Journal of Pollination Ecology, 23(9), 2018, pp 82-89

SPECIALIST NECTARIVOROUS BIRDS (*CINNYRIS OSEA*) STEAL NECTAR WHEREAS OMNIVOROUS BIRDS ARE POLLEN TRANSFER VECTORS OF *ANAGYRIS FOETIDA*

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Abstract—The ornithophilous *Anagyris foetida* is almost the only shrub in the eastern Mediterranean region that flowers in winter. We assessed the pollination potential of flower visitors by observing pollen loads on trapped animals and contacts with floral parts. Resident and wintering omnivorous bird species, together with honey bees (*Apis mellifera*), were found to carry the shrub's pollen throughout its long flowering period in Israel and thus might be legitimate pollinators. Spring-migrating omnivorous birds passing through Israel carried pollen. The Palestine Sunbird (*Cinnyris osea*) is the only specialist nectarivorous bird in the Middle East. It carries little pollen and is therefore primarily a nectar thief of *A. foetida*.

Keywords: Anagyris foetida, Palestine Sunbird, legitimate pollination, nectar theft, Mediterranean forest, Honeybees

INTRODUCTION

Mutualism between plant and pollinators occurs when the plant benefits from the pollinator's transport of pollen grains and the pollinator benefits from a food source in the form of nectar and/or pollen. Previous studies showed that specialized nectar-feeding birds have several morphological characteristics that enable them to feed efficiently and to act as legitimate pollinators of flowers with compatible morphologies. Characteristics of bills and tongues influence the speed and efficiency with which nectar is extracted from flowers, whereas body mass and the length and shape of the wings and legs influence the speed, efficiency and method of movement between flowers, and the techniques of perching or hovering (Collins & Paton 1989; Paton & Collins 1989; Geerts & Pauw 2009; Myers et al. 2010). On the other hand, morphological mismatch between the flower and visitor can lead to nectar theft, which is the consumption of nectar from flowers without contributing to its pollination (Inouye 1983; Irwin et al. 2010). Also, a growing array of research provides evidence of non-specialist nectar-feeding birds, typically passerines, that serve as pollen transport vectors, both in Europe and the Middle East (e.g., Valido et al. 2004; da Silva et al. 2014; Cecere et al. 2011) and more globally (e.g., Ragusa-Netto 2002; Kunitake et al. 2004; Johnson & Nicolson 2008; Fang et al. 2012).

Anagyris foetida is a leguminous shrub or small tree, deciduous in summer, with a Mediterranean and Irano-Turanian distribution (Valtueña et al. 2008). In Spain it is pollinated by three species of Passeriformes (Ortega et al. 2005; Valtueña et al. 2007; Valtueña et al. 2008). It is not uncommon to find ornithophily in Fabaceae, although the family is mainly bee-pollinated (Stone et al 2003; Tandon et al. 2003; Ragusa-Netto 2002; Arroyo 1981). Its flowers show typical ornithophilous attributes, such as diurnal anthesis, no odour, showy corollas, pseudo-tubular flowers with copious nectar located at the base of the floral tube, hard protective tissues surrounding the ovary and other flower organs and pendulous flowers (Faegri & Pijl 1979; Proctor et al. 1996; Ortega et al. 2005; Willmer 2011). The flowers copiously produce pollen and dilute nectar. Plants are self-compatible, and selfing may occur via geitonogamy or vector-facilitated self-pollination may occur, although the level of fruit production is generally higher after outcrossing (Ortega et al. 2005). *Anagyris foetida* has adaptations that can be found in autumnal and winter-flowering species, such as long exposure of flowers and ecologically generalized pollination system, which allow for the simultaneous use of floral resources by unrelated pollinators (Dafni 1996; Olesen & Jordano 2002; Galloni et al. 2008; Padyšáková et al. 2013).

Anagyris foetida pollination has not previously been studied in the eastern Mediterranean, where climate, diversity of bird species, and subspecies of other bird species differ from those in Spain. The shrub occurs in the central and northern parts of Israel and flowers from mid-November to mid-March (Shmida 2005).

