Short communication

The role of avian 'seed predators' as seed dispersers

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Seed dispersal is a central process in plant ecology with consequences for species composition and habitat structure. Some bird species are known to disperse the seeds they ingest, whereas others, termed 'seed predators', digest them and apparently play no part in dispersal, but it is not clear if these are discrete strategies or simply the ends of a continuum. We assessed dispersal effectiveness by combining analysis of faecal samples and bird density. The droppings of seed dispersers contained more entire seeds than those of typical seed predators, but over a quarter of the droppings of seed predators contained whole seeds. This effect was further magnified when bird density was taken into account, and was driven largely by one frequent interaction: the Chaffinch *Fringilla coelebs*, a typical seed predator and the most abundant bird species in the area and dispersed seeds of *Leycesteria formosa*, a non-native plant with berry-like fruits. These results suggest the existence of a continuum between seed predators and seed dispersers.

Keywords: Azores, Chaffinch, continuum, dispersal effectiveness, mutualism, seed dispersal.

Seed dispersal influences plant spatial structure, population dynamics and ultimately the long-term survival of plant species (Nathan & Muller-Landau 2000). Therefore, it is not surprising that many plants have evolved to attract seed dispersers, often by 'paying' for the seed dispersal service with a meal. Fleshy fruits and berries are well adapted to promote seed dispersal because they provide a nutritional reward, the pulp, to the disperser of the seeds. However, both seeds and pulp can be important sources of energy (Norconk *et al.* 1998) and many frugivores have the capacity to digest the seed content, thereby destroying most seeds they consume. These frugivores have been called 'seed predators' (Janzen 1971), 'opportunists' and 'exploiters' (McKey 1975), 'seed consumers' (Hampe 2001), 'granivores' (Bartuszevige & Gorchov 2006) and 'fruit thieves' (Howe 1980), and are generally considered to play a negligible role in seed dispersal. Therefore, for a long time, dispersing seeds or digesting them was regarded as a separate strategy (e.g. Hampe 2001, Herrera & Pellmyr 2001, Hulme 2002). It is now widely accepted that many animals do not fit this dichotomy strictly. For example, rodents often fail to recover buried seeds (Price & Jenkins 1986) and ungulates, primates and birds, despite being mainly seed predators, sometimes disperse viable seeds (Howe 1986, Clark *et al.* 2001, Guerrero & Tye 2009). However, the magnitude of this effect for avian seed predators has rarely been measured in the field and the process of seed dispersal has been considered negligible in this group (Norconk *et al.* 1998, Guerrero & Tye 2009).

Dispersal effectiveness is the result of two parameters: the quality of the service provided to the seeds and the quantity of seeds dispersed (Schupp 1993). The first component depends on the treatment given by the disperser to the seed (e.g. destruction, scarification) and on the quality of the deposition site. The second component is dependent on the number of seeds dispersed, which is in turn dependent on the density and the diet of the dispersers.

While conducting a dietary study on the birds living in the last remnant of native laurel forest in the Azores (Heleno *et al.* 2010) it became apparent that a large number of seeds observed in faecal samples from granivorous birds were intact. In this paper, we consider the role that granivorous birds may play in seed dispersal by combining the analysis of faecal samples with estimates of bird density to quantify the number of dispersed seeds.

METHODS

The study was conducted at Serra da Tronqueira, a mountainous district in the east part of the Island of São Miguel, Azores (37°47'N, 25°13'W), characterized by a temperate oceanic climate, with high relative humidity and a small temperature range (Tutin 1953). Sampling for seeds, birds and bird droppings was carried out in four sites representative of the main vegetation types present. For a full description of the study area see Heleno *et al.* (2010). Plots were 1 ha in size and sampling was repeated in each plot every 3 weeks from 1 May to 26 November 2005, covering the seeding season of most plants (Schäffer 2002).

