Are predatory birds effective secondary seed dispersers?

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We have studied the unusual phenomenon of secondary seed dispersal of *Lycium intricatum* seeds on a small oceanic Atlantic island (Alegranza, Canarian Archipelago) in which a small frugivorous lizard (*Gallotia atlantica*) and two different predatory birds participate, a shrike (*Lanius excubitor*) and a kestrel (*Falco tinnunculus*). Endemic lizards that are common prey of both bird species consume *Lycium* fruits. Lizard remains were significantly matched with the presence of *Lycium* fruits in the regurgitation pellets of the two predatory birds. Seeds were found in 7.3% of the lizard droppings, 31.0% of kestrel pellets and 55.7% of shrike regurgitations. The mean number of seeds per dropping or pellet was 4.8 ± 4 in lizard, 20.2 ± 34.5 in shrike and 6.7 ± 8.1 in kestrel. The percentage of viable seeds showed significant differences among all four treatments, decreasing in the following direction: seeds collected directly from plants (98.0%), shrikes (88.0%), lizards (72.3%), and kestrels (31.7%). Seeds from *Lycium* fresh fruits and shrike pellets showed significantly higher germination rates than those from lizard droppings and kestrel pellets. While lizards and shrikes are effective seed dispersers, kestrel gut treatment decreases seed viability. Seed viability is always higher than seed germination in each of the four treatments. In this island environment, *Lycium* seeds are under an important random influence during the seed dispersal process. Secondary seed dispersal seems to acquire a relevant dimension in small and remote insular environments or isolated continental systems where interactions among the different elements involved are intense, all of them are abundant native residents, and they have been coexisting for a long time. © 2002 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2002, 75, 345–352.

ADDITIONAL KEYWORDS: Canary Islands – *Falco* – *Gallotia* – germination – *Lanius* – *Lycium* – viability.

INTRODUCTION

Frugivores are often preyed upon by raptors. During this process, seeds contained in the gut of frugivores are passed on to the predator which may act as seed disperser (Ridley, 1930; Howe & Smallwood, 1982; van der Pijl, 1982). However, few papers have been published on this poorly understood matter (Damstra, 1986; Hall, 1987; Dean & Milton, 1988) and the majority of them have reported descriptive information and results were not interpreted in the ecological context. A similar and more known ecological phenomenon is the secondary seed dispersal by animals, in which seeds found in vertebrate droppings are redistributed through the activity of hoarding animals (often ants),

and where a redistribution of seeds is carried out after the first movement of the propagules (Levey & Byrne, 1993; Böhning-Gaese *et al.*, 1999).

Secondary seed dispersal may be favoured if it increases one or several components of seed dispersal 'effectiveness' (Schupp, 1993). These components include the number of seeds dispersed and seed viability, among others. However, the effectiveness of secondary seed dispersal has been rarely evaluated by examining several factors simultaneously. This is particularly true for secondary seed dispersal systems mediated through frugivore–predator interactions.

Some studies have been carried out on comparisons of germination with and without ingestion by dispersers (e.g. Lieberman & Lieberman, 1986; Barnea *et al.*, 1990, 1991; Izhaki & Safriel, 1990). Some general patterns have been observed and results obtained depending on the species involved in each

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interaction (see review of Traveset & Verdú, 2002). Other contributions have addressed the effects of different vertebrate groups of dispersers on germination of particular plant species, sometimes finding significant differences between the dispersal agents (Mandujano *et al.*, 1994; Traveset *et al.*, 2001) but not always (Lieberman & Lieberman, 1986; Traveset & Willson, 1997). Despite the interest in the secondary seed dispersal system by vertebrates preying upon frugivores, at the moment few contributions have studied the effect that birds can produce on the germination of seeds dispersed secondarily (Balgooyen & Moz, 1973; Nogales *et al.*, 1998).

