Some ecological implications of the broadening habitat and trophic niche of terrestrial vertebrates in the Canary Islands

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Two of the most important evolutionary tendencies of vertebrates in islands are the broadening habitat and trophic niche with regards to those relative species that live in continental ecosystems. Therefore, we present two cases related with these phenomenon and their ecological implications in the Canarian Archipelago. Common Raven (*Corvus corax*) is present in all environments of the Canary Islands where vegetation is highly structured according to altitude creating different types of macrohabitats. The role of the Common Raven (*Corvus corax*) (Corvidae) as a seed dispersal agent for plants in the Canary Islands was studied by means of analysing 2672 pellets collected from all islands of the archipelago. Seeds of 16 species of phanerogams were found (4 endemic to the Canaries, 3 endemic to the Macaronesian islands, 6 non endemic, and 3 introduced by humans). The quality of the transport of seeds between habitats was evaluated in a preliminary way by making use of the very high fidelity of the plant species to particular macrohabitats. Of the 102580 potentially fertile seeds (excepting the other 51061 infertile *Ficus carica* seeds) transported by Common Ravens, 76.5% were regurgitated in theoretically suitable habitat while the remaining 23.5% were taken to habitats that were not appropriate for the establishment. Considering results from germination and viability experiments and macrohabitat patterns of dispersal, the Common Raven seems to be an important disperser for 9 plant species: *Lycium intricatum* (Solanaceae), *Opuntia ficus-indica* (Cactaceae), *Rubia fruticosa* and *Plocama pendula* (Rubiaceae), *Juniperus turbinata* and *J. cedrus* (Cupressaceae), *Phoenix canariensis* (Arecaceae), *Asparagus pastorianus* (Liliaceae) and *Myrica faya* (Myricaceae).

Endemic Canarian lizards genus *Gallotia* show a clear tendency to consume vegetarian diet which contrast with the insectivorous feeding habits from the majority of continental lizard species. *G. atlantica* consume a high amount of *Lycium intricatum* (Solanaceae) fruits and these lizards are heavily predated by the shrike (*Lanius excubitor*). Indirect seed dispersal in the system: *Lycium*,

lizards and shrikes was studied in Alegranza, a xerophytic small island of the Canarian Archipelago. A total of 835 seeds (224 obtained from lizard droppings and 611 from shrike pellets) were found by analysing 123 droppings and 146 pellets respectively. *Lycium* fruit remains (including seeds) were observed in 31.7% of the lizard droppings and 50% of the shrike pellets. *Lycium* seeds were significantly matched with the presence of lizard remains in shrike pellets. Seeds in shrike pellets have come from fruit consumed by lizards which have been predated by the shrikes, and not directly from bird frugivory. Seeds from shrike pellets showed significantly higher germination rates than those from uneaten fruits and lizard droppings. It seems probable that different treatments in the guts of each species and retention time could be two of the main factors influencing the germination process. While gut pass time in *G. atlantica* has been estimated to be 2.42 days on average, the retention time of a seed inside a shrike gizzard is much shorter (45-55 min). This is a new case of the scarcely known phenomenon of indirect seed dispersal, which seems to acquire a relatively important role in small islands where the animal-plant interaction are very intense and all the elements of the system are native.
Keywords: trophic niche, habitats, ecology, evolution, islands, vertebrates, Canaries.

Algunes implicacions ecològiques de l'eixamplament del nínxol tròfic de vertebrats a les illes Canàries.
Dues de les més importants tendències evolutives de les espècies de vertebrats a les illes són l'eixamplament de l'hàbitat i del nínxol tròfic respecte els dels seus parents continentals. Presentam dos casos relacionats amb aquests fenòmens i discutim les seves implicacions ecològiques a l'arxipèlag canari.
El corb comú (*Corvus corax*) es troba a tots els ambients de les Illes Canàries, on la vegetació està molt estructurada d'acord amb l'altitud, creant diferents tipus de macrohàbitats. El paper dels corbs com a agents dispersors de llavors de plantes a les Illes Canàries va esser estudiat mitjançant l'anàlisi de 2672 egagròpiles recol.lectades a totes les illes de l'arxipèlag. Es varen trobar llavors de 16 espècies de fanerògames (4 endèmiques de Canàries, 3 endèmiques de les illes macaronèsiques, 6 no endèmiques i 3 introduïdes pels humans). La qualitat del transport de llavors entre hàbitats va esser avaluat d'una manera preliminar fent servir la fidelitat molt alta de les espècies de plantes als macrohàbitats concrets. De les 102580 llavors potencialment fèrtils (excloses les altres 51061 llavors no fèrtils de *Ficus carica*) transportades pels corbs, el 76,5 % varen esser regurgitades a hàbitats teòricament adequats, mentre que el 23,5 % restant varen esser duites a hàbitats que no eren apropiats per a l'establiment de les plantes. Si es tenen en compte els resultats dels experiments de germinació i viabilitat i els patrons de macrohàbitat de la dispersió, el corb sembla esser un dispersor important per a 9 espècies de plantes: *Lycium intricatum* (Solanaceae), *Opuntia ficus-indica* (Cactaceae), *Rubia fruticosa* i *Plocama pendula* (Rubiaceae), *Juniperus turbinata* i *J. cedrus* (Cupressaceae), *Phoenix canariensis* (Arecaceae), *Asparagus pastorianus* (Liliaceae) i *Myrica faya* (Myricaceae).
Les sargantanes endèmiques del gènere *Gallotia* presenten una tendència a tenir una dieta vegetariana, que contrasta amb els hàbits insectívors de la majoria de sargantanes continentals. *Gallotia atlantica* consumeix una quantitat elevada de fruits de *Lycium intricatum* (Solanaceae), i aquestes sargantanes són fortament depredades pel cap-xerigany (*Lanius excubitor*). A Alegranza, una petita illa xerofítica de l'arxipèlag canari, es va estudiar la dispersió de llavors indirecta al sistema *Lycium*, sargantanes i cap-xeriganys. Es va trobar un total de 835 llavors (224 provinents d'excrements de sargantanes i 611 d'egagròpiles de cap-xerigany) rera l'anàlisi de 123 excrements i 146 egagròpiles respectivament. Es