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Bird density was estimated using 8-min point counts, starting 1 min after arrival to the census point (Bibby *et al.* 2000). Four point counts were carried out at each plot in every 3-week period. Inside each plot, two fixed census points with good visibility were chosen and used alternately on two different days at 08:00 and 09:00 h. The density of each species was averaged across the four sites and the 10 sampling periods.

Bird diet was assessed by analysing faecal samples collected from mist-netted birds. Twenty mist-netting sessions were performed at 3-week intervals between May and November 2005 at each location. In each session, 72 m of mist-nets were opened for five consecutive hours starting at sunrise. Captured birds were kept inside bags for up to 20 min. All droppings produced were collected and the whole seeds in the droppings were identified under a dissecting microscope (magnification = 10–40×) by comparison with a reference collection of seeds. The viability of whole seeds of the most common plant species recovered from the droppings was assessed using germination trials.

Results are presented as the proportion of droppings that contained at least one whole seed of each species (frequency of occurrence), rather than the total number of seeds dispersed by each bird species. This measure is often used in seed dispersal studies as the latter approach can be hugely inflated by a large number of small seeds in a single dropping, which may not translate into high survival probability due to high intra-seed competition (Inouye 1980, Murray 1998).

Dispersal effectiveness was calculated for each bird species as frequency of occurrence of whole seeds multiplied by bird density. Germination trials were run with whole seeds from the most common plant species recovered from bird droppings. Seeds were identified and directly placed onto filter paper in Petri dishes, were inspected daily and moistened with tap water to keep them damp over a 13-month period, and the number germinating was recorded.

RESULTS

Overall, 664 droppings were collected from 815 mist-netted birds belonging to nine species (Table 1). From these, 2100 seeds of 30 plant species were identified. These seeds were dispersed by seven species of bird, four of these being traditionally classified as seed predators rather than seed dispersers. A list of all bird–seed interactions is shown in Table 1, which shows that most birds dispersed multiple seeds and most seeds were dispersed by several bird species in accordance with the diffuse nature of the dispersal process (Iwao & Rausher 1997). The densities we obtained for the nine bird species (Table 1) were very similar to those obtained by distance sampling and mist-netting in the same area (Ceia *et al.* 2009).

Droppings of typical seed dispersers (Eurasian Blackcap *Sylvia atricapilla*, Common Blackbird *Turdus merula* and European Robin *Erithacus rubecula*) contained entire seeds more frequently than droppings of other birds, being responsible for 73.9% of all droppings that contained entire seeds. However, over a quarter of the droppings that contained seeds (26.1%) were produced by the four species of granivorous bird species (Atlantic Canary *Serinus canaria*, European Goldfinch *Carduelis carduelis*, Chaffinch *Fringilla coelebs* and Azores Bullfinch *Pyrrhula murina*). Furthermore, if bird density is incorporated to include information on the 'quantity' component of seed dispersal, the importance of bird species typically considered seed predators increased from 26.1 to 36.2%. Although the small size of the community (seven bird species) hampers the interpretation of the results, when calculated in this manner, no significant differences existed between the dispersing effectiveness of seed predators and seed dispersers (one-way ANOVA: $F_{1,5} = 1.47$, $P = 0.280$). Ideally, the viability of all seed–bird combinations should be tested but viability trials could only be conducted on eight of these combinations:

1 *Vaccinnium cylindraceum* (30 seeds), *Acacia melanoxylon* (13 seeds), *Pittosporum undulatum* (30 seeds) and *Leycesteria formosa* (30 seeds), dispersed by Eurasian Blackcap;
2 *Duchesnea indica* (four seeds) and *L. formosa* (30 seeds), dispersed by Common Blackbird;
3 *Leycesteria formosa*, dispersed by European Robin (30 seeds) and Chaffinch (30 seeds), only the latter being a seed predator. However, 154 of the 197 (mean 78.2%, median 98.5%; *L. formosa* dispersed by Chaffinch = 96.7%) seeds that avoided physical destruction in the birds' beaks and grinding gizzards germinated within the study period, with no distinction being made between dormant and dead seeds at the end of the experiment.