Oceanic Islands, often represented by simple habitats, harbour ideal systems in which to study complex ecological interactions. Some studies have mentioned the important role of reptiles as seed dispersers on islands worldwide (Rick & Bowman, 1961; Iverson, 1985; Whitaker, 1987; Valido & Nogales, 1994; Traveset, 1995). To address the question of how birds affect the germination of seeds dispersed secondarily, we will focus on a unique system found in Alegranza Islet, a small island located in the north-east of the Canarian Archipelago (near Lanzarote Island), which is made up of a simple system where it is possible to study the effect of two different predatory birds, a shrike *Lanius excubitor* L. (O. Passeriformes) and a kestrel *Falco tinnunculus* L. (O. Falconiformes) as secondary seed dispersers of *Lycium intricatum* Boiss (Solanaceae) fruits. Both species of birds prey intensively upon the frugivorous lizard *Gallotia atlantica* Peters and Doria (Lacertidae) on Alegranza, where *L. intricatum* is practically the only fleshy-fruit plant species growing.

Gut enzymatic action is very variable depending on the type of predatory bird, being much stronger in the case of diurnal birds of prey compared with other non-specialized predatory birds (Brown *et al.*, 1993; Stuart & Stuart, 1994). This strong raptor stomach acidity can mineralize bones and therefore may affect germination through its influence on chemical or mechanical abrasion of the *Lycium* seed coat. Because diurnal birds of prey, such as the kestrels, have stronger enzymatic action and longer regurgitation time than the shrikes (see Balgooyen, 1971; Duke *et al.*, 1976; Yalden & Yalden, 1985; Olsson, 1984, 1985), and because of the apparent relative thickness of the seed coat of *Lycium* seeds, we expected that the kestrel would negatively affect viability and germination rates compared to shrikes. However, the contrary seed effect seems to occur with the gut treatment of the shrikes which function as effective seed dispersers, according to germination data obtained by Nogales *et al.* (1998).

The four main objectives of the present study were: (1) to confirm whether the presence of lizard prey remains and *Lycium* seeds both in shrike and kestrel

pellets reveal these predators as secondary seed dispersers (2) to assess the relative importance of lizards, shrikes, and kestrels in the primary and secondary dispersal of *Lycium* seeds (3) to evaluate the damage to the seeds eaten by all disperser agents and the viability after passing several gut treatments, and (4) to check for possible differences in germination rates of *Lycium* seeds exposed to the different dispersal treatments (directly collected from plants, lizard droppings, shrike and kestrel pellets). This is the first study we are aware of on secondary seed dispersal by vertebrates preying upon frugivores where viability and germination for all treatments of a dispersal system is systematically studied.

METHODS

STUDY SITE

The Canarian Archipelago is of volcanic origin and lies in the Atlantic Ocean about 100 km (at the nearest point) from the African continent. Alegranza is uninhabited and is the Northernmost island of the Canaries, being situated about 17 km from the north coast of Lanzarote. It comprises 10.5 km² with elevations ranging from 0 to 289 m a.s.l. The climate is semidesertic; mean annual temperature is around 21°C and total annual rainfall does not exceed 300 mm. The vegetation is sparse and dominated by xeric shrubs including *Chenoleoides tomentosa* (Lowe) Botshand, *Salsola vermiculata* L. (Chenopodiaceae), *Euphorbia obtusifolia* Poir. (Euphorbiaceae), *Lycium intricatum* and *Nicotiana glauca* Grah. (Solanaceae). For more information on Alegranza Islet and part of the system studied, see Martín & Nogales (1993) and Nogales *et al.* (1998), respectively.

PROCEDURES

Fieldwork was carried out during the springs of 1997 (28 April to 1 May) and 1998 (27 April to 1 May). We conducted extensive surveys of the island in search of *Lycium* fruits ($N = 314$) from 70 different plants, droppings of lizards ($N = 993$), and of shrikes ($N = 106$) and kestrel pellets ($N = 210$). In order to have a representative sample of the population involved in the process, we collected lizard droppings in at least 28 distant places, and shrike and kestrel pellets in 15 and three different and distant perches, respectively. Lizards (SVL: 61–95 mm; $N = 20$) are very abundant in Alegranza while shrike and kestrel breeding populations have been estimated in five and four pairs, respectively (data from 1998).