varen observar les restes de fruits de *Lycium* (llavors incloses) al 31,7 % dels excrements de sargantanes i al 50 % d'egagròpiles de cap-xeriganys. Les llavors de *Lycium* es trobaven significativament associades amb la presència de restes de sargantanes a les egagròpiles de cap-xerigany. Les llavors a les egagròpiles de cap-xerigany provenen de fruits consumits per les sargantanes depredades pels cap-xeriganys, i no per frugivoria ornítica directa. Les llavors provinents de les egagròpiles de cap-xeriganys presentaven unes taxes de germinació més elevades que les dels fruits no consumits i les dels excrements de les sargantanes. Sembla probable que tractaments diferents al tracte digestiu de cada espècie i el temps de retenció puguin esser els dos factors principals que influeixen en el procés de germinació. Mentre que el temps de pas pel tracte digestiu a *Gallotia atlantica* s'ha estimat en 2,42 dies com a promig, el temps de retenció d'una llavor al gavatx d'un cap-xerigany és molt més curt (45-55 minuts). Aquest és un nou cas del fenomen poc conegut de la dispersió indirecta de llavors, que sembla adquirir un paper relativament important a illes petites, on les interaccions planta-animal són molt intenses i tots els elements del sistema són nadius.

Paraules clau: Nínxol tròfic, Hàbitats, Ecologia, Evolució, Illes, Vertebrats, Canàries.

General evolutionary ecology tendencies of vertebrates in islands

Oceanic islands offer special opportunities for researching evolutionary ecology phenomena in terrestrial vertebrates that have adapted to this particular ecosystem. Some of the most important evolutionary tendencies of vertebrates that have evolved in islands are related with broader habitats and trophic niche, reduction of the clutch size, adaptative radiation, tendency to evolve to giant or dwarf forms, among others. Competition seems to restrict the abundance of a species and its utilisation of resources in continental areas. However, in island populations it could reach higher densities, to occupy different habitats and have broader niches than their mainland relatives (Gorman, 1979). This tendency among animals gives rise to different ecological interactions that have to do with three basic phenomenons, competition, predation and mutualism. The last process include two main aspects: 1) pollination, a critical step in the sexual reproduction of flowering plants, and 2) seed dispersal that may enhance parental fitness in several ways. Mutualisms on younger islands (e.g. volcanic ones) is probably more generalist than older islands with relict continental biotas such as Madagascar,

New Caledonia or New Zealand (Given, 1995).

Despite the great interest that pollination and seed dispersal show in islands environments, a small number of contributions have been carried out. Therefore, the two cases presented here are related with the first two evolutionary ecological aspects mentioned (broadening habitat and trophic niche) and we expose its ecological implications in the Canary Islands under the context of mutualism relationship. Previously to show these two cases and in order to get a general knowledge of the origin, situation, climate and natural history of the Canarian Archipelago, a general overview is presented.

THE CANARY ISLANDS

The Canary Archipelago, composed by seven main islands, is of volcanic origin and lies in the Atlantic Ocean about 100 km (at its nearest point) from the African continent (Fig. 1). The highest point is on Tenerife (Pico Teide: 3718 m a.s.l.), while the lowest island, Lanzarote, reaches only 671 m a.s.l. The largest island, Tenerife, is 2036 km^2 and the smallest, El Hierro, is 278 km^2. The climate on the Canaries varies distinctly with altitude. Mean temperature and annual precipitation ranges from about 21ºC and 100-300 mm,
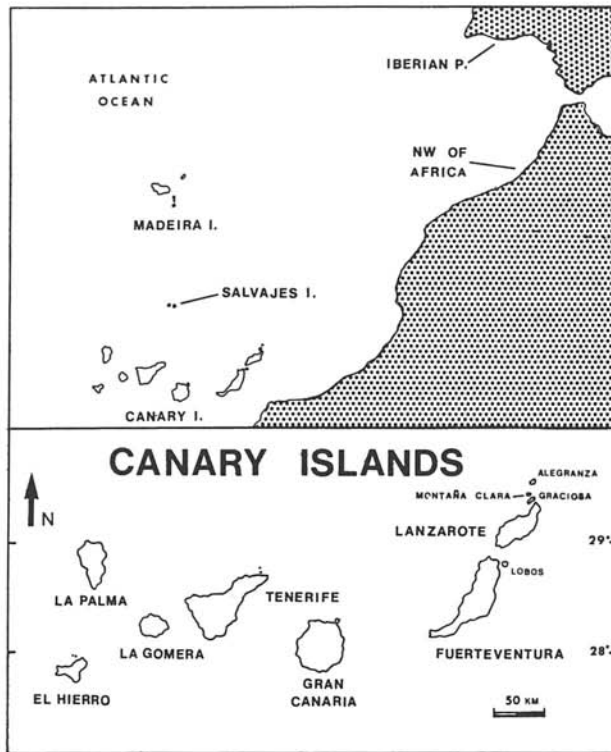
Figure 1. Situation of the Canary Islands in the Atlantic Ocean.
Figura 1. Situació de les illes Canàries a l'oceà Atlàntic.

