaronesian archipelagos (Canaries, Salvages and Madeira). It is distributed throughout the Canary Islands, including the islets of Alegranza, Montaña Clara and Roque del Este where it is rather scarce. The plant (≈ 0.5 –1 m plant cover) can reach about 1.5 m in height and the fruits are translucent berries (average length 7.5 mm; diameter 5.6 mm; fresh weight 0.2 g; dry weight 0.037 g; water content 81.5%; mean number of seed per fruit 1.4; individual seed weight 8.2 mg; $n = 40$ fruits; Nogales *et al.*, 1999). This biotype (characteristic of the larger island populations) contrast with the stunted plants existing in Los Islotes (≈ 25 –30 cm high and diameter plant cover). *Rubia fruticosa* and *L. intricatum* are only local plants that produce fleshy fruits. In the lowlands of the Canaries, fruits of *R. fruticosa* are consumed by several vertebrates, including lizards (Barquín *et al.*, 1986; Valido & Nogales, 1994; Valido, 1999), birds (Nogales *et al.*, 1999; N. Trujillo,

pers. comm.) and introduced mammals (Nogales *et al.*, 1995b).

Larus cachinnans is distributed from Eastern Europe, all Mediterranean, Iberia and Macaronesian islands (Azores, Madeira, Salvages and Canaries). It is the only regularly breeding species of gull in the Canaries. The total gull population of the archipelago was estimated in 1987 at about 4000–4700 breeding pairs, and the number on the islets varied (Alegranza: about 35–40 breeding pairs, Montaña Clara: 300; Roque del Este: 40; Roque del Oeste: perhaps one pair; La Graciosa: no breeding records exist although it is present; Delgado *et al.*, 1991). This gull and the plant are very abundant and well distributed in all the islands, coinciding widely in their geographic range in this archipelago.

MATERIAL AND METHODS

Fieldwork was conducted on Roque del Este in 1997 and 1998. We stayed on this small islet for 2 days in 1997 (30 April–1 May) and 6 days in 1998 (28 May–2 June). During these expeditions we collected a total of 81 recent pellets and 84 droppings from gulls and we counted the number of seeds in each sample (Table 1). We prospected all the surface of Roque del Este and we individually stored the samples (pellets and droppings) in aluminium foil and extracted the seeds manually.

Because of the fact that plants of *R. fruticosa* from Roque del Este consist in dwarf forms and fruit production is very scarce when it occurs, to perform germination experiments, it was necessary to collect seeds from plants on the neighbouring island of Lanzarote. To test possible differences in the germination curves from seeds obtained directly from plants, pellets and droppings, an experiment was performed using a greenhouse. Before planting, each seed was measured (diameter) and weighed in order to study any possible relationships between these metrics and the germination process. Seeds from plants were collected, in May 1997, from approximately 100 different plants in four localities on Malpaís de La Corona, on the neighbouring island of Lanzarote. The largest population of this plant species on this island is located in Malpaís de La Corona and it is the nearest nucleus to Los Islotes, therefore, it is presumably the place where the gulls consume most of their fruits. Seeds ($n = 208$ per treatment) were sown independently in a standard substrate (50% turf and 50% forest soil) and the experiment was followed daily during 3½ months.

Table 1 Number of *Rubia fruticosa* Ait. seeds obtained from pellets ($n = 81$) and droppings ($n = 84$) of *Larus cachinnans* Pallas in Roque del Este, during 1997 and 1998

Treatment	Number of seeds			
	Mean	Median	SD	Range
Pellets	598	537	285.1	150–1693
Droppings	146	97	150.0	15–691

We watered the seeds every 2 days and the night-day light period condition was similar to that found in the study area. In order to estimate the possible bias caused by the seed dormancy effect, a comparison of viability of randomly selected seeds from the three treatments (plants, pellets and droppings) was simultaneously carried out. Six-hundred and sixty-two seeds (plants: 217, pellets: 227, droppings: 218) were cut down the middle and included in a bio-indicator substance (2, 3, 5 triphenyl tetrazolium; Scharpf, 1970). Seeds were previously immersed in ethanol (70%) for 15 s and put into pure water for 8 h.

