Oikos 123: 1377–1383, 2014
doi: 10.1111/oik.01347

Subject Editor: Regino Zamora. Accepted 21 March 2014

Flower visitation by birds in Europe

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Most flowering plants depend on animal pollination. Several animal groups, including many birds, have specialized in exploiting floral nectar, while simultaneously pollinating the flowers they visit. 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 known to visit flowers, and several reports of flower visitation by birds in this continent prompted us to review available information in order to estimate its prevalence. 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 prevalence of bird flower-visitation, and thus potential bird pollination, is slightly more common in the Mediterranean basin, which is a stopover to many migrant bird species, which might actually increase their effectiveness as pollinators by promoting long-distance pollen flow. We argue that research on bird pollination in Europe deserves further attention to explore its ecological and evolutionary relevance.

Animal pollination is a key process in the reproduction of almost 90% of the 352 000 flowering plant species that 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). The main pollinating bird families are the Trochilidae, Nectariniidae and Meliphagidae, but there are other important bird pollinators such as Icteridae, Thraupidae, Drepanidini, Promeropidae, Zosteropidae, Dicaeidae and Loriini, being present in all continents except Europe and Antarctica (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 from the Eocene and the Oligocene suggest that birds close to the Trochilidae once lived in central Europe (Mayr 2004, 2005, Louchart et al. 2008). The reason why these birds disappeared from Eurasia is still unclear (Mayr 2005). Given that flowers are such an ubiquitous and abundant resource, the apparent paucity of flower–bird visitation records in the literature suggests that it is an uncommon phenomenon (Ford 1985). However, 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; botanists, by contrast, are those reporting most bird–flower interactions as they are focused on the plants (Straka 1989). Nectar is the major floral reward for most flower visitors, but pollen, floral oil, petals, water and flower-visiting arthropods may also attract birds and other potential pollinators (Grant 1996, Cecere et al. 2011c). Indeed, non-specialized nectarivorous birds are known to efficiently pollinate plants around the world (Fang et al. 2012). Bird flower visitation has also been reported in Europe, including some confirmation of effective pollination (Ortega-Olivencia et al. 2005), although 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 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 consequently a relatively low number of interactions. However, this might

be more common in the Mediterranean region where biodiversity is higher. Finally, we foresee a higher use of floral resources in winter and early spring, i.e. in 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 literature to assemble all records of flower visitation by birds in Europe, using all information available until the end of 2013. 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 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 respectively. 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 Angiosperm Phylogeny Group III system (Stevens 2001 onwards). 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), 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 the 18th 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 searching for nectar (Darwin 1874). Until 1959 all records originated from direct feeding observations. J. S. Ash was the first to record interactions based on the identification of pollen grains on bird feathers (Ash 1959, Ash et al. 1961). The first suggestions that European birds could be actively mediating pollination date to 1969 when *Turdus merula* was 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 to be potentially 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 insects and the exclusion of birds reduces fruit-set (Cecere et al. 2011a).

A quantitative analysis of bird–flower visitation in Europe

Our data compilation of bird–flower interactions (Table 1) includes 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; Supplementary material Appendix 1 Table A1). This represents 9% of the total European avifauna, 22% of passerine species (Cramp 2006, Crochet and Joynt 2012), and 0.76% and 0.61% of the total European and native floras, respectively (Winter et al. 2009). These are certainly underestimates, considering the low taxonomic resolution of many records and that few European plants have been surveyed for bird visits. Overall, these reports document 243 different interactions between birds and plants. Of this, only six plant species are known to be effectively pollinated by birds (Búrquez 1989, Ortega-Olivencia et al. 2005, 2012, Cecere et al. 2011a).

We further searched in our dataset for records of European bird or plant species with flower visitation obtained outside Europe (Table 1). We detected 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*

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

All records	Bird species	Plant species	Interactions
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

without any record of flower visitation in Europe and also at least 12 different plant species (Supplementary material Appendix 1 Table A1). Furthermore, some long-distance migratory European passerine species show a regular nectarivorous behaviour in their African stopover sites during spring migration (Salewski et al. 2006, Cecere et al. 2010). Moreover, some Mediterranean – west European plant species, such as *Arbutus* sp. and *Ulex* sp., were found to be visited and possibly pollinated by birds in their exotic ranges, for example by honeyeaters in Australia (Ford 1985).

Geographic and temporal patterns

We evaluated the geographical and temporal distributions of the interactions for which such information was available. Records based exclusively on pollen attached to feathers or bills were not included in this analysis, 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%) were from the Mediterranean region (Table 1). Thus, as expected, flower visitation seems slightly more common in the Mediterranean basin where biodiversity is higher. Moreover, many interactions were recorded at the end of winter and beginning of spring making it difficult to separate both seasons. This led us to group both seasons, and as hypothesized most records were obtained during winter and spring (93%).