respectively, in the coastal zone to about 9ºC and 500-800 mm, respectively, in the mountain zone. Longitude also plays an important role in climate variation. The eastern islands closest to Africa (Lanzarote and Fuerteventura) are low in altitude and highly influenced by dry winds from the Sahara Desert. Here vegetation is characterised by xerophytic shrubs that only occur in lowlands of the higher central and western islands of the Canaries (Gran Canaria, Tenerife, La Gomera, La Palma and El Hierro). These larger islands, however, have highly structured forest zones distributed basically as a function of altitude and orientation (Fig. 2). In the upper part of the xerophytic shrub, there are remains of a transition forest that was altitudinally located between the xerophytic shrub and the laurel forest (see Fig. 2). This macrohabitat, composed by species as *Juniperus turbinata* or *Phoenix canariensis*, has been drastically reduced due to human activities. The dense evergreen laurel forest found on the northern sides of larger islands, consists of nearly 20 species of trees and shrubs. Above the laurel forest and xerophytic shrub is a monospecific pine forest of the endemic *Pinus canariensis* forming an open, dry woodland. The vegetation of the highest parts is characterised by a sparse shrub of leguminous plants.

The flora of the Canaries has affinities with those of the archipelagoes of the Azores, Madeira, Salvages and Cape Verde, and all these have been grouped into the so-called 'Macaronesian Islands'. A large proportion of the floristic elements seem to have their origin in the Tertiary flora (especially that of the Pliocene and Miocene) which occupied the regions surrounding the Tethys Sea, primarily in the Mediterranean basin and North Africa (Bramwell, 1974).

Vertebrates broadening habitat and trophic niche in the Canary Islands: Ecological implications

The case of the seed dispersal by Common Ravens Corvus corax among island habitats.

The Common Raven (*Corvus corax*) (Corvidae) is markedly omnivorous through most of its range (Heinrich, 1989; Nogales and Hernández, 1997), and birds from different areas show qualitatively similar diets, although there are considerable quantitative differences (Nogales and Hernández, 1997). While diets in continental environments are dominated by vertebrates throughout the year, Common Ravens on certain subtropical oceanic islands (e.g. Canary Islands) include much wild fruit in their diet (Nogales and Hernández, 1994). This apparent broadening of trophic niche is a well-documented phenomenon in island birds (Grant, 1965; McArthur *et al.*, 1972).

On islands with important altitudinal differences, such as the Canaries, the vegetation is highly structured, creating different types of macrohabitats (Ceballos and Ortuño, 1951) (Fig. 2), and ravens readily move between these macrohabitats, allowing a study of large-scale seed movement. In contrast, most studies address dispersal effectiveness at the microhabitat level (Murray, 1988; Schupp, 1993; Ellison *et al.*, 1993).

The main objective in this case was to study the effects of Common Raven gut passage on the viability and germination of seeds and the reliability of delivering seeds to a macrohabitat appropriate for plant establishment.
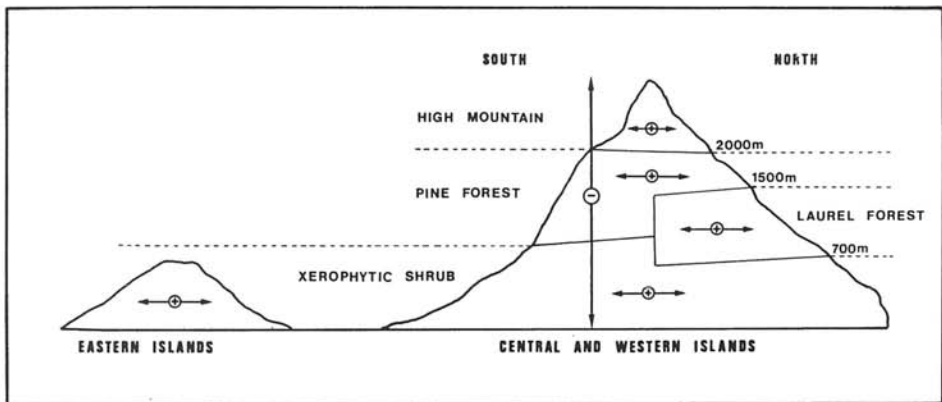

Figure 2. Altitudinal distribution of the main macrohabitats of the Canary Islands, and ecological implications of seed dispersal by Common Ravens (*Corvus corax*) in the various islands. (+): 'horizontal' dispersal in which the seeds remain in the same habitat. (-): 'vertical' dispersal in which propagules are displaced into different habitats. Central and western islands: Gran Canaria, Tenerife, La Gomera, La Palma and El Hierro. Eastern islands: Lanzarote and Fuerteventura.
Figura 2. Distribució altitudinal dels principals macrohàbitats de les illes Canàries, i implicacions ecològiques de la dispersió de llavors per corbs (Corvus corax) *a diferents illes. (+) dispersió 'horitzontal' en que les llavors romanen al mateix hàbitat. (-): dispersió 'vertical' en que els propàguls són desplaçats a diferents hàbitats. Illes centrals i occidentals: Gran Canaria, Tenerife, La Gomera, La Palma i El Hierro. Illes orientals: Lanzarote i Fuerteventura.*

Seeds were obtained from 2672 Common Ravens regurgitation pellets collected on the 7 main islands (Lanzarote: 248, Fuerteventura: 296, Gran Canaria: 491, Tenerife: 69, La Gomera: 352, La Palma: 13, El Hierro: 1032) and islets (Lobos: 40, La Graciosa: 69, Alegranza: 30, Montaña Clara: 28, Roque del Este: 4). Judging by the rapid disintegration of pellets over winter, the material collected during summer visits was probably produced in spring and summer, coinciding with fruiting of most plant species the Common Raven eats in the Canaries (Nogales and Hernández, 1994).