Sunbirds are a group of obligate nectar-feeding birds that can act as pollinators or thieves when consuming nectar from different plant species (Coombs et al. 2007; Coombs & Peter 2009; Padyšáková et al. 2013). Sunbirds generally perch while extracting nectar from flowers (Collins & Paton 1989). The Nectariniidae family is one of the major groups of pollinating

Received 28 August 2017, accepted 19 March 2018
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birds in Africa and Asia (Cronk & Ojeda 2008; Da Silva et al. 2014).

The Palestine Sunbird (*Cinnyris osea*) is the only member of the Nectariniidae that occurs in the Mediterranean. Its world distribution includes the west Arabian Peninsula as far as Yemen, Israel, Jordan, Lebanon, and Syria. In Israel, it had a very limited distribution within the Syrian-African Rift Valley until the 1940's. Following the urbanization and development of agriculture and domestic gardens in the last century, Palestine Sunbirds spread out all over Israel (Yom-Tov 2014). In late autumn and winter, the sunbirds tend to wander away from their breeding habitats to look for food sources (Hadoram 1976; Cheke & Mann 2010). The maximum distance record of a recaptured sunbird is 109 km from Jerusalem to Megadim (Israeli Bird Ringing Center Database, IBRC Code: IL007/16). The sunbirds' tendency to wander explains the relatively recent encounter with *A. foetida* flowers.

Cinnyris osea is a small bird weighing 6-7 grams, with a long, curved bill measuring 16-18 mm and a typically long tongue split at the end to enable nectar consumption (Yom-Tov 2014). The Palestine Sunbird is known to be either a pollinator or a thief (Eisikowitch & Nahari 1982; Vaknin et al. 1996; Tadmor et al. 2004). It usually feeds from a perching position and only occasionally while hovering. Apart from nectar, it eats insects and spiders, especially during the breeding season. This bird is a potential pollinator of *Loranthus acaciae* and might be its only pollinator in winter (Vaknin et. al 1996).

In winter and early spring, omnivorous birds can also be found in the Mediterranean forest. These include resident, wintering, and transient species of various families, including the Sylviidae, Turdidae, Pycnonotidae, Fringillidae and Passeridae.

This study evaluates the likely relative effectiveness of specialist sunbirds and omnivorous birds as pollinators of *A. foetida*.

MATERIALS AND METHODS

Study Areas

We studied two populations of native *A. foetida,* 17 km apart. Both were located in the Judean Plain: Ella Valley (31°40'58" N, 14°00'34" E), 290 m above sea level, and Hulda (31°49'14" N, 21°33'34" E), 120 m above sea level. In Ella Valley, ca 90 individuals of *A. foetida* are part of the Mediterranean shrub vegetation, spread across an area of ca 3 ha. In Hulda, ca 1000 individuals dominate an area of 5 ha. The average annual rainfall in Ella Valley and Hulda is 402 mm and 492 mm, respectively. In both study areas, the range of temperatures in winter is -4°C to 30°C but on only 10% of the days during winter did high temperatures remain below 14 °C. The average high temperature was 19.18 °C ± 4.54 SD and 19.49 °C ± 4.38 SD in Ella Valley and Hulda, respectively. Both study areas support honey bee hives. The Ella Valley study area is also subjected to grazing livestock in spring and summer.

Video recordings

Sunbirds start foraging on *A. foetida* at dawn, concentrating on the upper parts of the plants. Video recordings were done by an observer from a distance of ca 4 m with a high-definition video camera (HC-W850 Panasonic) mounted on a tripod. The video recordings were analysed according the following criteria: time spent on individual flowers, the perching position above or bellow the flower, and whether the bird opened the keel in the foraging process.

Pollen loads on the birds

Mist nets were erected in very close proximity to *A. foetida* bushes. Birds of all species were mist netted in compliance with the Israeli Bird Ringing Center (IBRC) regulations in order to check pollen loads on their bodies. Twenty-four ringing sessions (9 in Ella Valley and 15 in Hulda), were conducted between 3.12.2016 and 10.03.2017. Each session used on average 120 m of net and ran for four hours from dawn. All the birds were identified and ringed, and weight, wing length, age and sex were recorded. An adhesive transparent strip (cellotape) of 4 cm² was applied to the parts of the body on which the pollen could be transported: throat, forehead and bill, and then stuck onto a microscope slide. All the pollen grains that were identified as *A. foetida* were counted under the microscope. Levels of pollen load were evaluated from 0 to 3 whereby: 0 = no pollen grains; 1 = < 10 pollen grains; 2 = < 40 pollen grains; and 3 = > 200 pollen grains.