DISCUSSION

It is well established that avian seed predators can occasionally disperse seeds (Williams & Karl 1996), but our estimate that seeds dispersed by typical seed predators make up almost a third of all bird-dispersed seeds in one system was unexpected. Even if the ecological role of typical seed dispersers remains indisputable, it is remarkable that the four seed predators in our study all successfully dispersed entire seeds, and that their collective role was far from negligible. The interpretation of the results is, however, complicated by two factors. First, the importance of seed predators was largely influenced by one frequent interaction: the Chaffinch, a typical seed predator, dispersing seeds of *L. formosa*, an alien plant with berry-like fruits. This bird species is likely to be genuinely more effective at dispersing seeds than other typical seed predators, given that it is both very common (in the

Table 1. List of all seed–seed disperser interactions quantified in terms of the number of droppings with whole seeds. Biogeographical status refers to the distribution of each species following Borges *et al.* (2005): (i) introduced, (n) native, (E) endemic to the Azores, (M) endemic to Macaronesia, (d) doubtfully native. Abundance and number of droppings analysed of each bird species are presented.

| Bird species (density birds⁄ha) [droppings analysed]	Species	Plant family	Biogeographical status	No. of droppings where present
Blackcap (2.37) [59]	*Acacia melanoxylon*	Fabaceae	i	1
	Duchesnea indica	Rosaceae	i	7
	Hedychium gardneranum	Zingiberaceae	i	3
	Leycesteria formosa	Caprifoliaceae	i	21
	Pittosporum undulatum	Pittosporaceae	i	3
	Solanum nigrum	Solanaceae	i	1
	Gen. sp. Indet. (seed 1)	Unknown		3
	Calluna vulgaris	Ericaceae	n	1
	Fragaria vesca	Rosaceae	d	3
	Hedera azorica	Araliaceae	E	4
	Juncus effusus	Juncaceae	n	1
	Juniperus brevifolia	Cupressaceae	E	1
	Myrica faya	Myricaceae	n	4
	Myrsine africana	Myrsinaceae	n	1
	Rubus ulmifolius	Rosaceae	i	3
	Vaccinium cylindraceum	Ericaceae	E	5
Blackbird (2.25) [100]	*Acacia melanoxylon*	Fabaceae	i	1
	Cryptomeria japonica	Taxodiaceae	i	1
	Duchesnea indica	Rosaceae	i	11
	Leycesteria formosa	Caprifoliaceae	i	12
	Pittosporum undulatum	Pittosporaceae	i	1
	Gen. sp. Indet. (seed 1)	Unknown		2
	Gen. sp. Indet. (seed 2)	Unknown		1
	Calluna vulgaris	Ericaceae	n	1
	Centaurium erithraea	Gentianaceae	d	1
	Fragaria vesca	Rosaceae	d	2
	Hedera azorica	Araliaceae	E	1
	Ilex perado	Aquifoliaceae	E	11
	Juniperus brevifolia	Cupressaceae	E	6
	Laurus azorica	Lauraceae	n	1
	Myrica faya	Myricaceae	n	1
	Potentilla erecta	Rosaceae	n	2
	Rubus ulmifolius	Rosaceae	i	3
	Vaccinium cylindraceum	Ericaceae	E	11
	Viburnum tinus	Caprifoliaceae	E	1
Canary (3.91) [37]	*Conyza bonariensis*	Asteraceae	i	1
	Duchesnea indica	Rosaceae	i	1
	Holcus lanatus	Poaceae	i	2
Goldfinch (0.52) [11]	*Sonchus tenerrimus*	Asteraceae	i	1
Chaffinch (8.20) [176]	*Acacia melanoxylon*	Fabaceae	i	1
	Leycesteria formosa	Caprifoliaceae	i	16
	Pittosporum undulatum	Pittosporaceae	i	1
	Solanum nigrum	Solanaceae	i	5
	Gen. sp. Indet. (seed 3)	Unknown		1
	Carex viridula	Cyperaceae	M	2
	Carex vulcani	Cyperaceae	E	1
	Potentilla erecta	Rosaceae	n	2
Robin (2.09) [44]	*Duchesnea indica*	Rosaceae	i	1
	Leycesteria formosa	Caprifoliaceae	i	6
	Solanum nigrum	Solanaceae	i	1
	Vaccinium cylindraceum	Ericaceae	E	1
Azores Bullfinch (0.49) [24]	*Hypericum humifusum*	Hypericaceae	n	3
Yellow Wagtail *Motacilla flava* (0.87) [25]				
Goldcrest *Regulus regulus* (6.90) [188]				
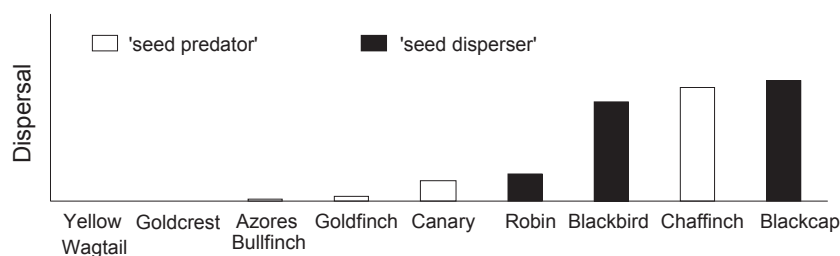
Figure 1. Dispersal effectiveness of the forest birds in the Azores suggesting the seed predator–disperser continuum.