In order to test the effect of regurgitation from the digestive tract of the Common Raven on seed germination, regurgitated seeds were sown by utilising a standard substrate (lapilli, turf and forest soil). This experiment was performed in a greenhouse every day for 3 months (90 days), until no further germination was detected (for more information on the germination method see Valido and Nogales, 1994). Since germination of seeds from pellets varied extremely, we also performed a comparison of viability of randomly selected seeds from pellets and seeds from plants ($n = 70$ respectively) with the 2, 3, 5 triphenyl tetrazolium test (Scharpf, 1970).

The effect of transport of seeds by the Common Raven between macrohabitats was evaluated by comparing the potential ecological possibilities for establishment provided by the habitats where the seeds were regurgitated with those of the most probable typical habitat. All the plant species consumed by Common Ravens show high fidelity to particular macrohabitats (e.g. Rivas-Martínez, 1983; Bramwell and Bramwell, 1990). We can assess a measure of effectiveness of dispersal (sensu Schupp, 1993) at a large geographic scale: the proportion of a population's seeds that are dispersed into an unsuitable macrohabitat.

Although it is not easy to determine the significance of dispersal simply by observation of birds eating or transporting fruits,

Herrera and Jordano (1981) and Schupp (1993) cite some basic requirements. From the quantitative point of view, seed dispersal depends on 1) the number of visits made to the plant by a disperser, and 2) the number of seeds dispersed per visit. From the qualitative point of view, seed dispersal depends on 1) the quality of treatment given to a seed in the mouth and gut, and 2) the quality of seed deposition as determined by the probability that a deposited seed will survive and become adult.

In our case the quantitative requirements mentioned seem to be satisfied (see Table 1, and Nogales and Hernández, 1994). A total of 153641 seeds of 16 species were recovered from regurgitated pellets and 73.4 % contained at least one seed. Of the 16 species of phanerogams represented in the pellets, 7 (43.8%) were taxa endemic to the Canaries or to the Macaronesian islands (4 and 3 respectively), 6 (37.4%) were native but not endemic, and another 3 (18.8%) have been introduced by humans (Table 1). The most common seed was *Opuntia ficus-indica* which has been introduced. *Ficus carica* had the second largest number of seeds in the pellets ($n = 51\,061$). Because it is infertile in the Canaries, it is not considered further. Among the native plants, *Rubia fruticosa* showed the largest representation.

The number of seeds transported in each visit to a plant is positively correlated with the size of the birds (Howe and Steven, 1979). The large Common Raven can ingest many fruits, showing a large capacity of seed delivery. Given the large interspecific variation in the size of seeds obtained from the pellets, it seems likely that Common Ravens do not have great problems with the burden imposed by different-sized fruit, although this factor is very important in the selection of fruit by small and medium-sized birds (Herrera, 1981; Snow and Snow, 1988). This low level of selection by size conforms with that described by Moermond and Denslow (1985) for dispersal by large birds.

With respect to the qualitative requirements, the effect of the Common Raven on the seeds -either through manipulation or regurgitation- does not produce large losses in most plant species, as demonstrated by the viability tests. The percentage of viable seeds did not differ significantly for any species between pellet seeds and seeds obtained directly from the plants (G-test; df = 1; $P > 0.05$ for each species and treatment respectively). This may be partly due to the lack of strongly developed musculature in the gizzard of the Common Ravens (Oelhafen-Gandolla and Ziswiler, 1981). Furthermore, the treatment provided by the digestive tract of this corvid improves seed germination in 6 species, has a negligible effect in 4, and reduces germination in 3 (Table 1). Few studies on birds have compared the germination of seeds eaten with controls collected directly from the plants, despite the potential importance of this research field (e.g. Howe *et al.*, 1985; Katusic-Malmborg and Wilson, 1988; Schupp, 1993; Ellison *et al.*, 1993). The results obtained in these studies vary and depend to a large extent on the species of plants and animals involved (Lieberman and Lieberman, 1986; Izhaki and Safriel, 1990; Ellison *et al.*, 1993).

With regards to the second aspect mentioned on the quality of seed dispersal, an important factor determining the importance of dispersal are the movements of the birds after eating the fruit (Howe and Primack, 1975). Table 1 summarizes number of seeds potentially dispersed to habitats that appear to be ecologically suitable for the establishment and growth of each species. Without taking into account the infertile seeds from *F. carica*, 76.5% of the 102580 seeds transported by the Common Ravens in all the islands were regurgitated in their original habitat types, and the remaining 23.5% were moved into habitats inadequate for establishment.

Considering whole data of the islands, more than 90% of the seeds of 9 species were moved to suitable macrohabitats and only 2 species had less than 50% dispersed to an appropriate macrohabitat. The dispersal path

followed by the seeds in the mountainous islands of the Canaries, described in the present case, show that the majority of seeds dispersed by Common Ravens are not displaced out of their native habitats. Data on viability, germination and seed delivery to appropriate habitats suggest that Common Raven act as an apparently important seed disperser for 8 species (*L. intricatum, O. ficus-indica, R. fruticosa, J. turbinata, J. cedrus, Phoenix canariensis, M. faya* and *P. pendula*) (see Table 1). Even if the effect of the bird significantly reduces germination for *A. pastorianus*, the other results (seed viability and habitat suitability) suggest that dispersal may be important. Nevertheless, some other species do not seem to benefit. For instance, most seeds of *O. dillenii* and *Pinus canariensis* are moved into unfavourable habitats, although Common Ravens improve germination in *O. dillenii*. Species typical of the laurel forest (*V. mocanera, L. azorica, I. canariensis* and *R. inermis*), were consumed only rarely and no seed germination was observed after passing through the gut of the Common Raven.