To learn the gut pass time (hereafter GPT) of the *R. fruticosa* seeds, we held two gulls for 4 days in individual cages (80 × 50 × 90 cm) where the presence of pellets or defecations was easy to see and record. Gulls were each hand force-fed with 750 glass beads (similar in size to *R. fruticosa* seeds), a number that corresponded with the sum of the means of seeds counted in a pellet (about 600) and a dropping (150) (see Table 1) together with some food. Because characteristics of food consumed affect the speed at which food is moved through the gut (Clench & Mathias, 1992), and considering the omnivory of gulls, we carried out two different experiments, simulating two types of diets: (1) carnivore (sardines) and (2) vegetarian or frugivore (ripe grapes). This last trial was important because of the high composition of fleshy fruits in the gull's diet in Roque del Este during the spring. We made four feeding trials per animal (two with the carnivore diet and two with the vegetarian diet) using in each case a different colour of beads to separate the experiment types. Feeding trials were performed every 12 h, the first in the morning and the second in the afternoon. Cages were examined every hour and pellets or faeces were visually recorded; all individuals had *ad libitum* access to the diet previously mentioned, water and grit. GPT was defined as the average time from consumption until appearance in the pellets or droppings of all glass beads regurgitated or defecated in both treatments (carnivore and vegetarian diet).

RESULTS

Diet and importance of moved seeds

Different types of food items were identified from the gull pellets, including fish bones, small Coleoptera remains (Curculionidae and Tenebrionidae), gastropod shells, one seed of *P. patellaris* (Chenopodiaceae) and inorganic material (glass, grit, aluminium foil and plastic). However, all the pellets and droppings contained seeds from *R. fruticosa* and most of them were composed entirely of these seeds. We counted a total of 48,460 seeds from this plant species in the 81 gull pellets and 12,219 seeds in the 84 dropping samples collected in Roque del Este. The mean number of seeds was about five times larger in pellets than in droppings, and statistical differences were recorded (Mann–Whitney test, $Z = 9.81$, $P < 0.001$; Table 1). However, the defecation rate was clearly higher than regurgitation rate (see data on GPT experiments).

Table 2 Size and weight of *Rubia fruticosa* seeds collected on the plants and extracted from the pellets and droppings of *Larus cachinnans* in Roque del Este

	Plants			Pellets			Droppings		
	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>
Diameter (mm)	2.33	0.22	208	2.47	0.24	208	2.50	0.26	208
Weight (g)	0.0062	0.0015	208	0.0058	0.0015	208	0.0059	0.0014	208

Seed traits

The size and weight of the seeds found in the pellets, droppings and those extracted directly from fruits collected on the plants are shown in Table 2. The diameter of seeds collected from plants was smaller than that of seeds from the other two treatments (ANOVA, $F = 28.92$, $P < 0.001$), and no significant differences were recorded between seeds from pellets and droppings. However, the smallest seeds from the plants were heavier than those obtained from pellets and droppings (ANOVA, $F = 4.03$, $P = 0.018$), and no differences were detected between the last two ($P > 0.05$). To calculate the lost weight of the seeds expelled via pellets or droppings it was necessary to consider only the seeds collected on the fruit plants because they had not been consumed. Therefore, and taking into account only these seed plants, we performed a correlation (Pearson correlation coefficient, $r_p = 0.81$, $P < 0.001$) and a posterior regression analysis (Weight = 0.0057 Diameter – 0.0072 ; $R^2 = 0.67$). Then, we substituted in this formula the mean diameter of the seeds obtained from the pellets and droppings in order to calculate the theoretical weight for both types of seeds separately. From the differences between these results and those observed in the pellets and droppings, we noted that the consumed seeds lost about 15.7% (in the case of the droppings) and 14.7% (in the pellets) of the weight. The weight probably was lost to dehydration.