Azores and throughout the Western Palaearctic), and highly generalist in its feeding habits (Newton 1972). Furthermore, *L. formosa* is also a generalist species in the sense that it is highly attractive to many frugivorous birds, which in part explains its worldwide success (Williams & Karl 1996). Secondly, in this study we did not quantify the proportion of destroyed seeds. It is commonly accepted that seed predators destroy a larger proportion of ingested seeds than seed dispersers. However, if the total number of viable seeds that reaches the ground is a more important metric for the reproductive success of the plant, which is particularly true for highly fecund trees, then this might be a price that many plants are 'willing' to pay (Crawley 1992). Particular cases where the impact of high seed predation may lead to no measurable reduction in the number of recruiting plants are when recruitment is microsite-limited or when there are high seed densities (Crawley 1992).

The most commonly dispersed seeds (*L. formosa* and *V. cylindraceum*) came from berries. Berries tend to be more appealing to seed dispersers and therefore have higher dispersal rates (Rejmanek & Richardson 1996). Furthermore, birds are more likely to disperse seeds from berries than seeds from drupes because berries produce many seeds, which increases the probability that some will be defecated intact (Crawley 1992).

Wheelwright and Orians (1982) suggested that the often-assumed predator–disperser dichotomy obscured the fact that frugivores represent a continuum in terms of their contribution to seed dispersal. Hulme (2002) developed this idea further and suggested that seed predators and seed dispersers should be seen as two extremes along a continuum of mutualistic (dispersal) to antagonistic (predation) interactions. However, none of the authors presents empirical evidence of such a continuum. The results presented here, even if dominated by the large contribution of a single species (Chaffinch), suggest that the dispersal effectiveness of forest birds in the Azores is better described by a gradient from poor to good dispersers (Fig. 1), akin to the distribution predicted by Wheelwright and Orians (1982) and Hulme (2002). Whether this result is a local phenomenon arising from the simplified avian community of an isolated island or a more general pattern should be further investigated. This study highlights the need to evaluate the dispersal capabilities of avian seed predators on seed dispersal studies. There is currently great interest in ecosystem services such as seed dispersal. If we want to conserve and utilize these services, it is critically important that we accurately identify the species that provide them (Kremen & Hall 2005). Using untested assumptions to assort species to discrete ecological roles such as seed predator and seed disperser may not accurately describe their function. Charles Elton (1927) stated 'when an ecologist says "*there goes a badger*" he should include in his thoughts some definite idea of the animal's place in the community to which it belongs'. Here we suggest that the place of seed predators in the community may not be as clear-cut as previously thought.

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