Title: **Flowers as food source by birds in Europe**

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Abstract

Most plants depend on animal pollination. Several animal groups, including many birds , have specialized in exploiting floral nectar simultaneously pollinating the visited flowers. These specialized pollinators are present in all continents except Europe and Antarctica, and thus, insects are often considered the only ecologically relevant pollinators in Europe. Nevertheless, generalist birds are also know to visit flowers, and several reports of flower visitation by birds in Europe prompted us to review available information in order to estimate its prevalence of this phenomenon. We retrieved reports of flower-bird interactions from 62 publications. Forty-six bird species visited the flowers of 95 plant species, 26 of these being exotic to Europe, yielding a total of 243 specific interactions. The ecological importance of bird-flower visitation in Europe is still unknown, particularly in terms of plant reproductive output, but effective pollination has been confirmed for several native and exotic plant species. We suggest nectar and pollen to be important food resources for several bird species, especially tits (*Cyanistes*), and *Sylvia* and *Phylloscopus* warblers during winter and spring. The reported use of flowers as food sources to birds, and, as a consequence bird pollination is more common in the Mediterranean basin, which is a stopover to many migrant bird species, and the flower visitation by these might promote long-distance pollen flow. We argue that bird pollination in Europe is a promising research topic and that further studies are needed to explore its ecological and evolutionary relevance.

Introduction

Animal pollination is a key process in their reproduction of The approximately 90% of the 352,000 flowering plant species form the foundation of most terrestrial ecosystems (Knight et al. 2005, Sargent and Ackerly 2008(Ollerton et al. 2011).

Together with insects, birds are prominent pollinators of many plant species. Globally, at least 500 plant genera are known to be pollinated by over 900 bird species (Sekercioglu 2006), and the actual number of flower-visiting birds may reach 1100 (Carstensen and Olesen 2009). In the face of the accentuated decline of some bird groups around the world, including Europe, it is increasingly relevant to evaluate what ecological functions might be at risk (Sekercioglu 2006). The main pollinating bird families are the New World Trochilidae, the Palaeotropical and Pacific Nectariniidae and the Austro–Oceanian Meliphagidae, but there are other important bird pollinators such as the New World Icteridae and Thraupidae, the Hawaiian Drepanidini, the South African Promeropidae, the sub-Sahara African and southern and eastern Asia Zosteropidae, the Oceanian and south-eastern Asia Dicaeidae and Loriini (see Olesen and Valido 2003, Ortega-Olivencia et al. 2005, Carstensen and Olesen 2009).

Although there are no specialized nectarivorous bird species in Europe (Ortega-Olivencia et al. 2005, Cramp 2006), fossil records suggest that birds close to the Trochilidae where once presentin Central Europe (Mayr 2004, 2005, Louchart et al. 2008). The reason why these birds, disappeared from Eurasia is unclear (see Mayr 2005).The apparent paucity of flower-bird visitation records in the literature suggests that it is a rare phenomenon (Ford 1985). a confirmation bias may also play a role, i.e. people see what they expect to see, and that goes for ornithologists as well. When a bird visits a flower an ornithologist expects it to be foraging for insects and does not value or report the interaction, but botanists, on the other hand, are focused on the plant and more often report nectar intake by birds (Straka 1989). Flowers are an abundant resource in Europe and many non specialized nectar-drinkers might visit flowers for their pollen, floral oil, petals, water and flower–visiting arthropods (Grant 1996, Schwilch et

al. 2001, Cecere et al. 2011c,). Indeed, many non-specialized birds are known to efficiently pollinate plants around the world (e.g. Fang et al. 2012). , Bird flower visitation has also been reported in Europe, including some confirmation of effective pollination (e.g. Ortega Olivencia et al. 2005), but its actual extent, richness and ecological relevance is still unknown (Ford 1985). Here we make an exhaustive review on the use of flowers as food source by birds in continental Europe and discuss their role as pollinators. We expect a low number of generalist and non-hovering bird species interacting with flowers (Fleming and Muchhala 2008) and consequentially a relative low number of interactions. However this might be more common in the Mediterranean region were biodiversity is higher. Finally we foresee a higher use of floral resources in winter and early spring, periods with low numbers of invertebrates, plant pollinators and food source for birds (Cronk and Ojeda 2008, Cecere et al. 2011c).