Seed viability, germination and GPT experiments

The presence of broken seeds of *R. fruticosa* was negligible in the three treatments and we performed several tests of viability and germination for all of them (Table 3). More than 95% of seeds were viable in all treatments, and no statistical differences were recorded (Likelihood ratio test, $G = 3.24$, $P = 0.19$). In the germination trials, germination

Table 3 Seed rates of viability and germination of *Rubia fruticosa* for the three treatments (seeds from plants, and seeds from pellets and droppings of *Larus cachinnans*)

	Plants	Pellets	Droppings
Viable	210 (96.8)	221 (97.4)	216 (99.1)
Non-viable	7 (3.2)	6 (2.6)	2 (0.9)
Germinated	170 (81.7)	181 (87.0)	191 (91.8)
Non-germinated	38 (18.3)	27 (13.0)	17 (8.2)

Values are given as number (%).

rates were higher than 80% in all treatments and significant differences were only recognized between those seeds from plants and from droppings (higher germination percentages in the latter ones) ($\chi^2 = 9.24$, d.f. = 1, $P = 0.002$). Seeds from droppings also germinated earlier than those from pellets and plants (Kolmogorov–Smirnov tests, $K-S = 2.29$, $P < 0.001$ and $K-S = 2.92$, $P < 0.001$, respectively) and seeds from pellets also germinated earlier than those from plants ($K-S = 2.21$, $P < 0.001$; Fig. 2).

The only relationship found between the metrics of the seeds and the germination pattern was in seeds collected from plants. These exhibited a direct correlation between weight, size and germination rate (Table 4).

The GPT experiments indicated that seeds remain in the intestinal tract of gulls for a mean of 9.51 h (SD = 10.66, range = 1–47) if they are expelled via regurgitation and 16.92 h (SD = 11.13, range = 2–72) if they are expelled via cloaca (Table 5). Despite the small sample size ($n = 2$ gulls), GPT was in both cases (regurgitation and defecation) higher in the feeding trials made with carnivore diet than the herbivore diet. Furthermore, the defecation rate was nine times higher than regurgitation rate (mean = 1.20 per hour, SD = 1.10, range = 0–4, $n = 24$ h vs. mean = 2.7/24 h, SD = 2.3, range = 0–4, $n = 96$ h, respectively) and the total number of glass beads ejected by the cloaca was similar to the number expelled orally in each feeding trial.

Figure 2 Germination patterns of *Rubia fruticosa* Ait. seeds obtained from fleshy fruits and *Larus cachinnans* Pallas droppings and pellets in Roque del Este.

Table 4 Relationships between seed size and seed weight of *Rubia fruticosa* on the germination process for the three treatments (plants, pellets and droppings of *Larus cachinnans*) in Roque del Este. Seeds per each treatment was $n = 208$

	Plants				Pellets				Droppings			
	Diameter (mm)		Weight (g)		Diameter (mm)		Weight (g)		Diameter (mm)		Weight (g)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Seeds												
Germinated	2.35	0.22	0.0064	0.0015	2.47	0.23	0.0058	0.0014	2.50	0.27	0.0059	0.0015
Non-germinated	2.28	0.17	0.0056	0.0014	2.45	0.30	0.0057	0.0020	2.46	0.20	0.0059	0.0013
Student's test	1.77		2.66		0.48		0.34		0.74		0.14	
<i>P</i>	0.079		0.008		0.63		0.73		0.46		0.89	

Table 5 Results of gut pass time experiments performed on two individuals of gulls *Larus cachinnans*. Each gull was fed 750 glass beads in each of the two treatments

Statistical parameters	Transit times (h)					
	Regurgitation			Defecation		
	Sardines	Grapes	Total	Sardines	Grapes	Total
Mean	16.86	3.63	9.51	23.63	12.17	16.92
Median	22	2	5	22	9	14
SD	11.93	3.58	10.66	12.03	7.40	11.13
Range	2–47	1–22	1–47	2–72	5–44	2–72

DISCUSSION

The vegetarian component of the diet of gulls

The spring diet of gulls in Roque del Este was omnivorous, but we emphasize the high frequency and abundance of *R. fruticosa* seeds. Although the diet of *L. cachinnans* and related species in other areas is based mainly on food of animal origin, the presence of plant material in pellets has often been reported, such as fibre from terrestrial plants (Harris, 1965; Nogales *et al.*, 1995a), commercial seeds proceeding from rubbish dumps (Munilla, 1997), etc. Part of this material, such as grass, is associated in the pellets with the presence of sharp and caustic objects, such as marine invertebrate shells, beaks of cephalopods or elytron of insects, suggesting that the consumption of this poor nutritive food could provide a buffer for these material (Munilla, 1997). These plant fibres may contribute to the formation of pellets, avoiding injuries in the digestive tract, and facilitating the accumulation and posterior expulsion of the indigestible remains (Nogales *et al.*, 1995a).