Bees

Honey bees' (*Apis mellifera*) foraged on *A. foetida* flowers only when temperatures were higher than ca 14°C (Joshi & Joshi 2010; Abou-Shaara et al. 2012). Three parameters were recorded while visiting an individual flower: duration of flower visits, pollen or nectar collection, and success or failure in opening the keels of the flowers. The honeybee visits were observed by eye from 20–50 cm. Some video recordings were taken as well.

RESULTS

Phenology

Anagyris foetida flowers bloomed from the last week of November 2016 until mid-March 2017 (Fig. 1). Three resident bird species (Palestine Sunbird (*Cinnyris osea*), Sardinian Warbler (*Sylvia melanocephala*), White-spectacled Bulbul (*Pycnonotus xanthopygos*)) and three wintering species Blackcap (*Sylvia atricapilla*), Chiffchaff (*Phylloscopus collybita*), Spanish Sparrow (*Passer hispaniolensis*)) were present throughout the flowering period of *A. foetida* (Fig. 1). Four migrant species (Common Whitethroat (*Sylvia communis*), Lesser Whitethroat (*Sylvia curruca*), Ruppell's Warbler (*Sylvia rueppelli*), Orphean Warbler (*Sylvia crassirostris*) were present only from mid-February onward. All ten of these species were also observed foraging on the plant.

The arrival of sunbirds to the research sites preceded anthesis by ca two weeks (e.g., the first catch of sunbirds in

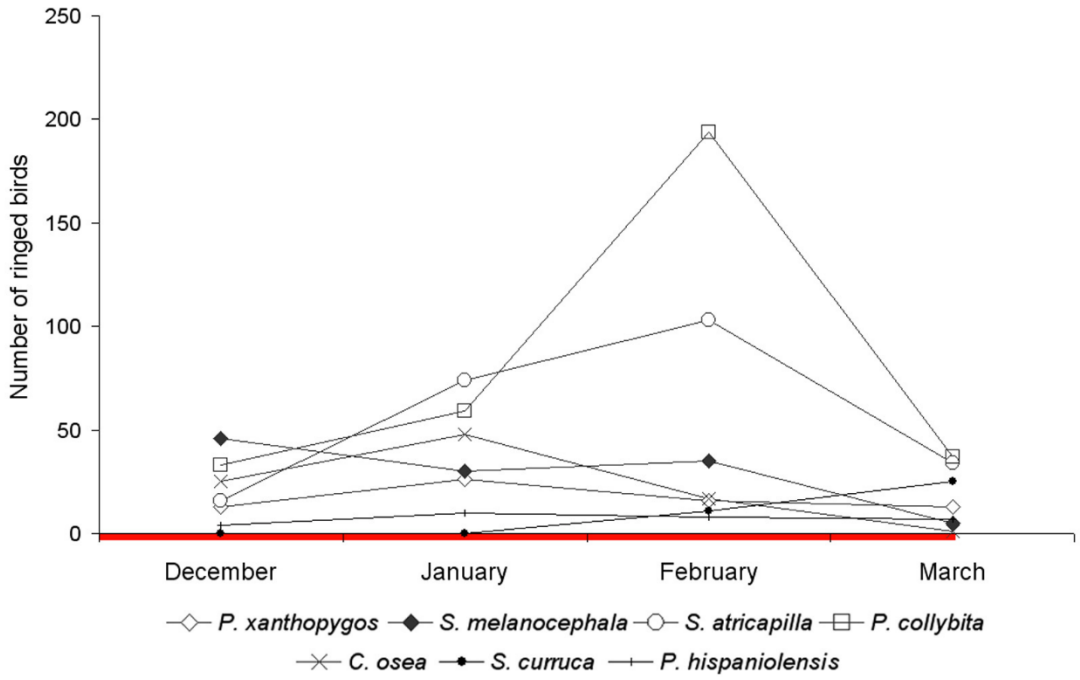

FIGURE 1: Birds presence during the flowering season of *A. foetida*, 2016/2017. (In red the flowering period of *A. foetida*)

FIGURE 2: Downward (A) and upward (B) approaches of Palestine Sunbird to *A. foetida* flower

Ella Valley was 18 November 2014, 23 November 2015, 1 December 2016). A sharp decline in the presence of sunbirds at the research sites occurred in mid-February.