Methods

We reviewed the scientific literature to assemble all records of flower visitation by birds in Europe. Searches were conducted in www.scholar.google.com, www.isiknowledge.com, and "grey" publications, i.e. informally published, written material. In addition, we included unpublished personal observations. We limited the geographic extent of the searches to continental Europe, i.e. east to the Ural Mountains, including continental islands, but excluding any territories outside the European continental shelf. We compiled all records of birds feeding on open flowers or parts of open flowers (i.e. excluding flower buds), and also records of pollen attached to bird feathers or being present in faeces. Whenever available, the following information was retrieved: species or higher taxon of birds and plants, country or region and month of the observation, and type of interaction, i.e. nectar drinking, damaging the flower to access the nectar, nectarivory, or florivory. We included all bird species with persistent populations in Europe, including introduced species with self-sustained populations

(Cramp 2006, Crochet and Joynt 2012). Plant taxonomy followed Stevens (2001), . When plant taxonomy was only available to supra-specific levels (most often genus) we considered the plant as native if there was any native European member of the taxon.

Evidence for bird flower visitation in Europe

Our search revealed 62 publications describing flower visitation by wild European birds. These came from general ecology journals (e.g. *Oikos*), and from specific botanical (e. g. *Annals of Botany*) and ornithological literature (e.g. *Ardea*,*Ibis*), including regional publications (e.g. *Avocetta, British Birds*).

Following some initial information from the end of XVIII century on European bird-flower visitation (White 1789; Darwin 1791), there was no new information on this subject until 1874 when Charles Darwin noticed the particular way that some flowers were bitten, suggesting that this resulted from the behaviour of birds when searching for nectar. However, until 1959 all records originated from direct feeding observations (Ash 1959, Ash et al. 1961). John Ash was the first to identify pollen grains on bird feathers. The first suggestions that European birds could be actively mediating pollination dates back to 1969 when *Turdus merula* were recorded visiting the flowers of the exotic *Puya chilensis*, which is pollinated by hummingbirds in its natural range in South America (Ebbels 1969). Twenty years later, the native *Rhamnus alaternus* was also reported as being likely pollinated by *Sylvia atricapilla* and *S. borin* (Calvario et al. 1989). However, these studies did not evaluate the efficiency of birds as pollen vectors. In 1989, bird pollination was finally confirmed in Europe: *Cyanistes caeruleus* was shown to be a pollinator of the ornithophilous *Fritillaria imperialis*, introduced from Turkey and Asia (Búrquez 1989), and later other tit species were also suggested to pollinate this plant species (Peters et al. 1995). Recently, the native legume *Anagyris foetida* was observed to be pollinated by *Phylloscopus collybita*, *Sylvia melanocephala* and *S. atricapilla* (Ortega-Olivencia

et al. 2005). Several continental species of *Scrophularia* also have a mixed pollination system consisting mainly of insects but also birds (Ortega-Olivencia et al. 2012). On the Italian Ventotene Island, the agriculturally important *Brassica oleracea* group (e.g. cabbage, broccoli, cauliflower) is more often visited by birds than by insects and exclusion of birds reduces fruit-set (Cecere et al. 2011a). This latter example suggests that non-specialized nectar birds might play a role in the pollination of economically important plants. This is also known for the fruit tree *Eriobotrya japonica* in China (Fang et al. 2012).