Seed dispersal by gulls

The gull consumption of grain and weed seeds has been mentioned (Gillham, 1952; Andersson, 1970, and references therein), and some researchers have pointed out the role of gulls in dispersing plants to islands in temperate latitudes (Gillham, 1956; Morton & Hoggs, 1989 and references therein). Gillham (1956) cited the presence of 14 seed plant species in the Pembrokeshire Islands of Wales while

Morton & Hoggs (1989) found a total of 24 different seed plant species (21 in pellets and three in droppings) in the Great Lakes (Canada) and most of these species corresponded to weedy plants in both cases. In our GPT experiments, at least half of the *R. fruticosa* seeds were ejected via cloaca, which increases the gut retention time and therefore the potential distance of seed dispersal. Furthermore, the lack of differences in size and weight between seeds from pellets and droppings is probably because of the small size of these propagules, which are able to pass intact through the digestive tract.

Morton & Hoggs (1989) managed to germinate 19 plant species from seeds that had been ingested by gulls, indicating the legitimate role of these birds as seed dispersers. These data coincide with our results in all three treatments (seeds from fruit plants, pellets and droppings) high viability and germination rates were observed. All seems to indicate that gulls produce a digestive mechanical abrasion on the seed coat causing a probable dehydration effect on the seeds that were ejected by regurgitation or via cloaca. This process was very important for enhancing the speed germination process compared with those seeds collected directly from fruit plants. Although it is known that bigger seeds show a higher germination rate (Silvertown, 1981), this pattern was confirmed in the case of the non-ingested seeds and this tendency was masked when the seeds were consumed by the gulls. Data from the speed of germination indicate that seeds ejected via cloaca or expelled by regurgitation germinated earlier than those from plants. This temporal pattern could have a beneficial effect on the seed germination in arid ecosystems, where rain is unpredictable (see Nogales *et al.*,

1998; Traveset, 1998). In these environments, seeds must be ready for germination with the arrival of the first precipitations (Izhaki & Safriel, 1990).

Biogeographical considerations

The data presented in this contribution strongly support the hypotheses of the gulls as one of the main agents of *R. fruticosus* dispersal, both among the islands of the Canaries and for the colonization of the Macaronesian archipelagos from the African mainland. However and before widely treating this phenomenon, it would be interesting to consider that another potential disperser could be the raven (*Corvus corax* L.), a species that also eats fruits from this plant species (Nogales *et al.*, 1999). Although this corvid could play a certain role in seed dispersal among islets and islands, its consumption is lower, the population is much smaller and the species shows a more sedentary behaviour pattern (Nogales & Hernández, 1994; Nogales *et al.*, 1999). It is also interesting to note that lizards from the endemic genus *Gallotia* have colonized all the islands of the Canaries and they could also have dispersed seeds among them inside the gut, although this means of transport seems to be clearly less frequent than the gulls. Furthermore, Los islots constitute one of the main places for the passing of migratory birds and some of them are clearly frugivorous (warblers, thrushes, etc.). Therefore, some of these species also could have participated in the colonization of the archipelago by this plant species from the African continent.

As far as we know, the number of seeds (thousands) of *R. fruticosus* dispersed to Roque del Este are much greater than the number of seeds of any plant species moved by gulls in the world. The dispersal of this Rubiaceae also has been observed in the neighbouring islands of Montaña Clara (pers. obs.) and Alegranza (Jorge *et al.*, 2000) but the volume of seeds has been lower. This suggests that *L. cachinnans* is one of the main agents responsible for the presence of *R. fruticosus* in all the mentioned islets. However, it is important to consider that the eastern Canary Islands (Fuerteventura, Lanzarote and surrounding islets) were joined during the glacial periods on several occasions (García-Talavera, 1997). Therefore, the current distribution of *R. fruticosus* in the islets could have originated as long as 18,000 years ago, and is not wholly the results of dispersal by birds. Nevertheless, the current dwarf form of the plants in these islets, whose fruit production is very scarce when it occurs, suggests that this population has originated from the numerous seeds that are transported every year by the gulls from the neighbouring island of Lanzarote. Furthermore, the spatial distribution of these small plant populations in Roque del Este, Montaña Clara and Alegranza coincides in all cases with those of the main colonies of gulls on these islets. A larger spatial pattern that supports the idea of the gulls as one of the main agents of dispersal of *R. fruticosus*, both among the islets of Los Islots and the rest of the Canary Islands, is the fact that both the plant and the bird are very abundant and well

distributed in all the islands, coinciding widely in their geographical range throughout each island of this archipelago.