Foraging behaviour of sunbirds on A. foetida

297 different visits of Palestine Sunbirds to *A. foetida* flowers in 18 different sessions were recorded. The birds did not hover but perched on the branches to collect the nectar. In 235 visits (79.12%), the birds approached the flower from above, inserting their bills between the short standard and the wings, elevating the angle of the flower to ease nectar consumption. After the visit, the flower parts returned to their original position (Fig. 2A). In 62 visits (20.88%), the sunbirds approached the flowers from below following the same procedure (Fig. 2B). 26 visits (8.75%) were recorded to flowers with apparently high level of nectar. The time spent consuming nectar from these flowers was 3.86 sec ± 1.04 sec SD. All other visits were much shorter (ca 0.5 sec), probably to flowers having less nectar or none at all.

When young, *A. foetida* flowers are closed, green-yellowish and their keel has two blackish spots. After anthesis the flowers open and become yellow with reddish-black spots (Valtueña et al. 2008, Ortega et al. 2005). The sunbirds bypassed all yellow flowers with reddish spots on the standard and with open keels. Instead, they nectar in the greenish flowers, of which most had closed keels. The sunbirds did not make any visible contact with the anthers or stigmas

Pollen load

Pollen loads were sampled from 643 birds from 10 species: 3 resident, 3 wintering and 4 "pure" migrating species (Table 1A and Fig. 3). The Palestine Sunbird and Chiffchaff only rarely carried substantial amounts of pollen. The Blackcap, Bulbul and Sardinian Warbler were quite often found to carry large amounts of pollen grains (level 3 in Table 1A). The migrating birds, which appeared at the research sites only at the end of the flowering season, were often found with large amounts of pollen grains (level 3 in Table 1A). The

TABLE 1: (A) Level of pollen load found on different bird species. (B) Level of pollen load found on recaptured birds. (Pollen load: 0 = 0 pollen grains, 1 = < 10 pollen grains, 2 < 40 pollen grains, 3 > 200 pollen grains)

(A)

Species	N	Status	0 load	1 load	2 load	3 load	% 2+3 load	% 3 load
Blackcap (*Sylvia atricapilla*)	209	wintering	29	4	9	167	84.2	79.9
Chiffchaff (*Phylloscopus collybita*)	144	wintering	123	17	2	2	2.7	1.4
Common Whitethroat (*Sylvia communis*)	11	migrating	4	1	0	6	54.5	54.5
Lesser Whitethroat (*Sylvia curruca*)	35	migrating	15	0	0	20	57	57
Orphean Warbler (*Sylvia crassirostris*)	4	migrating	1	0	1	2	75	50
Palestine Sunbird (*Cinnyris osea*)	90	resident	60	23	5	2	7.7	2.2
Ruppell's Warbler (*Sylvia rueppelli*)	2	migrating	0	0	0	2	100	100
Sardinian Warbler (*Sylvia melanocephala*)	82	resident	20	3	2	57	71.9	69.5
Spanish Sparrow (*Passer hispaniolensis*)	14	wintering	10	0	1	3	28.5	21.5
White-spectacled Bulbul (*Pycnonotus xanthopygos*)	52	resident	5	1	4	42	88.5	80.7

(B)

Species	N	0 load	1 load	2 load	3 load	% 2+3 load	% 3 load
Blackcap (*Sylvia atricapilla*)	30	1	0	2	27	96.6	90
Chiffchaff (*Phylloscopus collybita*)	34	30	4	0	0	0	0
Lesser Whitehroat (*Sylvia curruca*)	3	0	0	0	3	100	100
Sardinian Warbler (*Sylvia melanocephala*)	33	3	2	1	27	84.8	81.8
White-spectacled Bulbul (*Pycnonotus xanthopygos*)	5	0	0	0	5	100	100

Spanish Sparrow can be regarded as an occasional carrier of pollen grains.

Recaptures

Some birds did not carry pollen grains the first time they were captured. We assumed that they were new arrivals to the research area. After getting familiar with the *A. foetida* flower, these birds began consuming its nectar and were found to carry pollen grains the second time caught (Table 1B). Only recaptures between ringing sessions are included in Table 1B. Apart from the Chiffchaff, birds from each species were found to have more pollen on average on the second capture. No Palestine Sunbird was recaptured.