Seeds were manually extracted and counted from the different lizard droppings and predatory birds pellets individually. Seeds recovered from fruits and

from the three vertebrate species were examined for their viability and ability to germinate. We performed a comparison viability experiment using 2, 3, 5 triphenyl tetrazolium (TTC) test (Scharpf, 1970) on seeds, collected in spring 1998, from the four treatments ($N = 199$ seeds collected directly from plants or uningested, 191 from lizard droppings, 200 from shrike pellets and 187 from kestrel pellets). Seeds were previously immersed in water during 24 h before being included in TTC and kept in the dark during the same time period. Additionally, we ran a germination experiment in a greenhouse, including seeds from spring 1997, of the same four seed treatments ($N = 104$ seeds, from each). Every seed was planted in an individual pot and we used a standard substrate (lapilli, turf and forest soil in a ratio of 1–1–2); the experience was examined daily for three months until no germination was found. Seeds were watered every two days and night-day light period conditions were those naturally found in the study area. Germination was defined as the emergence of any seedling part from the soil surface.

To test whether seeds of *Lycium* in the two predators occurred in association with lizard bones, we recorded their presence in each pellet individually and we used Chi-square tests to assess such association. This analysis was also used to identify possible differences in viability and germination from seeds belonging to the four treatments. We used a Kolmogorov-Smirnov test to study the germination speed among different seed types. All analyses were performed by using SPSS (version 9.0).

RESULTS

PLANT AND SEED DISPERSAL SYSTEM

Lycium intricatum is a common thorny solanaceous shrub that can reach 2 m in height in the xerophytic coastal Canarian areas. Fruits ripen in winter/spring,

turn red (measure: 7.75 ± 1 mm in length; mean ± 1 SD, 5.17 ± 2 mm in diameter, 0.12 ± 0.1 g in fresh weight, a water content of $71.72 \pm 7\%$; seed length is ≈ 2 mm; number of seeds present in fresh fruits range between 1 and 17, mean = 7.43 ± 3 ; $N = 40$ fruits).

Lycium seeds were found in 7.3% of the lizard droppings analysed (993 in total) and mean number of seeds per droppings was 4.8 ± 4 (range = 1–22). Frequency of occurrence of lizard remains was found to be the same for shrike and kestrel pellets (74%). The two predatory bird species are secondary dispersers of *Lycium* seeds according to the high association found between seeds and lizard remains in the pellets of both species (Table 1). This association was consistent between the two years and in 49.1% of shrike pellets and 31.0% from kestrel pellets were matched (Table 1). Frequency of seed occurrence and mean number of seeds per pellet was higher in shrike than in kestrel ones (Table 2).

SEED VIABILITY AND GERMINATION

The external visual damage produced by lizards to *Lycium* seeds was very small and a similar effect was observed in the case of the regurgitated seeds from the two predatory birds after a second treatment (Table 2). Highly significant differences were observed in seed viability among all combinations of the four treatments, decreasing in the following direction: uningested seeds, shrikes, lizards, and kestrels (Fig. 1 and Table 3).

A total of 233 seeds (56.0%) germinated of the 416 seeds planted (Fig. 1). Seeds from kestrel pellets suffered a reduction in germination of one third relative to those obtained from lizard droppings and of about one fourth relative to shrike seeds and uningested *Lycium* seeds. Furthermore, a smaller reduction of the seeds taken from lizard droppings with regards to those from shrike regurgitations and

Table 1. Results of Chi-square tests for association of *Lycium intricatum* seeds and *Gallotia atlantica* remains in regurgitation pellets from *Lanius excubitor* and *Falco tinnunculus* on Alegranza

