

Blue tits, *Parus caeruleus*, as pollinators of the crown imperial, *Fritillaria imperialis*, in Britain

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It is proposed that the crown imperial (*Fritillaria imperialis* L.) is a plant pollinated by passerine birds in its native range. The high rate of secretion of sugar (up to 2.1 mg sugar h⁻¹ flower⁻¹), the nectar solute concentration (4–10% w/w), the absence of sucrose from the nectar, and the low amino-acid concentration, point to the passerine bird pollination syndrome. In Britain, this introduced plant is visited by blue tits (*Parus caeruleus* L.), and bumblebees. The fit of the birds in the flower, and the geometry of the flower, strongly suggests that this plant possesses morphological adaptations to ornithophily. This is confirmed by the fact that flowers visited by blue tits are efficiently pollinated and fertilized, while those visited only by insects, or isolated from visitors, do not produce fruits. This is probably the most northerly case of ornithophily yet reported.

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Introduction

Until the last decade there were no records of bird pollination in Europe (e.g., Proctor and Yeo 1973). Evidence of birds visiting flowers in Europe was collected by Ford (1985). He discussed the various hypotheses proposed to explain this apparent lack of passerine-bird pollination.

In Europe the idea that birds visit flowers to catch insects or to eat fleshy parts of the flowers, rather than to drink nectar, is much more deeply ingrained than in any other region (e.g., Lowe 1896, Swynnerton 1916, Campbell 1963). This situation is similar to that prevalent in Australia ca. 15 yr ago, when most ornithologists thought that honeyeaters visited the flowers to eat insects rather than to drink nectar (H. A. Ford, pers. comm.). The behaviour of birds visiting flowers or exploiting new sources of food, such as the sap of damaged trees (Mylne 1959, Soper 1969), or milk in bottles (Fisher and Hinde 1949, Hinde and Fisher 1952), has been described as novel or unusual (Thorpe 1956). From the point of view of a floral ecologist, the devel-

opment of new forms of search and the variation in the exploitation patterns are expected from a pollinator. Blue tits (*Parus caeruleus*) have been repeatedly recorded as flower visitors throughout Europe (e.g., Ford 1985, Kay 1985). They have been described as using a wide variety of habitats (Perrins 1979, Gibb 1954), and as resorting to new and unusual ways of foraging (Thorpe 1956, Fisher and Hinde 1949, Hinde and Fisher 1952).

In this study a relationship between blue tits and the crown imperial (*Fritillaria imperialis* L.) is described. Proof of the role of blue tits as pollinators, and evidence of a passerine bird pollination syndrome in the crown imperial, is offered. Finally, the role of birds visiting flowers in Europe is discussed.

Material and methods

The plant

The crown imperial (*Fritillaria imperialis* = *Imperialis coronata* Dum.-Cours; Liliaceae) is a stout erect plant

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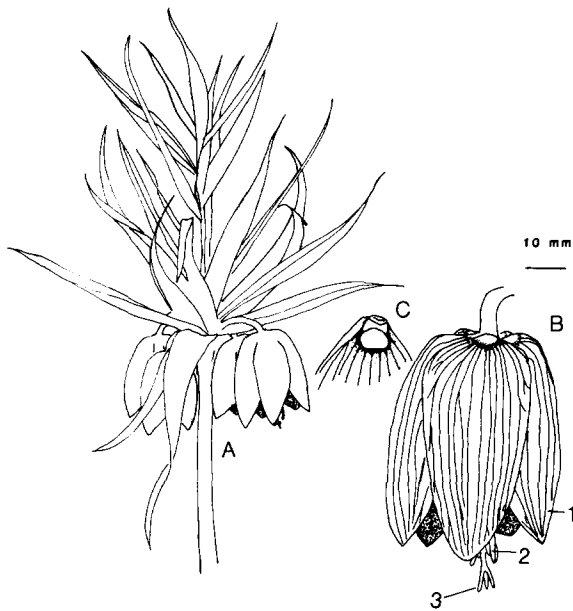


Fig. 1. Flower of *Fritillaria imperialis* L. A. inflorescence, B. 1. perianth segment, 2. anthers, 3. stigma, C. Internal view of a perianth segment showing the nectary.