Common Ravens seem to play an important role in the dispersal of certain endemic plants in the Canaries. For the endemic *J. cedrus* -a species considered "endangered" by IUCN- no other dispersal agent is known at the moment in the islands. For this reason, the future of the species could partially depend on the number of Common Ravens, whose populations are gradually undergoing a major decline in the Canarian Archipelago (Nogales, 1992). The results presented provide additional evidence that effective dispersal does not necessarily depend on specialist frugivores as has been indicated by some authors (Moermond and Denslow, 1985). A particularly clear case of the importance of a non-specific dispersal agent concerns *O. ficus-indica*, a species introduced by humans into the Canaries in the 19th century. This cactus has now become a characteristic feature of some Canary Island landscapes in dry areas.

The phenomenon presented in this case could be relevant and extended to those areas

Species	Biogeogr. Range	Nº of seeds dispersed	% seeds dispersed	% seeds moved to suitable habitats	Maxim. % seeds of each plant species dispersed in the context of one island	% of Germination Raven	% of Germination Plant	G-test	P^a	% viable seeds from Raven pellets
Apas	NNE	1 336	1.30	100.0	50.5(F)	67.1	94.0	14.1	<<0.001	100.0
Lint	NNE	1 504	1.47	96.9	39.7(F)	44.3	44.0	0.019	0.98	90.0
Ppen	CE	541	0.53	92.1	6.0(C)	52.0	26.0	7.20	0.007	96.4
Rfeu	ME	17 947	17.50	100.0	22.1(H)	52.9	60.0	0.72	0.39	100.0
Jced	CE	79	0.077	69.6	29.6(P)	16.0	4.3	4.79	0.029	0.0
Jtur	NNE	1 765	1.72	89.0	2.2(H)	10.1	0.0	9.37	0.014	50.0
Phocan	CE	262	0.26	100.0	6.7(G)	54.9	2.6	36.31	<<0.001	90.2
Odill	TIH	6 556	6.39	35.3	44.5(T)	12.9	0.0	13.09	<<0.001	96.6
Ofic	TIH	68 886	67.15	72.5	90.1(G)	30.0	8.6	10.82	0.001	100.0
Vmoc	ME	538	0.52	97.0	0.7(H)	0.0	5.7	5.43	0.020	-
Mfay	NNE	2 919	2.84	83.9	3.7(H)	35.7	28.6	0.82	0.36	90.0
Ican	ME	61	0.059	100.0	0.075(H)	0.0	0.0	-	-	-
Lazo	NNE	14	0.013	100.0	5.2(P)	0.0	0.0	-	-	-
Rine	NNE	13	0.012	100.0	0.4(G)	0.0	38.0	10.73	0.001	-
Pincan	CE	159	0.16	42.8	0.5(C)	44.1	35.7	0.82	0.41	25.0

a. analysis correspond to chi-square tests

Table 1. Germination, viability and number of seeds observed in the pellets of Common Ravens (*Corvus corax*) in the Canary Islands. Plant species = **Apas**: *Asparagus pastorianus* (Liliaceae), **Lint**: *Lycium intricatum* (Solanaceae), **Ppen**: *Plocama pendula* (Rubiaceae), **Rfru**: *Rubia fruticosa* (Rubiaceae), **Jced**: *Juniperus cedrus* (Cupressaceae), **Jtur**: *Juniperus turbinata* (Cupressaceae), **Phocan**: *Phoenix canariensis* (Arecaceae), **Odill**: *Opuntia dillenii* (Cactaceae), **Ofic**: *Opuntia ficus-indica* (Cactaceae), **Vmoc**: *Visnea mocanera* (Theaceae), **Mfay**: *Myrica faya* (Myricaceae), **Ican**: *Ilex canariensis* (Aquifoliaceae), **Lazo**: *Laurus azorica* (Lauraceae), **Rine**: *Rubus inermis* (Rosaceae) and **Pincan**: *Pinus canariensis* (Pinaceae). Islands = F:

Fuerteventura, T: Tenerife, C: Gran Canaria, G: La Gomera, P: La Palma, H: El Hierro. Biogeography range = CE: Canary endemism, ME: Macaronesian endemism, NNE: native, non-endemic taxon, TIH: taxon introduced by humans. *Ficus carica* (Moraceae) seeds are excluded from this table because they are infertile. Seeds from that species are not included in the calculations presented here.

Taula 1. Germinació, viabilitat i nombre de llavors observades a egagròpiles de corb (Corvus corax) *a les Illes Canàries. Espècies de plantes* = *Apas:* Asparagus pastorianus *(Liliaceae),* *Lint:* Lycium intricatum *(Solanaceae),* ***Ppen:*** Plocama pendula *(Rubiaceae),* ***Rfru:*** Rubia fruticosa *(Rubiaceae),* ***Jced:*** Juniperus cedrus *(Cupressaceae),* ***Jtur:*** Juniperus turbinata *(Cupressaceae),* ***Phocan:*** Phoenix canariensis *(Arecaceae),* ***Odill:*** Opuntia dillenii *(Cactaceae),* ***Ofic:*** Opuntia ficus-indica *(Cactaceae),* ***Vmoc:*** Visnea mocanera *(Theaceae),* ***Mfay:*** Myrica faya *(Myricaceae),* ***Ican:*** Ilex canariensis *(Aquifoliaceae),* ***Lazo:*** Laurus azorica *(Lauraceae),* ***Rine:*** Rubus inermis *(Rosaceae) and* ***Pincan:*** Pinus canariensis *(Pinaceae). Illes* = *F: Fuerteventura, T: Tenerife, C: Gran Canària, G: La Gomera, P: La Palma, H: El Hierro. Categories biogeogràfiques* = *CE: Endemisme canari, ME: Endemisme macaronesi, NNE: tàxon nadiu, no endèmic, TIH: tàxon introduït pels. S'han exclòs d'aquesta taula les llavors de* Ficus carica *(Moraceae) per mor que no són fèrtils. Les llavors d'aquesta espècie no s'han inclòs als càlculs que presentam.*

where small habitat surfaces are highly differentiated altitudinally, such as the high oceanic islands and even elevated mountain zones of continental areas.