Items	<i>Lanius</i>			<i>Falco</i>		
	1997	1998	Pooled	1997	1998	Pooled
<i>Lycium</i> and lizard	16	36	52	19	46	65
<i>Lycium</i> alone	2	5	7	0	0	0
Lizard alone	11	9	20	25	66	91
None	17	10	27	28	26	54
Total pellets	46	60	106	72	138	210
χ^2	9.2	9.2	22.9	14.3	14.2	30.6
P	0.002	0.001	<0.0001	<0.0001	<0.0001	<0.0001

Table 2. *Lycium intricatum* seeds found in the droppings of *Gallotia atlantica* and the pellets of *Lanius excubitor* and *Falco tinnunculus* on Alegranza

Parameters	<i>Gallotia</i>	<i>Lanius</i>	<i>Falco</i>
Number of droppings/pellets studied	993	106	210
Droppings/pellets with seeds (%)	7.3	55.7	31.0
Number of seeds per droppings/pellets (mean $\pm$ SD)	4.8 $\pm$ 4	20.2 $\pm$ 34.5	6.7 $\pm$ 8.1
Range of seeds per droppings/pellets	1–22	1–134	1–39
Total number of seeds found	331	1202	389
Damaged seeds (visual inspection %)	3.0	1.2	1.3

Table 3. Statistical results obtained from the viability tests (2, 3, 5 triphenyl tetrazolium) and germination experiments of *Lycium intricatum* seeds based on the four seed treatments on Alegranza

Seed treatment	Viability			Germination		
	χ^2	d.f.	<i>P</i>	χ^2	d.f.	<i>P</i>
<i>Lycium</i> vs. <i>Gallotia</i>	49.69	1	<0.0001*	8.61	1	0.003*
<i>Lycium</i> vs. <i>Lanius</i>	13.76	1	<0.0001*	0.40	1	0.527
<i>Lycium</i> vs. <i>Falco</i>	220.89	1	<0.0001*	67.09	1	<0.0001*
<i>Gallotia</i> vs. <i>Lanius</i>	14.34	1	<0.0001*	5.37	1	0.020
<i>Gallotia</i> vs. <i>Falco</i>	85.93	1	<0.0001*	31.04	1	<0.0001*
<i>Lanius</i> vs. <i>Falco</i>	158.67	1	<0.0001*	58.61	1	<0.0001*

*Significant at Bonferroni-corrected *P* level (0.05/6 = 0.008).

Figure 1. Viability and germination observed in the *Lycium intricatum* seeds from the four treatments (fresh fruits, droppings of *Gallotia atlantica*, and regurgitation pellets of *Lanius excubitor* and *Falco tinnunculus*) on Alegranza.

Lycium fruits was observed (Table 3), being only statistically significant with respect to the latter. There were no significant differences between seeds of these two last treatments.

Seeds from *Lycium* fruits germinated significantly earlier than those from the other three treatments

(Kolmogorov-Smirnov tests, $P < 0.0001$) (Fig. 2). Seeds from shrike pellets emerged sooner than those from lizard droppings ($Z = 4.47$, $P < 0.0001$) and kestrel pellets ($Z = 4.83$, $P < 0.0001$). Seeds from lizard droppings germinated earlier than seeds from kestrel pellets ($Z = 4.74$, $P < 0.0001$). These results were also significant at Bonferroni-corrected *P* level (0.05/3 = 0.016).