Honeybees

190 visits of Honeybees to *A. foetida* flowers were recorded in both study sites when the ambient temperature between 10:30 and noon was 15–20°C. In 167 visits (87.9%) they tried to open the keels of the flowers, indicating that they were seeking pollen (Fig. 4). The average time they spent on a flower was 8.91 ± 6.81 sec (range of 2-29, $N = 78$) if they failed to open the keels and 19.51 ± 14.33 sec (3-70, $N = 78$) if they succeeded. Alternatively, 12.1% of the bees appeared to be seeking nectar only; these inserted their heads under the standard.

DISCUSSION

If an animal picks up pollen from one flower and its body is adapted for pollen transport to the stigma of another flower of the same species, it can be regarded as a true pollinator (Ortega et al. 2005). In order to extract nectar in a legitimate way from the fabaceous flower of *A. foetida,* a bird has to insert its bill into the flower under the short standard and into the pseudo-tubular perianth all the way into the hypanthium.

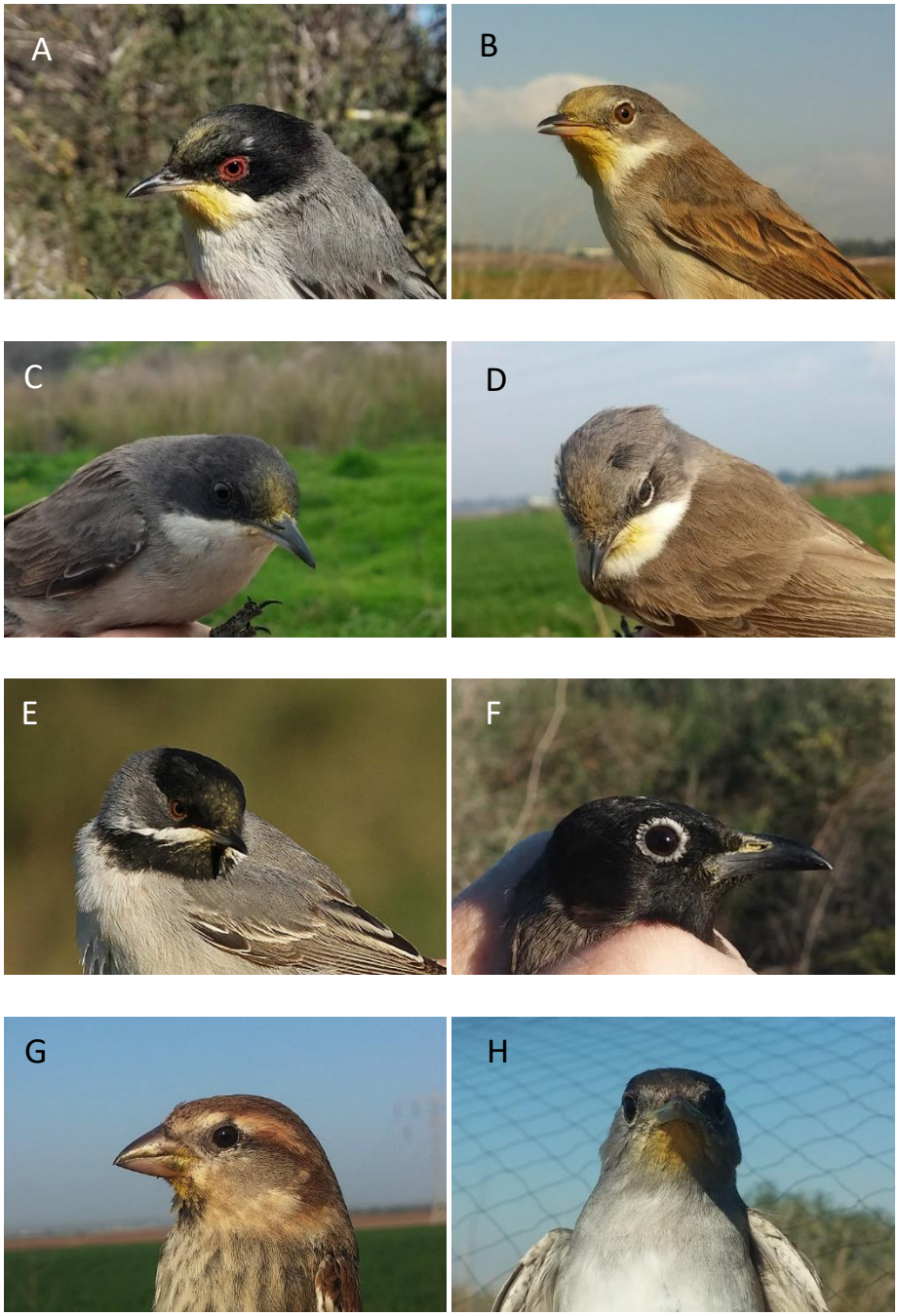

FIGURE 3. Pollen of *A. foetida* on feathers of (A) *Sylvia communis,* (B) *Sylvia melanocephala,* (C) *Sylvia crassirostris,* (D) *Sylvia curruca,* (E) *Sylvia rueppelli,* (F) *Pycnonotus xathophygos*, (G) *Passer hispaniolensis,* (H) *Sylvia atricapilla*