The case of the indirect seed dispersal of shrikes, lizards and Lycium intricatum (Solanaceae) fruits on the lowlands of the Canaries (Alegranza I.).

Island ecosystems, often represented by relict fauna and flora, harbour some important examples of herbivory by lizards (e.g. Sadek, 1981; Machado, 1985; Feller and Drost, 1991; Naranjo *et al.*, 1991; Sáez and Traveset, 1995). Several studies have emphasized the importance of these reptiles as seed dispersers in different islands worldwide (Rick and Bowman, 1961; Iverson, 1985; Whitaker, 1987; Traveset, 1995) and in the Macaronesian islands in particular (Barquín and Wildpret, 1975; Barquín *et al.*, 1986, Valido and Nogales, 1994). Frugivorous reptiles are preyed upon by an array of raptors that act as secondary seed dispersers in a variety of habitats (Ridley, 1930; Howe and Smallwood, 1982; van der Pijl, 1982). The few papers published on this matter reported birds as intermediate seed vectors (Damstra,

1986; Hall, 1987; Dean and Milton, 1988). All these studies, largely based on descriptive information, were carried out in continental habitats, and results were rarely, if ever, interpreted in the context of plant-animal interactions.

Previous studies of indirect seed dispersal in the different habitats of the Canary Islands have focused on the interaction of an introduced top predator (*Felis catus*) with the endemic frugivorous lizards belonging to the genus *Gallotia* (Nogales *et al.*, 1996). It was shown that the secondary seed vector does not seem to have a great quantitative effect on natural regeneration of plants when comparing direct vs. indirect seed dispersal. Virtually nothing is known about the relevance of indirect seed dispersal, at species or community level, in complex or even in apparently simple arrays of interacting species. Nevertheless, the phenomenon may be important for the effective dissemination of certain animal-dispersed plants on small islands. Here we deal with a system in which the players are an endemic frugivorous lizard species and one of its main natural predators (a shrike), whose interactions potentially influence the seed dispersal and establishment

of the only available fleshy-fruited plant species. Alegranza, a small island located in the north east of the Canary Islands, where the fleshy-fruited plant *Lycium intricatum* (Solanaceae) coexists with a small lizard *Gallotia atlantica* and a shrike *Lanius excubitor*, provides this apparently system framework. The main target pursued is to demonstrate the indirect seed dispersal and to study the quality of the dispersal carried out by the different disperser agents.

Field work was conducted in the mentioned island, the northernmost component of the archipelago located about some 17 km north of Lanzarote, with an area of about 10.5 km² and a maximum altitude of 289 m a.s.l. (La Caldera volcano). Alegranza is uninhabited and its climate is semidesertic with dry summers (Pérez and Henríquez, 1974).

L. intricatum is a common fleshy-fruited, thorny shrub up to 2 metres in height, typical of coastal habitats in the Canaries. It produces berries (average length ± SD = 7.75 ± 0.82 mm; diameter = 5.17 ± 1.76 mm; fresh weight = 0.12 ± 0.05 g; water content = 71.72 ± 6.24 %; seed length: ~ 2 mm; n = 40 fruits), which are red when ripe (in winter); this plant is the only fleshy-fruited species on the island.

Lizard droppings and bird pellets, and also *Lycium* ripe fruits, were collected between April 30 and May 3, 1996. Previous inspections indicated the presence of *Lycium* seeds both in pellets of *Lanius* and in *Gallotia* droppings. We also examined a number of shrike pellets which had been collected on Alegranza in 1994 (April 23-28) and 1995 (April 3-5).

A germination experiment was conducted in order to test possible differences in the germination curves of *Lycium* seeds, isolated both from *Lanius* pellets and *Gallotia* droppings, and those collected directly from the plants. In this assay only seeds from 1996 were used. This allowed us to compare germination rates of seeds passed through the gut of lizards with those that had later been ingested by shrikes and with the control groups

(uningested seeds collected directly from plants). For each treatment, 210 seeds were planted in individual pots with a standard substrate (lapilli, turf and forest soil in a ratio of 1-1-2) (For mor details on the germination methods, see Valido and Nogales, 1994).

All lizard species belonging to the genus *Gallotia* in the Canary Islands seem to be omnivorous (Machado, 1985; Molina, 1986 a and b; Naranjo *et al.* 1991; Valido and Nogales, 1994) although *G. atlantica* shows a certain tendency to an insectivorous diet (Molina, 1986b; A. Valido, M. J. Bethercout and J. De Urioste pers. comm.). *Lycium* fruits are heavily consumed by the abundant lizard *G. atlantica* in Alegranza and remains of *Lycium* fruits were found in 31.7% of the lizard droppings analysed (n = 123), and 30% contained at least one seed (n = 224 seeds).