A quantitative analysis of bird-flower visitation in Europe

Our data compilation of bird-flower interactions (Table 1) found 46 bird species, all but one belonging to the Passeriformes order (here we consider *Passer italiae* as a true species), feeding on flowers of 95 plant species in Europe, 66 native and 29 exotic (including cultivated and invasive plants; see Supplementary material Appendix 1, Table A1). This represents 9% and 22%of the total European avifauna and passerine species diversity, respectively, (Cramp 2006; Crochet & Joynt 2012), and 0.61% and 0.76% of the native, and total European floras, respectively(Winter et al. 2009). These are certainly underestimates, once that few European plants have been surveyed for bird visits and due to the low taxonomic resolution of many records. Overall, these reports document 243 different interactions between birds and plants. However, only six plant species are yet confirmed to be effectively pollinated by birds (Búrquez 1989, Ortega-Olivencia et al. 2005, 2012, Cecere et al. 2011a).

In our data compilation, we further searched records of European bird species with bird-flower visitation obtained outside Europe (Table 1). In this additional search, we found four bird species, two native passerines (*Iduna pallida*/*I. opaca* -formerly regarded as a single species - and *Sylvia crassirostris*) and two exotic species, *Estrilda astrild* and *Psittacula krameri* without any information of flower visitation in Europe and also at least 12 different plant species (see Supplementary material Appendix 1, Table A1). Furthermore, the long-distance

migratory European passerine species seem to show a regular nectarivorous behaviour in their African stopover sites during spring migration (Salewski et al. 2006, Cecere et al. 2010). Additionally we found that the flowers of some Mediterranean-West European plant species, such as *Arbutus* sp. and *Ulex* sp., are visited and possibly pollinated by birds in their exotic ranges, for example by honeyeaters in Australia (Ford 1985).

Geographic and temporal patterns

We have evaluated the geographical and temporal distributions of the interactions for which such information was available. Records based on pollen attached to feathers or bills were not included as the interaction might have occurred several months before and on a different region from where it was recorded. (e.g. pollen found in feathers of *Sylvia* and *Phylloscopus* warblers (thereafter: warblers) in Denmark contained pollen from Mediterranean plant species, and one bird carried pollen from spring flowering plants in August (Laursen et al. 1997)).

Eighty-eight interactions (55%) are from the Mediterranean region (Table 1). Thus, as expected, flower visitation seems slightly more common in the Mediterranean basin where biodiversity is higher, but it is also well represented in higher latitudes, potentially due to the paucity of alternative insect food.

Many interactions were record during the end of winter and the beginning of spring making difficult a separation per season, so we chose to group both seasons. As we hypothesized most records were obtained during winter and spring (93%). According to Laursen et al. (1997), this might be particularly common in especially cold springs poor in insects.

Ecological relevance of bird-flower interactions

As expected, the 50 flower-visiting bird species (46 in Europe and four species recorded from outside Europe) were trophic generalists, with flexible or opportunistic feeding habits that change throughout the year according to food availability (Cramp 2006). The bird species with most records of flower visitation are included in Table 2, and belong mostly to *Sylvia* (almost all European species visit flowers, but especially *S. atricapilla*, *S. borin*, *S. melanocephala*, *S. communis* and *S. curruca*), *Phylloscopus* (*P. collybita* and *P. trochilus*) and tits (*particularly C. caeruleus*). Most of these birds are mainly insectivorous or frugivorous, depending on the season. Typical granivorous bird species, particularly finches and sparrows, visit flowers too (for the complete list of interactions see the Supplementary material Appendix 1, Table A1). The number of flower–visiting birds is certainly underestimated and the scarce information from some regions may reflect a paucity of studies rather than flower visitation. For example, *Sylvia* and *Phylloscopus* are prominent flower visitors in Western Europe, and it is most likely that ecologically/morphologically related taxa play a similar role in Eastern Europe. We also found bird species in which flower visitation probably occur rarely, such as *Muscicapa striata*, *Hippolais icterina*, *Erithacus rubecula* and *Saxicola rubetra*. Several studies have analysed many samples of feathers and faeces of these species but pollen was rarely present (Schwilch et al. 2001, Cecere et al. 2011c). In these publications, several other passerine species were also inspected for pollen, but showed no evidence of flower visitation, including ; these species include, for instance, *Phoenicurus phoenicurus*, *Luscinia megarhynchos, Anthus trivialis*, *Oenanthe oenanthe*, *Ficedula hypoleuca*, *Acrocephalus scirpaceus* and *Acrocephalus schoenobaenus* (Schwilch et al. 2001).