whose distribution extends from the mountains of Turkey to the Himalayas. It is widely planted in gardens in the temperate world, particularly in Europe. It has long been known in cultivation. It even appears cited in a list of spring flowers in "A winter's tale" (Shakespeare 1623, in Rix 1971). Its ecology, taxonomy and horticultural properties are described by Beck (1953), Furse (1960) and Rix (1971). *F. imperialis* grows vigorously in early spring from underground bulbs. Rix (1971) reported that it takes at least 8 yr from germination to flowering. It has a strong odour, most noticeable in the bulbs, but present in most vegetative structures. A stem free of leaves in its median zone carries the flowers of *F. imperialis*. These are symmetrical with 6 large, thick perianth segments. The flowers hang from curved pedicels under a crown or dense whorl of leaves, well above the basal foliage (Fig. 1). The flowers are yellow or dark orange. Flower colour seems to be associated with the colour of the flowering stems and the time of flowering. Yellow-flowered plants flower relatively late, and have unpigmented stems. Each perianth segment bears a round nectary in a depression at its base (Fig. 1). Flowers last several (5–8) days, and are strongly protogynous. Although wasps and bumblebees have been invoked as pollinators of some species in this genus (Rix 1971, Rix and Rast 1975, Hedström 1983), the pollinators of *F. imperialis* are unknown. However, Porsch (1924), Vogel (1954), and Yeo (1972) deduced from morphological features of the flower that *F. imperialis* might be pollinated by birds.

In Cambridge, *F. imperialis* flowers from mid-April to

mid-May. The study plants were growing in the display and experimental areas of the Cambridge University Botanic Garden, and in private gardens around the city. The stands in the display area were well established, being in the same locations for many years. Observations were made throughout the whole flowering season in the spring 1986, 1987, and 1988. Records of visitors, nectar secretion and experimental pollination were made during at least 8 d in each year. In most cases observations lasted from 04 00 to 24 00 GMT.

Nectar measurements

Nectar was extracted with autoclavable flexible nylon tubing (Portex, Hythe, Kent). Nectar solute concentration was measured as sucrose equivalents on a weight per total weight basis with a Bellingham and Stanley pocket refractometer. Sugars were analysed by thin layer chromatography using Gelman plates (silica gel on fibreglass) run with chloroform/methanol 60/40 v/v, and visualised by spraying with aniline-diphenylamine (and later developing in an oven at 90°C for 10 min, see Lewis and Smith 1969). The amino acid content was assessed by liquid chromatography, comparing the retention times with a known sample of the 26 most common amino acids. To make my observations comparable with those of Baker and Baker (1973, 1983) the total amino-acid content was also evaluated by the histidine scale method.

Experimental pollinations

Flowers were bagged with fine bridal veiling from the bud stage. Two days after the flowers opened, when the stigmatic surface was exposed and moist, and the anthers were shedding pollen grains, several experimental pollinations treatments were performed: 1) Flowers were left bagged until the perianth segments were dry to test for auto-pollination (bagged controls). 2) Flowers were pollinated with their own pollen by means of a fine brush and then bagged again (self-pollinated). 3) Flowers were pollinated with pollen from at least four other plants and then they were bagged again (cross-pollinated). 4) Flowers were uncovered and left exposed until they had received one pollinator visit, and then covered again. When the perianth segments were dry and papery, the bags were removed. Fruit set was recorded on month later.

Results

Behaviour of visitors and flower morphology

The visitors observed comprised two bumblebee species (*B. ombus terrestris* (L.) and *B. lapidarius* (L.)) and three bird species (*Parus caeruleus* L. and two unidentified species of Fringillidae). The only species which fits the flowers, by its size, behaviour, and geom-



Fig. 2. Postures adopted by blue tits (*Parus caeruleus*), when visiting flowers of *Fritillaria imperialis*. Traced from photographs.

etry allowing the contact of anthers and stigma with the body, is *Parus caeruleus*. The other visitors fail to contact the anthers or stigma, because of their small size, or because of their illegitimate visiting behaviour. When visiting the flowers, blue tits perched on the main stem just below the overhanging flowers. They rapidly introduced their heads into the campanulate flowers to probe the nectaries at the base. In doing so, they contacted the anthers and stigma (Fig. 2). Several flowering stems were visited in this fashion in a single bout. On very rare occasions insects other than bees were seen inside the flowers, visits to the flowers were obviously made to drink the nectar. Nectar standing crop was

lower in flowers recently visited by blue tits. However, the disparity between the density of birds and flowers made impossible both the evaluation of the quantity of nectar ingested in each visit, and the rates of visit to individual flowers. In the Botanic Garden, three large clumps were monitored. Birds were seen visiting flowers within a clump, and then flying to other clumps or nearby trees. The visits by birds began in the morning (after 0700 GMT), and persisted with discrete bursts of activity throughout the day. The other birds, probably finches, were seen perching on top of the flowers, tearing apart the perianth segments, or piercing holes to reach the nectaries from outside the flower. This behaviour did not lead to pollination because the bird never contacted the reproductive structures of the flower. Moreover, once a flower nectary was damaged, its nectar secretion decreased dramatically (usually secretion stopped completely).