Lycium fruits have a high water content (average = 71.7%; n = 40 fruits) and in xeric islands, this trait makes them an important water source for reptiles since limited locomotion restricts their ability to move to permanent watering points, only three of which exist in this island. Milton (1992) and Valido and Nogales (1994) have also recorded this process in xerophytic habitats. In contrast to the lizards on islands, most Lacertidae are insectivorous in continental zones (e.g. Avery, 1966; Pérez-Mellado, 1982; Valakos, 1986), and a few appear to be omnivorous (Hernández, 1990).

The diet of *Lanius excubitor* from 1994 to 1996 in Alegranza island, revealed *G. atlantica* as its main vertebrate prey there. In 1994, 84% and 93% of shrike pellets at two sites contained lizards remains (n = 60 pellets; N. Puerta and M. N. Zurita, pers. comm.), compared with 91% at a single site in 1995 (n = 31 pellets; T. Barrera and R. González, pers. comm.), and 95% in 1996 (n = 55 pellets; present study). In continental zones their diet is quite similar but lizards are substituted by rodents (Cramp and Perrins, 1993). Plant material is very scarce in the shrike diet, although fleshy fruits of some species (genus *Prunus, Rosa, Symphoricarpos*) are sporadi-

cally consumed (see Cramp and Perrins, 1993). In some continental sites shrikes can prey on birds such as finches or legitimate seed dispersers such as *Sylvia* spp. and *Erithacus rubecula* L. (Hernández, 1995) and are more likely to act as indirect seed dispersers.

Two of the factors that have been mentioned as most important in germination ability have been retention time in the gut of the disperser (Levey, 1986; Barnea *et al.,* 1992) and the morphological features of the seed coat (Barnea *et al.*, 1990; Barnea *et al.*, 1991). In the present system, the external damage produced by lizards to *Lycium* seeds was negligible. Subsequently, seed treatment in the shrike gizzard resulted in damage to only 3.1% of seeds (Table 2), so we consider that seeds were deposited virtually intact after a two-gut transit. Over half the seeds germinated ($n = 353$; 56%) from the total planted ($n = 630$). Furthermore, a significantly higher number of seeds from the bird pellets (135, 64.3%) germinated compared with those collected from plants (114, 54.3%) and lizard droppings (104, 49.5%) ($\chi^2 = 9.67$; df = 2; $P = 0.0079$) (Fig. 3). The differences observed in germination rates among treatments can be attributed to different treatment in the guts of each species and gut retention time of the dispersers. The criteria that define the effectiveness of direct seed dispersal in many seeded plants involve qualitative and quantitative factors. Qualitative factors include the differential mobility of disperser species involved in the interaction, as well as their differential promotion of germination dependent on seed treatment in the mouth and gut (Schupp, 1993). The quantitative factor (i.e. number of seeds dispersed by both lizard and shrike), clearly appears in our indirect dispersal system, to devolve mainly upon the lizard, because the bird rarely eats *Lycium* fruits. In the absence of lizard remains, we found seeds in only two shrike pellets. Association of seed with presence of lizard remains in shrike pellets was high (Table 3), although seeds of *Lycium* were present in only 73 (50%) of 146

shrike pellets analysed (3 years pooled data). The frequency of occurrence of pellets with at least one seed differed significantly between 1994 and 1996 ($\chi^2 = 28.54$; df = 2; $P \ll 0.001$; see Table 3), despite the fact that there were no significant among-year differences in the number of seeds present per shrike pellet (Kruskal-Wallis test; K = 4.845; $P = 0.0887$). This suggests fruits were consumed consistently by lizards among years. Thus, although it varied in extent, indirect seed intake by *Lanius* occurred during all three years, indicating that *G. atlantica* is a key intermediate seed vector in the sequential dispersal of *Lycium* seeds by this bird. This could also be the case of other birds, such as raptors, also reported as indirect seed dispersers worldwide (Damstra, 1986; Hall, 1987; Dean and Milton, 1988). In this sense, indirect seed dispersers of *Lycium* seeds in Alegranza may include *Falco tinnunculus*; seeds have been found in Kestrel pellets in spring 1995 (T. Barrera and R. González, pers. comm.).

The quantitative importance of seed dispersal by secondary agents, may however be masked, for certain species by more critical effects of direct dispersers on seed shadows. One of the tasks is to find out to what extent direct dispersal contributes to a seed shadow, in comparison with indirect vectors. In our study area, shrikes apparently preferred to regurgitate their pellets on the top of small hills. In 12 of the 14 perches where pellets were collected, we observed at least one plant of *Lycium*. However, some plants found on these prominences could also have come from seeds previously dispersed directly by lizards. Seed shadows produced by the two species may be qualitatively different because the movements are shorter, and the home range smaller for the lizard (Valido and Nogales, 1994) than for the bird. This may imply a mobilisation of *Lycium* seeds to differentially suitable microhabitats, depending on the pattern of movement of each seed vector and its habitat selection (Schupp, 1993).

Leaving aside the disperser's 'external' behaviour, germination ability, which is

	1994	1995	1996
Number of pellets studied	60	31	55
% of pellets with seeds ± 95% CL	25	55	75
Mean number of seeds per pellet ± SD	4.66±8.00	7.76±8.68	9.97±12.10
Range of seeds per pellet	1-32	1-35	1-60
Total number of seeds found	70	132	409
% of damaged seeds	10	0	2.9