Most bird-flower visitation in Europe occurs while birds are perched, as opposed to specialized nectarivory birds which normally hover in front of the flowers (Fleming and Muchhala 2008). The only exceptions are *Phylloscopus* and *Regulus* that can feed either while

186 perched or hovering (Rodríguez-Rodríguez and Valido 2008, Ortega-Olivencia et al. 2012).
187 While some species, such as the warblers, mainly drink nectar from the flowers, acting as
188 legitimate pollinators (Ortega-Olivencia et al. 2012), others such as finches and sparrows are
189 mostly nectar robbers, tearing parts off the perianth or piercing holes to reach the nectar,
190 often without touching the reproductive structures of the flower, thus damaging most visited
191 flowers (e.g. Búrquez 1989). Finally, some species such as tits, are both legitimate and
192 illegitimate visitors, most likely depending on the flower structure and position (Búrquez 1989,
193 Fitzpatrick 1994). Even when flowers are damaged during the visit, many of them might still
194 produce fruits, and the visit might still result in increased fitness to the plant (e.g. Swynnerton
195 1917). INCLUIR AQUI A FRASE SOBRE O DON-FAFE

196 In most flower-visiting birds, pollen is adhered to the bill and feathers around upper
197 mandible and on forehead, face, chin, sometimes even on breast feathers (Ash et al. 1961,
198 Laursen et al. 1997, Schwilch et al. 2001). However, in finches they often occur half-way out on
199 the mandibles and sometimes only on the lower mandible (Ash et al. 1961). If pollen loads are
200 large and humidity is high, birds may accumulate a hornlike structure on the forehead known
201 as a pollen horn (Laursen et al. 1997). Pollen horns can persist on the birds for long periods,
202 storing information on bird-flower visits until feathers get shed.

203 Flower visitation seems to be more common during the early stages of an ecological
204 succession, when annual plants and flowers are more abundant (Cecere et al. 2010). During
205 their spring migration, at least *S. borin* and *S. communis* seem to prefer nectar to insects
206 (Schwilch et al. 2001). This choice might be explained by the chemical content of nectar, i.e.
207 water and simple sugars, being readily absorbed by the digestive tract of the birds, which is
208 reduced during migration (Schwilch et al. 2001, Cecere et al. 2011c). Finally, handling time of
209 flowers is shorter than that of insects, and flowers may also be easier to locate (Cecere et al.
210 2010, 2011c). Although *Cyanistes caeruleus* does not prefer nectar as its major food source, it

211 is even able to select the most productive flowers (Fitzpatrick 1994). Finally, the low insect
212 availability during winter and cold springs may force birds to feed on flowers.

213 The most common pollen grains found on European birds belong to the genera
214 *Brassica*, *Citrus* and *Eucalyptus* (Ash et al. 1961, Laursen et al. 1997, Schwilch et al. 2001,
215 Cecere et al. 2011b, Provost et al. 2012). Their flowers are certainly among the most important
216 to nectar-foraging birds. However, their importance for bird populations cannot be easily
217 estimated, due to regional variation in flower, arthropod and seed abundances and in the
218 incomplete sampling of this interaction type. Most flowers visited by birds are mostly insect
219 pollinated, and while some have bird-pollination characteristics such as the Crown Imperial
220 (Búrquez 1989, Peters et al. 1995), most have insect-pollination traits such as *Brassica* or wind-
221 pollination traits such as *Quercus* sp. (Cecere et al. 2011a, b).. The majority of the plants
222 reported do not require bird pollination, so it is expected that birds are the most benefited in
223 these interactions, the exception is *Anagyris foetida*. The fact that x% of the plants visited by
224 birds are exotic (Table 1), raises interesting ecological questions such as how important are
225 birds for the pollination and subsequent expansion of these exotic plants, and the role of these
226 exotic plants to wintering and migrating bird population in the Mediterranean area. On the
227 other hand, the y% native plants visited by birds offer an equally stimulating research topic
228 with evolutionary implications. Besides the potentially contribution for plant reproduction, it is
229 particularly relevant to know how important are native flowers for bird survival and
230 reproduction in exceptionally cold years. Studies using a combination of methods, as direct
231 observations and pollen load in birds, should be able to tackle these and other ecological and
232 evolutionary questions.