Nectar composition

The presence of abundant, dilute nectar has been associated with plant pollination by vertebrates. In *Fritillaria imperialis*, the quantity and the concentration of nectar have the values expected from passerine bird pollinated plants (a secretion rate of up to 2.1 mg sugar h⁻¹ flower⁻¹, 4–10% nectar solute concentration as sucrose equivalents by weight, and a nectar standing crop volume up to 4–8 ml flower⁻¹ [Búrquez 1988]). The nectar of *F. imperialis* is mainly a mixture of glucose and fructose; sucrose is absent. My results regarding the composition of sugars in the nectar agree with the findings of Percival (1961, 1965) and Rix and Rast (1975).

Both colour morphs show a relatively small amino acid total content and range (Tab. 1). The main amino acid was aspartic acid. Strong differences were detected between the yellow and red morphs, notably the absence of phenylalanine, isoleucine, leucine, and histidine in the yellow flowers. This difference is most marked in the case of histidine which is the second major constituent of the red morphs. To make the scores comparable with those proposed by Baker and

Tab. 1. Amino-acids in the nectar of *Fritillaria imperialis* in mg·l⁻¹. The letters Y and R followed by a number indicate independent samples from the yellow and red phenotypes respectively. The dash indicates aminoacids not detected in the sample.

Amino-acid	Y1	Y2	Y3	R1	R2	R3
Asparagine	–	–	9.44	45.36	15.20	21.54
Arginine	26.50	55.20	17.84	44.00	63.98	40.00
Aspartic acid	150.46	255.80	87.42	159.06	275.40	167.06
Glutamic acid	1.56	4.00	2.88	17.82	6.74	8.32
Alanine	–	2.30	–	4.68	19.28	2.90
Phe+Iso+Leu	–	–	–	9.43	81.46	68.00
Ornithine	–	5.18	1.16	6.08	8.62	7.32
Histidine	–	–	–	104.78	189.32	123.40
Lysine	3.84	13.12	2.94	3.62	6.36	2.26

Tab. 2. Analysis of variance for the total amino-acid content in red and yellow flowers of *Fritillaria imperialis*. Nectar solute concentration is due to the sugars in solution in the nectar.

Source of variation	SS	DF	MS	F	P
Covariates:					
nectar solute concentration	46.78	1	46.78	19.85	0.001
Red vs yellow flowers	4.69	1	4.69	1.99	0.184
Explained	51.47	2	25.73	10.92	0.002
Residual	28.28	12	2.36		
Total	79.75	14	5.70		

Baker (1973, 1983), the total amino-acid content was also evaluated by the histidine scale technique. Scores of 4–5 for the yellow morphs and 6–7 for the red morphs were obtained. There were significant differences in total amino-acid concentration between the red and yellow morphs, but when total nectar solute concentration (mainly sugars) was used as a covariate in the analysis of variance, these differences disappeared (Tab. 2). Hence, the amino-acid concentration as a percentage of total nectar solutes did not differ significantly between morphs.

Breeding system and pollinator effectiveness

Experimental pollination treatments showed that blue tits were the only visitors capable of pollination. Flowers covered from the bud stage with bridal veiling bags, and then only visited by blue tits produced a high fruit-set. Contrastingly, no fruit was produced by flowers isolated from the bud stage, or pollinated with their own pollen, or visited only by bumblebees (Tab. 3).

Discussion

Several traits of nectar quality and composition have been associated with passerine-bird pollination. The ab-

sence of sucrose from the nectar has been correlated with pollination by passerine birds (Baker and Baker 1975, 1982, 1983, Freeman et al. 1983a, Lammers and Freeman 1986). This correlation is now supported by experimental evidence indicating that passerine birds are very inefficient at degrading sucrose when compared with hummingbirds (Karasov et al. 1986, Martínez del Río et al., in press). It is remarkable that *F. imperialis* is the only species in this genus reported to have a nectar devoid of sucrose (Percival 1961, 1965, Rix and Rast 1975, among 34 species studied). This single trait is a strong indication of its passerine-bird patronage.

The amino-acid content of the nectar in bird pollinated plants has been found to be lower than that in nectars of entomophilous plants (Baker and Baker 1973, 1983). The number and concentration of amino-acids in the nectar of *F. imperialis* is low. The absence of cistic acid, taurine, proline, gamma amino-butyric acid, cystine and threonine is remarkable. All of these have been reported for species pollinated by bats and passerine birds (Baker and Baker 1975, 1986, Cruden and Toledo 1977, Freeman et al. 1983b, 1985). However, arginine, histidine and aspartic acid, the most important constituents of the nectar of *Fritillaria*, are among the most important amino-acids found in the nectar of plants (e.g., Baker and Baker 1983). The total amino-acid scores on the histidine scale are similar to the values reported for bat and passerine-bird flowers (Baker 1978, Baker and Baker 1983, Freeman et al. 1983b).