Table 2. Analysis of *Lanius excubitor* pellets showing numbers of *Lycium intricatum* seeds removed, and the proportion of damaged seeds over a three year period on Alegranza Island (Canary Archipelago).
Taula 2. Anàlisi d'egagròpiles de Lanius excubitor *on es mostren els nombres de les llavors de* Lycium intricatum *obtingudes, i la proporció de llavors fetes malbé sobre un periode de tres anys a l'illa d'Alegranza (arxipèlag canari).*

important to the fitness of the plant, is partially a function of the retention time in the gut of each disperser species (Levey, 1986; Barnea *et al.*, 1992). In laboratory conditions (12 hours daylight and 26-28 °C), gut pass time (GPT) of a solid piece (glass beads) similar in size to *Lycium* seeds in *G. atlantica* is on average 2.42 days (Valido and Nogales, unpubl. data). Seed retention time inside the gizzard of *L. excubitor* is much shorter (45-55 min) (Olsson, 1984 and 1985) and significant seed losses inside the shrike gizzard are prevented by the lack of strong muscles characteristic of grain-eating birds (Oelhafen-Gandolla and Ziswiler, 1981). Overall retention time may, therefore, be shorter when a lizard is predated by a shrike. The difference in seed germination time between seeds passed through lizard and shrike is thus more likely to be attributable to a different treatment in the guts, possibly due to differential enzymatic actions of lizards vs. shrikes.

Seed passage through the disperser gut has been shown to have different results depending on the species. In some plants, seed ingestion by reptiles promotes an increase in germination (Rick and Bowman, 1961; Cobo and Andreu, 1988; Valido and Nogales, 1994), while in other species no effect was detected (Whitaker, 1987; Traveset, 1990;

Valido and Nogales, 1994). No significant differences were found between *Lycium* seeds consumed by *Gallotia galloti* and seeds collected from the plants (*n* = 70 seeds/treatment) in Tenerife island (Valido and Nogales, 1994). The present study suggests that for a complete approach to the seed dispersal system associated with this single fleshy-fruited plant species on this restricted oceanic habitat, we should measure not only frugivory by direct dispersers but also indirect dispersal by birds (including winter migrants). We must also consider the effects of potential secondary seed vectors (i.e. *Lanius, Falco* spp.) on the seed shadows and their relative contribution to plant fitness. Further efforts should concentrate on the patterns of plant visitation and the dispersal behaviour (i.e. patterns of seed deposition) of the main vertebrate species present during the plant fruiting season. In view of the complex array of this system and their temporal consistency in the use of an intermediate seed vector, we cannot therefore expect, *a priori*, to observe a weak effect of indirect seed dispersal on *Lycium* reproductive fitness. Despite the fact that we have only studied the phenomenon on Alegranza, it is likely that this process occurs in practically all the lowland Canary Islands due to the high similarities among these habitats.
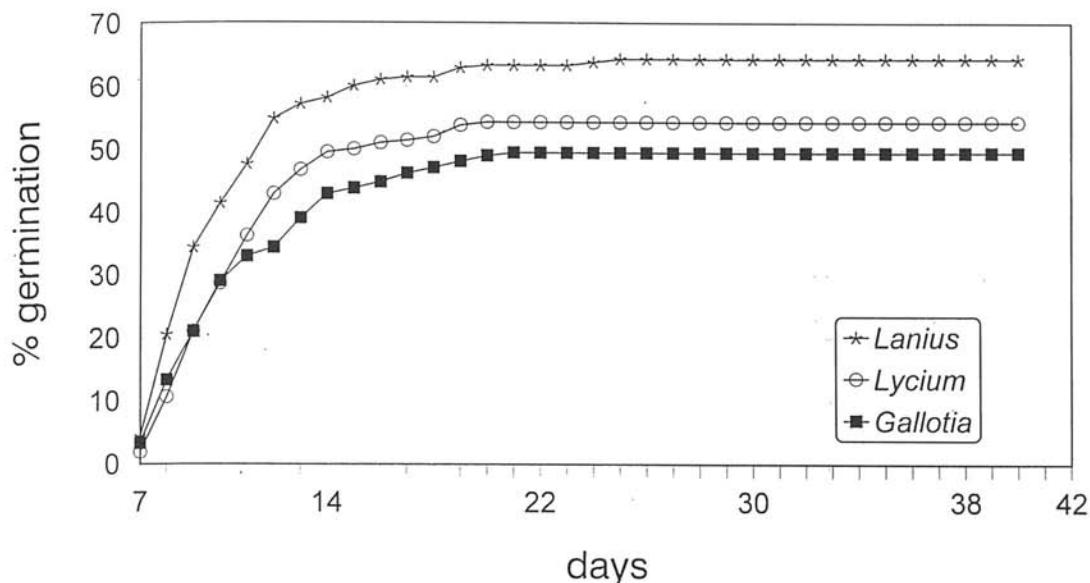
Figure 3. Rates of germination of seeds from *Lycium intricatum* collected from fresh fruits, *Gallotia atlantica* droppings and *Lanius excubitor* pellets in Alegranza (*n* = 210 per treatment).
Figura 3. Taxes de germinació de llavors de Lycium intricatum *recol.lectades de fruits frescs, excrements de* Gallotia atlantica *i egagròpiles de* Lanius excubitor *a Alegranza (n = 210 per tractament).*

	1994	1995	1996	Prooled
Lycium+Gallotia	15	17	39	71
Lycium alone	1	0	1	2
Gallotia alone	38	9	13	60
None	6	5	2	13
Total pellets	60	31	55	146
G	0.69	9.14	2.15	9.93
P	0.40	0.0025	0.14	0.0016

Table 3. Results of G-tests for association of *Lycium intricatum* seeds and *Gallotia atlantica* remains in *Lanius excubitor* pellets analysed. Figures are pellet numbers.
Taula 3. Resultats de les proves G d'associació de llavors de Lycium intricatum *i restes de* Gallotia atlantica *a les egagròpiles de* Lanius excubitor *analitzades. Les xifres són nombres d'e-gagròpiles.*

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