233

234 **General remarks**

Records of flower-visiting birds in Europe have been frequently considered to be rare and with reduced ecological relevance.. We show that the relationship between birds and flowers is richer and more widespread than hitherto thought. European flower-visiting birds are mainly food generalists that in harsh seasons and insect–poor environments, may expand their food niche and explore flowers for nectar,pollen and even insects. Floral resources may be crucial to winter and spring migration, and breeding of many bird species. Many of the plant species visited are exotic which might have ecological implications, and % are native with likely evolutionary and ecological implications, opening two promising research topics.. Due to their high mobility, birds may fulfil an important function as long–distance pollen vectors, much more efficiently than insects (Yates *et al.* 2007). However, our understanding of the ecological relevance of bird-flower interactions in Europe seems to be still on its infancy.

Acknowledgment

LPS was supported by the grant SFRH/BD/77746/2011 of the Fundação para Ciência e Tecnologia (FCT). RH was supported by the grant SFRH/BPD/76037/2011 of the FCT and the Marie Curie Action FP7-PEOPLE-2012-CIG-321794. We would like to thank Joana Alves, Vanessa Mata, Nickolas Waser and two anonymous referees (for all suggestions and corrections on the manuscript.

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Supplementary material (available online as Appendix OXXXXX at <www.oikosoffice.lu.se/appendix>). Appendix A1 (Table A1.xlsx: All recorded interactions between birds and flowers (x interactions)

Table 1 – Number of bird and plant species and bird-flower interactions recorded, in all data, and data with geographic and temporal information.

			Bird species	Plant species	Interactions
All records	Europe	Total	46	95	343
		Native	46	66	220
		Exotic	0	29	98
	Outside Europe		13	14	30
Records with geographical information		Total	31	56	160
		Mediterranean	22	25	88
		North and Central Europe	20	32	72
Records with temporal information		Total	27	40	108
		Winter and Spring	26	36	100
		Summer and Autumn	8	5	8

Table 2 – Recorded interactions between the most common flower visitors and plants, the complete interaction matrix (x interactions) is available as Supplementary Data due to space constraints. **f** - pollen observed on feathers, forehead, bill or breast; **o** -feeding observation; **ns** - not stated; **fe** - pollen in faecal sample; **st** - stomach content; ? - most likely plant taxa; bold - exotic species; ( ) - record outside Europe; * - pollination confirmed.