DISCUSSION

RELATIVE IMPORTANCE OF EACH DISPERSER

Secondary seed dispersal is a very little known phenomenon in which mainly birds (Ridley, 1930; Damstra, 1986; Hall, 1987; Dean & Milton, 1988; Stiles, 1992; Nogales *et al.*, 1998) and mammals (Nogales *et al.*, 1996) participate as secondary dispersers. The majority of cases described in the process of secondary seed dispersal by vertebrates involve frugivorous passerine birds as primary dispersers. In the present system, a frugivorous lizard achieves the first step. Our results show that shrikes and kestrels act as potential secondary seed dispersers due to the high association found between *Lycium* seeds and lizard remains in their pellets. Furthermore, lizards are

Figure 2. Seed germination rates from *Lycium intricatum* obtained from fresh fruits, droppings of *Gallotia atlantica*, and regurgitation pellets of *Lanius excubitor* and *Falco tinnunculus* on Alegranza.

common prey in the diet of shrikes and kestrels on Alegranza (Nogales *et al.*, 1998; M. N. Zurita & N. Puerta, unpub. data), reaching 18.1% and 13.5% of the total prey consumed and representing a total biomass of 64.3% and 50%, respectively (T. Barrera & R. González, unpubl. data).

In order to assess the efficiency of the three different vertebrates involved in this particular system, one of the most important factors in seed dispersal is the number of seeds transported by each dispersal agent (Schupp, 1993). In this system, frequency of apparition of *Lycium* seeds was approximately four times greater in the pellets of both predatory bird species than in lizard droppings (Table 2). Furthermore, lizards and kestrels have a similar mean number of seeds per dropping (4.8 and 6.7, respectively) whereas shrike pellets have four-fold more. Although defecation and regurgitation rates range between one and two droppings per day for the three disperser species (Duke *et al.*, 1976; Olsson, 1984, 1985; A. Valido & M. Nogales, unpubl. data), a higher number of seeds is probably transported by lizards due to their great abundance in the islet.

SEED DEPOSITION

Seed deposition, referred to as the mean number of seeds per dropping, seems to be very different when comparing lizard and kestrel droppings with shrike pellets, being clearly higher in the latter (see Table 2). If we consider that seed clumping has important and negative implications for seed survival, germination and seedling competition (Jordano, 1992), these results suggest that lizards and kestrels are more beneficial as dispersers than shrikes in this particular

aspect of the dispersal system. However, the two predatory birds produce a more seed clumped spatial distribution than lizards since they frequently use perches. In any case, the combination of both primary and secondary seed dispersers in this system results in a more heterogeneous seed shadow than that expected if interactions were only with lizards.

DISPERSER EFFECTIVENESS AND SEED GERMINATION

The viability tests performed in our study indicate that while lizards and shrikes (direct and secondary, respectively) do not affect the viability and germination of the *Lycium* seeds negatively, kestrels clearly do. These results are consistent with those showing that many vertebrate frugivorous species do not affect seed viability when they ingest seeds (Stiles, 1992; Traveset, 1998). Despite the utility of the viability test in seed germination studies, few contributions have examined seed viability before performing germination (Holthuijzen & Sharik, 1985; Nogales *et al.*, 1999).

With regards to secondary seed dispersal systems previously described, Hall (1987) observed that the majority of seeds secondarily ingested by raptors were apparently unharmed. Furthermore, the capacity of germination of seeds of the grass *Calamagrostis canadensis* (Michx.) Beauv. after suffering a double digestion of a frugivorous passerine and an American Kestrel (*Falco sparverius* L.) has been anecdotically mentioned by Balgooyen & Moz (1973).

In general, two of the main factors that affect seed germination are retention time in the gut of each species (e.g. Levey, 1986; Barnea *et al.*, 1992) and treatment effects in the digestive tract of every disperser (Schupp, 1993). Furthermore, it is known that

seed regurgitation time by frugivorous birds is short (5–20 min), while seeds that are defecated spend a longer period being digested, usually in the range 20–90 min (Levey, 1986; Snow & Snow, 1988; Jordano, 1992). Seeds that have been voided rapidly seem more likely to germinate than those that have been under a long gut retention time (e.g. Murray *et al.*, 1994). In our system, species involved show very different gut passage time (GPT) in lizards and regurgitation time (RT) in predatory birds. Lizard GPT was measured in laboratory conditions (12 h daylight, 26–28 °C, $N = 20$ individuals) by giving a glass bead, similar in size to a *Lycium* seed, and it yielded an average time of 2.4 days (A. Valido & M. Nogales, unpubl. data). In contrast, shrike RT is rather short (45–55 min; Olsson, 1984, 1985). For kestrels, Balgooyen (1971), Duke *et al.* (1976) and Yalden & Yalden (1985) observed a period of 12–23.5 h.