When legitimate visitors enact such a visit (Fig. 5), their head or throat touches the closed keel and opens it (Ortega et al.2005). In a successful pollination visit to *A. foetida* (Valtueña et al. 2008), two major events occur: 1. the stigma cuticle is ruptured, which is necessary to allow pollen germination 2. pollen is deposited on the bird's feathers.

The presence of pollen grains was easily observed with the naked eye on the bird's forehead, throat or bill (Fig. 3.) Captured birds frequently carried thousands of grains (level 3 in Table 1A). We consider a species to be a major potential pollinator if it fulfils the following criteria: 1. the species was present in the field in large numbers (can reach over 10 birds per ringing session) during major periods of the flowering season; 2. Over 70% of the species' individuals were found to carry large amounts (level 2 and level 3) of pollen on their feathers. Of the ten bird species sampled (Table 1A), only the Blackcap and the Sardinian Warbler meet these criteria as major potential pollinators of the *A. foetida*.

Palestine Sunbird

The bill length of *C. osea* (16-18 mm) is longer than the tubular structure of the *A. foetida* flower (ca 10 mm). Warblers' bills are shorter than those of *C. osea*: 13 mm for

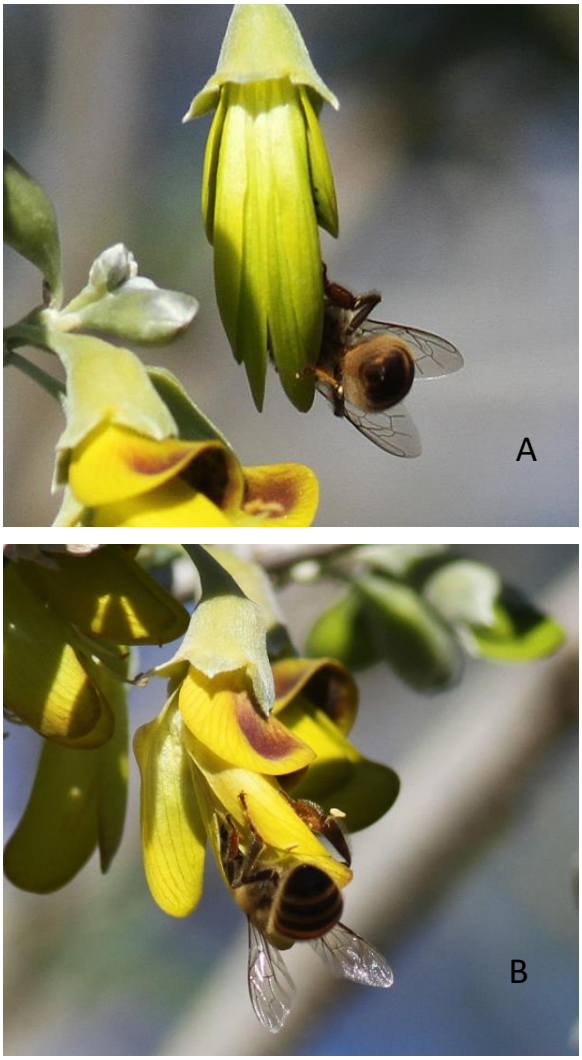

FIGURE 4. Honey bees foraging pollen of *A. foetida*. (A) Trying to open the keel. (B) Inside the keel.