The movement of seeds by gulls acquires even greater importance on the western island of El Hierro, where both plant and bird are very widely distributed and the gulls consume a high quantity of fruits and seeds. On this island, many young plants get established after the dispersal process in suitable habitat, while this does not occur on the xerophytic islets of Los Islots where suitable habitat for this plant is relatively scarce. A clear example can be observed in Roque del Este where despite the arrival of thousands of seeds every year, the population of *R. fruticosus* is only 22 stunted plants. It is very probable that this dwarf biotype is related to the adverse habitat conditions, characterized by high sunshine and salinity, scarce precipitation, and poor soil because of the steep terrain.

According to the GPT results, seeds remain in the intestinal tract of gulls about 9.51 h if they are regurgitated or 16.92 h if defecated (general mean of both feeding trials). These data concur quite well with those given by Proctor (1968) for similar seed and bird sizes. Taking into account that the gulls have a cruise flight speed of 31–40 km h⁻¹ (Meinertzhagen, 1955; Campbell & Lack, 1985), they could cover a distance of 295–677 km before expelling the seeds. The Canaries, Salvages, Madeira, and the NW coast of Africa are all well within this range (Fig. 1). Furthermore, the cruise flight speed from the north-west of Africa to the Canaries is favoured by the NE trade winds, which sometimes reach gale-force. In this regard, Martín & Lorenzo (2001) mention the presence in Africa (Dakhla, Western Sahara) of gulls ringed in Canaries (Tenerife) and how gulls cross to the islands following ships.

It is important to consider that experimental GPT results obtained during our experiments (in captivity conditions) could be different from those that occur in the wild. However, in a wider geographical context, and considering the maximum GPT value observed in our experiments (72 h) and the fastest cruise flight speed previously mentioned (40 km), gulls could carry seeds to islands located at 2880 km distant from the continent. Other genera of Rubiaceae, such as *Bobea*, *Canthium*, *Coprosma*, etc. have been considered to be dispersed by birds in the Pacific Ocean (Gulick, 1932; Carlquist, 1965, 1967). The fleshy, non-floating fruits of these plants have moderate-sized seeds suitable for ingestion and dispersal by these animals.

In summary, the results of our study of seeds from the gull colony of Roque del Este support the hypotheses that gulls (*L. cachinnans*) could have been one of the main agents responsible for the movements of *R. fruticosus* seeds among the islands of the Canaries and for the colonization of the Macaronesian archipelagos by this plant from the African mainland. Finally, this study suggests that generalist feeding seabirds with high capacity for seed transport and high power displacements, like the gulls, could have played a more important role than that currently recognized in the colonization of oceanic islands by some plants whose genetic origins were located in distant continental masses.

ACKNOWLEDGMENTS

Aurelio Martín shared with us the two expeditions carried out to Roque del Este. Francisco Valdés advised us on all referent to the viability tests. Ignacio Munilla provided important gull references, Elena Mateo collected the plant fruits from Lanzarote and Concepción Nieves gave logistic support during the GPT experiments. Bernard Zonfrillo, Alfredo Valido and Robert Whittaker read and offered very valuable comments and suggestions to improve the manuscript. The Unidad de Medio Ambiente del Cabildo Insular de Lanzarote permitted our access to the islet and gave logistic support, in particular Luis Pascual; and the Unidad de Medio Ambiente del Cabildo Insular de Gran Canaria facilitated the gulls for doing the GPT experiments, particularly Pascual Calabuig and Loly Estévez. The editor (Philip Stott) and two anonymous referees offered all kinds of useful suggestions and comments to improve the manuscript.

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