Ecological relevance of bird-flower interactions

As expected, the majority of the 50 flower-visiting bird species (46 in Europe and four from outside Europe) were trophic generalists, with flexible or opportunistic feeding habits that change throughout the year depending upon food availability (Cramp 2006). The most recorded bird flower visitors are included in Table 2, and belong mostly to the genus *Sylvia* (almost all European species visit flowers, but especially *S. atricapilla*, *S. borin*, *S. melanocephala*, *S. communis* and *S. curruca*), genus *Phylloscopus* (*P. collybita* and *P. trochilus*) and former genus *Parus* (*particularly C. caeruleus*). Most of these birds are mainly insectivorous or frugivorous, depending on the season. Typical granivorous bird species, particularly finches and sparrows, also visit flowers (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 of 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 which rarely visit flowers, such as *Muscicapa striata*, *Hippolais icterina*, *Erithacus rubecula* and *Saxicola rubetra*. Many studies have analysed several samples of feathers and faeces of these species and rarely found pollen in them (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, 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 perching, as opposed to specialized nectarivory birds, which normally hover in front of flowers (Fleming and Muchhala 2008). The only exceptions are the genus *Phylloscopus* and *Regulus* that can feed either while perched or hovering (Rodríguez-Rodríguez and Valido 2008, Ortega-Olivencia et al. 2012). While some species, such as warblers, mainly drink floral nectar and act as legitimate pollinators (Ortega-Olivencia et al. 2012), others such as finches and sparrows are mostly nectar robbers, often damaging flowers by tearing parts off the perianth or piercing holes to reach the nectar, without touching the flower reproductive structures (Búrquez 1989). Finally, some species as *C. caeruleus*, can be both legitimate and illegitimate visitors depending on the flower structure and position (Búrquez 1989, Fitzpatrick 1994). Even when flowers are damaged during a visit, many of them may still produce fruits (Swynnerton 1917). Other bird species, such as the *Phyrrula phyrrula*, are well known to eat flower buds. During this process, they may touch nearby open flowers and potentially transfer pollen between plants (these cases, however, were not included in our dataset).

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

Flower visitation seems to be more common during the early stages of an ecological succession, when annual plants and flowers are more abundant (Cecere et al. 2010). During their spring migration, at least *S. borin* and *S. communis* seem to prefer nectar to insects (Schwilch et al. 2001). This choice might be explained by the chemical content of nectar, i.e. water and simple sugars, being readily absorbed by the digestive tract of the birds, which is reduced during migration (Schwilch et al. 2001, Cecere et al. 2011c). Finally, handling time of flowers is shorter than that of insects, and flowers may also be easier to locate (Cecere et al. 2010, 2011c). Although *Cyanistes caeruleus* does not prefer nectar as its major food source, it is even able to select the most productive flowers (Fitzpatrick 1994). Finally, the low insect availability during winter and cold springs may force birds to feed on flowers.

The most common pollen grains found on European birds belong to the genera *Brassica*, *Citrus* and *Eucalyptus* (Ash et al. 1961, Laursen et al. 1997, Schwilch et al. 2001, Cecere et al. 2011b, Provost et al. 2012). Their flowers are

Table 2. Recorded interactions between the most common flower visitors and plants, the complete interaction matrix (× 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

Continued

Table 2. Continued.

Order	Family	Lower taxa	*Cyanistes caeruleus*	*Phylloscopus collybita*	*Phylloscopus trochilus*	*Sylvia atricapilla*	*Sylvia borin*	*Sylvia. communis*	*Sylvia curruca*	*Sylvia melanocephala*
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						

certainly among the most important to nectar-foraging birds. However, their importance for bird populations cannot be easily estimated, due to regional variation in flower, arthropod and seed abundances and in the incomplete sampling of this interaction type. While some bird-visited flowers have bird-pollination characteristics such as *Fritillaria imperialis* (Búrquez 1989, Peters et al. 1995), most have insect-pollination traits such as *Brassica* or wind-pollination traits such as *Quercus* sp. (Cecere et al. 2011a, b). Most plants reported do not require bird pollination, so it is expected that birds are the most benefitted in the interactions. The fact that almost one third of bird-visited plants are exotic and involved in approximately one third of the recorded interactions (Table 1), raises interesting ecological questions such as which is the role of these exotic plants to wintering and migrating bird populations, and how important birds may be for the pollination and subsequent expansion of these exotic plants. On the other hand, native plants visited by birds offer an equally stimulating research topic with evolutionary implications. It would be particularly interesting to know not only how many plant species are benefitting from birds, but also to what extent, and how important their flowers are to birds. Studies using a combination of methods, as direct observations and pollen load in birds, should be able to answer these and other ecological and evolutionary questions.

General remarks

Records of flower-visiting birds in Europe have been frequently considered to be rare and with reduced ecological relevance. This work shows that the relationship between birds and flowers is richer and more widespread than hitherto thought. European flower-visiting birds are mainly food generalists that may expand their food niche and explore flowers for nectar and other floral resources. Floral resources may be crucial to winter and spring migration survival, and the early reproductive phase of many bird species. Nearly one third of the plant species visited are exotic, and are involved in almost the same proportion of the total interactions, which might have important ecological implications. On the other hand, the bird–flower interaction with native flora is still poorly understood and likely has 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 (Yates et al. 2007). However, our understanding of the ecological relevance of bird–flower interactions in Europe is still in its infancy.

Acknowledgements – 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, Nickolas Waser and Vanessa Mata for all suggestions and corrections on the manuscript.

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Supplementary material (available online as Appendix oik.01347 at <www.oikosjournal.org/readers/appendix>). Appendix 1 (Table A1.xlsx: All recorded interactions between birds and flowers (× interactions).