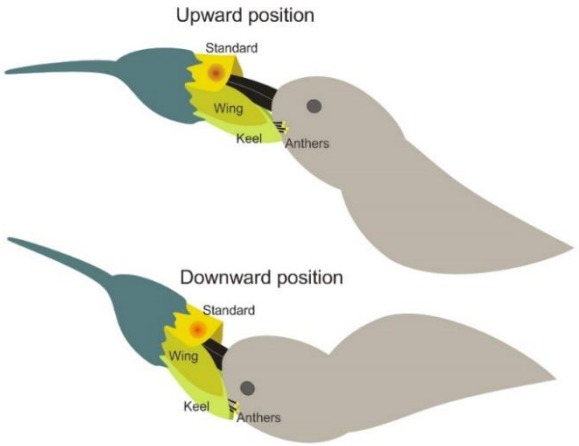

FIGURE 5. Diagram of downward and upward legitimate approaches of pollinating birds to *A. foetida* flower.

S. curruca, 14.7 mm for *S. atricapilla*, 14.3 mm for *S. melanocephala* (Hadoram et al. 2001). Video recordings of sunbirds foraging for nectar in *A. foetida* flowers show that the bird usually inserts its bill in the proper position to collect nectar without damaging the flower tissues. But, due to its long and curved bill, it does not touch the keel from either perching positions (Fig. 2). Only two netted Palestine Sunbirds (2.2% of trapped sunbirds) showed high amounts of pollen grains (level 3 in Table 1A). Thus, only rarely does it act as a pollinator in carrying pollen grains on its feathers or bill. Therefore, our study showed that, despite being the most specialized nectar feeder, Palestine Sunbirds are primarily nectar thieves of *A. foetida*.

The immense quantity of flowers—which can reach over 100,000 flowers for the season on an individual plant of *A. foetida* (Valutena et al. 2008)—and the large quantity of daily nectar production— that can reach over 40 µl per flower (Ortega et al. 2005)—are an ideal combination of features for foraging sunbirds (Wolf et al. 1975).

The role of omnivorous birds as pollen transport vectors

The omnivorous, all-year resident and wintering, bird species were present in the research area throughout the flowering season of *A. foetida* (Fig. 1). In autumn and winter (October–March) these birds rely almost entirely on fleshy fat-rich fruits and play an important role as seed dispersers of western and eastern Mediterranean plants (Herrera 1995; Izhaki 2002). Nectarivory by non-nectarivorous species is observed when resources such as insects, fruits or seeds are in short supply and nectar is abundant, e.g., during winter or early, cold springs (Valido et al. 2004). We found heavy pollen loads on foreheads, throats, or bills of these birds, indicating a high probability of successful pollination of *A. foetida.*

The White-spectacled Bulbul is a resident generalist species seen in groups of up to five birds in both research areas. *Anagyris foetida* pollen grains were found mainly on its bill and forehead (Fig. 3). As in the case of the Chinese Bulbul (*Pycnonotus sinensis*) (Fang et al. 2012) and the Red-whiskered Bulbul (*Pycnonotus jocosus*) (Olesen et al. 1998), the White-spectacled Bulbul was seen both consuming flower parts and inserting its bill in the proper position. More than 80% of trapped birds carried a large amount of pollen grains (Table 1A) and thus can be considered a potential pollinator.

Two subspecies of Sardinian Warblers, *S. m. momus* and *S. m. melanocephala* (local breeding and wintering/migrating, respectfully), were present in the research areas throughout the flowering season and bore pollen on both their foreheads and throats. We suggest that there are high chances that this species is a pollinator of *A. foetida* as approximately 70% of the birds were caught with high levels of its pollen grains (Table 1A) and more than 80% of recaptured birds had high levels of its pollen grains (Table 1B). *S. melanocephala* was also found to be nectar feeding from, and an effective pollinator of, *Isoplexis canariensis* in the Canary Islands (Rodrigues & Valido 2008).