Although birds are known to visit flowers in Europe, they are not known to pollinate them. Bird pollination involves an interaction between a nectar-seeking bird and a flower with such a geometrical arrangement of parts to allow pollination by birds.

Birds whose diet is dominated by nectar are generally confined to regions where the climate permits nectar-feeding in all seasons (usually by local altitudinal migrations), or they penetrate northern latitudes only as summer migrants (e.g. several hummingbird species in North America). The bird fauna of northern Europe lacks such specialists, but does include species that visit

Tab. 3. Percentage fruit set and absolute number of fruits produced after different pollination treatments in *Fritillaria imperialis*. *Parus* and *Bombus* treatments refer to flowers bagged from the bud stage, briefly exposed when receptive, and bagged again after a visit by *Parus caeruleus* or *Bombus* spp., respectively. The different letters after the treatment indicate groups with similar characteristics.

Treatment		Number of flowers in which fruits were:		Percentage fruit set	N
		Produced	Not produced		
Bagged control	a	0	10	0	10
Self-pollinated	a	0	10	0	10
<i>Bombus</i>	a	0	6	0	6
<i>Parus</i>	b	4	3	57	7
Cross-pollinated	b	7	3	70	10

flowers for nectar occasionally. These are (or are closely related to) migrant species that visit flowers more regularly in the Mediterranean or in Macaronesia. It appears that such common birds as *Sylvia* spp., *Phylloscopus* spp., and *Parus* spp. have been studied by naturalists much more in their northern summer locations, where they are mainly insectivorous, than in their winter retreats, where they seem to be at last partly nectarivorous (e.g., Thake 1980, Cortés 1982).

It has been shown that some Sylviidae and other species arrive in Britain in spring carrying large pollen loads of *Citrus* and other south European flowers (Ash 1959, Ash et al. 1961). Observations of birds visiting flowers in Europe extend well into the past. In many instances, blue tits and other passerine birds have been noted in Europe as nectar robbers (Ludwig 1897, Swynerton 1916, Yeo 1972). However, many birds are remarkable in visiting a large number of plant species for their nectar, without causing any visible injury to the flowers (Gibb 1954, Campbell 1963, England 1969, Visik 1977, Laursen 1978, Perrins 1979, Thake 1980, Cortés 1982, Holm and Laursen 1982, Garcia in Ford 1985, Kay 1985; see also citations in Tab. 1 in Ford 1985). One of the common names of some *Phylloscopus* spp. (particularly *P. collybita*) in Spain is 'picaflores', referring to their flower visiting habit (Peñas et al. 1984). Also, many birds in Britain take honey readily (Soper 1969), or drink the sap of trees (Mylne 1959). Although some authors have suggested that birds, in northern Europe at least, visit flowers searching for insects (Lowe 1896, Campbell 1963), the evidence shows overwhelmingly that their main goal is the search for nectar. Moreover, it has been shown that the tongue of warblers (Sylviidae) is remarkably similar to that of obligate nectarivorous birds such as the hummingbirds (Holm and Laursen 1982). It is likely that after the glaciations, some partly nectarivorous birds returned to Europe (and still do so, see Järvinen and Ulfstrand 1980), but the plants they visited did not. In the Canary Islands where the glaciations had little impact, several plant genera have been positively identified as ornithophilous (Vogel 1954, Yeo 1972, Vogel et al. 1984, Olesen 1985). Also, in Madeira, the endemic genus *Muschia* seems to be ornithophilous (particularly *M. wollastoni*, according to Vogel 1954, although Elvers (1978) noted that *M. aurea* is visited by lizards).

In the native flora of temperate Europe, ornithophilous flowers are absent, perhaps because of failure of post-glacial reinvasion (see Ford 1985). In the garden flora of this region, ornithophilous flowers are numerous, but most are long-tubed hummingbird or sunbird flowers, which short-billed native birds cannot pollinate. The cultivated ornithophilous flowers with an open corolla would be accessible to native bird species. I have shown that *Fritillaria imperialis* belongs to this category. It will be interesting to see if native birds can also exploit other passerine-bird flowers grown in gardens in Europe.

In so far as nectar feeding is opportunistic rather than obligate for birds in Europe, it parallels other opportunistic feeding habits such as the opening of milk bottles and the opportunistic use of milk as a resource by tits (Fisher and Hinde 1949, Hinde and Fisher 1952). For a nectarivorous bird a reward in the nectary of a flower is comparable with that in a milk bottle; both rewards are hidden, and learned is involved in their capture. Opportunistic foraging behaviour by blue tits is, in this case, comparable to the use of floral resources by small generalist lizards that become herbivorous for a short time when easily digestible flowers are available (Búrquez et al. 1986).

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