Order	Family	lower taxa	Cyanistes caeruleus	Phylloscopus collybita	Phylloscopus trochilus	Sylvia atricapilla	Sylvia borin	Sylvia. communis	Sylvia curruca	Sylvia melanocephala
Apiales	Apiaceae	Ferula communis		o	o	o; fe	o; fe	o; fe	o	o
		Oenanthe sp.			o					
	Araliaceae	Hedera helix		f						
	Pittosporaceae	**Pittosporum tobira**					o	o		
Asparagales	Asparagaceae	**Agave americana**			o					
		Yucca sp.				o				
	Iridaceae	**Chasmanthe aethiopica**					(o)			
		Freesia laxa		o						
	Xanthorrhoeaceae	**Aloe arborescens**	o	o		o				o
		Aloe sp.					ns	f?		
		Kniphofia sp.	o							
Asterales	Asteraceae	tribe Anthemideae		f						
		sub-family Cichorioideae				f				
Brassicales	Brassicaceae	Brassica fruticulosa				o; fe	o; fe	o		
		Brassica incana		o		o	o	o		o
		Brassica oleracea*					o	o		
		Family Brassicaceae		f	f	f	f		f	
	Capparaceae	**Maerua crassifolia**		(o)	(o)			(o)		
Buxales	Buxaceae	Buxus sp.		f		f				
Caryophyllales	Caryophyllaceae	Family Caryophyllaceae		f						
Dipsacales	Adoxaceae	Sambucus sp.		f						
		Viburnum sp.		f		f				
Ericales	Theaceae	**Camellia sp.**	o							
Fabales	Fabaceae	**Acacia sp.**		f						
		Anagyris foetida*	f	f; o; fe		f; o; fe				f; o; fe
		Erythrina tomentosa					(o)			
		Parkia biglobosa			(o)					
Fagales	Betulaceae	Betula sp.	o	f	f	f	f		f	
	Fagaceae	Quercus sp.		f	f	f	f		f	
	Myricaceae	Myrica faya		f						
		Myrica gale		f						
Lamiales	Bignoniaceae	**Tecoma capensis**	o							
		Tecoma sp.				(o)			(o)	
	Oleaceae	Fraxinus excelsior	o							
		Fraxinus sp.		f	f	f				
		Jasminum nudiflorum				o				
	Plantaginaceae	Plantago lanceolata		f						
	Scrophulariaceae	Scrophularia grandiflora*				o				o
		Scrophularia sambucifolia*		o		o				o
		Scrophularia trifoliata*				o				o
Liliales	Liliaceae	**Fritillaria imperialis***	o		o	o	o		o	
Malpighiales	Euphorbiaceae	**Euphorbia pulcherrima**		o						
	Salicaceae	Populus sp.		f		f				
		Salix caprea	o	o		o				
		Salix cinerea	o							
		Salix sp.	o	f	f	f				
Malvales	Malvaceae	**Abutilon sp.**				(o)				
		Hibiscus sp.	o							
		Lavatera arborea				o	o	o		o
		Malva sylvestris					o			
Myrtales	Myrtaceae	**Callistemon sp.**				(o)				
		Eucalyptus globulus		o						
		Eucalyptus sp.		f; o	f	f; (o)	f		f; (o)	
	Onagraceae	**Fuchsia sp.**				o	o			
Pinales	Cupressaceae	Juniperus phoenicea			f?					
	Pinaceae	Pinus sp.		f	f	f	f		f	
Proteales	Proteaceae	**Grevillea robusta**			(o)		(o)			
Ranunculales	Berberidaceae	**Mahonia japonica**	o			o				
Rosales	Cannabaceae	**Cannabis spp.**		f					f	
	Rhamnaceae	Rhamnus alaternus				o	o			
	Rosaceae	Crataegus sp.			st	f; st	ns; st	st	st	
		Eriobotrya japonica	o	o		o				o
		Prunus dulcis	o			o				
		Prunus sp. or Sorbus sp.		f	f	f				
		sub-family Amygdalaceae		f	f	f	f		f	
	Ulmaceae	Ulmus glabra	o							
	Urticaceae	Urtica sp.		f		f	f		f	
Sapindales	Rutaceae	**Citrus aurantium**						f?		
		Citrus sinensis				(o)				
		Citrus sp. (not C. aurantium)						f		
		Citrus sp.		f	f	f	f	f	f	

	Sapindaceae	Acer pseudoplatanus						f?	
		Acer platanoides				o	o		
		Acer sp.		f					ns
Saxifragales	Grossulariaceae	**Ribes sanguineum**	o						o
		Ribes uva-crispa	o						
Solanales	Convolvulaceae	Calystegia sp.		f; o					