Gut enzymatic action of diurnal raptors is clearly stronger than in other types of birds (Duke *et al.*, 1976; Brown *et al.*, 1993; Stuart & Stuart, 1994). In our case it seems clear that the gut effect on secondarily ingested seeds is lower for shrike pellets than for kestrels. However, despite the fact that lizards showed a GPT which was about twice the Kestrel RT, this raptor reduced seed viability and germination rate to about one third. In this respect, it is also interesting to note that seed retention time, and therefore lizard gut treatment, is shorter when a bird predaes a lizard (Nogales *et al.*, 1998). This fact has an important implication in seed germination (Fig. 1), and Nogales *et al.* (1998) found similar results for germination pattern and percentages on part of the system presented here (plant–lizard–shrike).

Viability rates are higher than germination rates in all four *Lycium* seed treatments in this study (Fig. 1), so they could be influenced by an inhibitory process that reduces germination. Inhibitory effects in germination have been recorded by several authors in some species from temperate habitats (e.g. Livingston, 1972; Smith, 1975). Germination may be inhibited by several causes: anaerobic atmospheres, extreme temperatures, dry conditions, different acid types, among others (Murdoch & Ellis, 1992). Nevertheless, mechanisms underlying promotion and inhibition by chemical factors are largely unknown (Karssen & Hilhorst, 1992).

The fact that primary and secondary dispersal agents alter the speed of germination (Fig. 2) is difficult to interpret although it could have ecological implications as in the length of exposure to postdispersal seed predators, the finding in ephemeral seedling microsites (Schupp, 1993) or advantages in seedling size (Traveset *et al.*, 2001). Furthermore, early germination might be related to arid ecosystems where rain is unpredictable (Izhaki & Safriel, 1990).

In the xeric islet of Alegranza, we observed significant differences among the four treatments, in order of emergence: seeds from shrikes, *Lycium* fresh fruits, lizards and kestrels.

GENERAL ECOLOGICAL CONSIDERATIONS

As mentioned in the introduction, secondary seed dispersal by vertebrates preying upon frugivores shows relative analogies with the secondary seed dispersal in which seeds found in vertebrate droppings are redistributed though the activity of hoarding animals (e.g. ants; Levey & Byrne, 1993; Böhning-Gaese *et al.*, 1999). However, secondary seed dispersal by vertebrates includes a second digestion of seeds which does not occur in the hoarding process. Furthermore, secondary seed dispersal by hoarding animals modifies seed shadow less intensively because the second movement is performed on a smaller spatial scale. In the case of the secondary seed dispersal by predatory birds, the seeds are clearly dispersed at larger distances as a consequence of the second seed movement. In this respect, and on a larger spatial scale, Moore (1999) mentioned that movement of seeds from lizards to birds increases the opportunities for island-dwelling plants, giving them a greater chance of moving to new islands. Although this process might occur rarely and it would be very difficult to demonstrate, this author has considered that like other events in island biology, given enough time it can probably come about.

On our insular environment scale, *Lycium* seeds are under an important random component during the seed dispersal process. Dissemination can be done directly by a lizard, or secondarily by a shrike or a kestrel providing different ecological advantages (under the legitimacy view) depending on the disperser type. In general, this complex dispersal system can be considered advantageous for *L. intricatum*, considering the wide distribution that this species enjoys in all the Canary Islands and islets, and its abundance in all the lowland habitats of the Archipelago.

Finally, despite being poorly known, secondary seed dispersal by predatory birds may acquire an important dimension in small and remote insular environments or isolated continental systems where interactions are quite intense; all the participants are abundant, native residents, which have been interacting for a long time.

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