Among the wintering species, only the Blackcap (*Sylvia atricapilla*) could be regarded as a major potential pollinator. 80% of the trapped birds carried a considerable amount of pollen grains on both their foreheads and throats (Table 1A)

and had a high likelihood of touching the stigma (Fig. 3). Blackcaps were abundant throughout the flowering season. Recaptured birds carried a high amount of pollen grains in 90% of the cases (Table 1B). The Blackcap was found to visit *Isoplexis canariensis* and *Musschia wollastonii* Lowe flowers for nectar in Macronesia (Valido et al. 2004).

The Chiffchaff (*Phylloscopus collybita*) was caught in large quantities throughout the flowering season, but fewer than 2% carried substantial amounts of pollen grains (Table 1A, Table 1B). Chiffchaffs might best be regarded as non-pollinating visitors of *A. foetida* in Israel, where the weather might enable it to rely on its regular insect diet without consuming nectar.

The Spanish Sparrow (*P. hispaniolensis*) was seen and caught rarely, and only ca 20% (Table 1A) carried large amounts of pollen grains of *A. foetida* on their throats and bills (Fig. 3). It can be concluded that this species might be an occasional pollinator of this plant. This species was found pollinating introduced bird flowers such as *Strelitzia, Hibiscus*, *Aloe*, *Nicotiana* and *Agav*e in Macaronesia (Valido et al. 2004).

Migrating birds

Various studies have already shown that many migrating birds are looking for nectar as an easy, energetic resource. They may act as pollinators in the process (Schwilch et al. 2001; Salewski et al. 2006; Cecere et al. 2011; Da Silva et al. 2014).

The beginning of spring migration coincided with the end of the flowering season of *A. foetida*. In the overlapping period, four species of migrating warblers were trapped with *A. foetida* pollen grains on their feathers (Fig. 3): Lesser Whitethroat, Common Whitethroat, Orphean Warbler and Ruppell's Warbler (Table 1A). The Lesser Whitethroat was more common than all the other migrating species. Pollen was found on both its forehead and throat (Fig. 3). 54.5% of the individuals caught carried level 3 of *A. foetida* pollen (Table 1A). Therefore, the Lesser Whitethroat is the only migrant that can be regarded as a major pollinator.

Honey bee (Apis mellifera) as a pollen vector

The distance between the beehives and the *A. foetida* bushes was 0–350 m in Hulda and 40-250 m in Ella Valley. Every day when temperatures were high enough (above ca 14°C), the bees foraged for food. As the *A. foetida* was almost the only flowering plant in the area, the bees were all over it, despite the fact that it is considered as only moderately attractive for bees looking for pollen (Keasar & Shmida 2009).

88% of the observed honey bees collected and carried pollen grains after successfully opening of the keel. It is likely they touch and rupture the stigma while entering into the keel and collecting pollen grains.

The high presence of honey bees on *A. foetida* flowers throughout the flowering season makes them important pollinators of this plant. A mixed pollination system between Hymenoptera and passerine birds was found in the Canary Islands in a variety of plants (Ortega et al. 2011).

Conclusions

Anagyris foetida, having an ecologically generalized pollination system, attracts a large array of potential pollinators including resident, wintering and migrating birds, and honey bees.

The variety of visitors to *A. foetida* and their role as potential pollinators differes from what Ortega et. al. (2005) found in Spain. This is probably due to differences in biogeography in terms of latitude, climate, diversity of bird species and subspecies, and the routes of bird migration.

Of the three bird species found in Spain as major pollinators, the Blackcap and Sardinian Warbler have higher chances of being important pollinators of *A. foetida* in Israel as well. However, the Chiffchaff appears to be a poor pollinator of *A. foetida* in Israel. Climate differences are probably also responsible for the different roles honey bees have in the pollination of *A. foetida*. The mild Israeli winters enable honey bees to be active outside their hives from late morning and to forage pollen and nectar.

To conclude, all omnivorous bird species (excluding the Chiffchaff) were highly suspected as legitimate pollinators, whereas only the nectarivorous Palestine sunbird acted as a nectar thief.

ACKNOWLEDGEMENTS

We would like to thank Tomas Rodriguez- Riano and Dan Eisikowitch for their helpful comments on a draft of this paper. We would also like to thank Carmel Zitronblat and many other bird ringers who joined the efforts of the winter ringing sessions.

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