*Ardeola* 57(1), 2010, 143-157

# NECTAR EXPLOITATION BY SONGBIRDS AT MEDITERRANEAN STOPOVER SITES

## EXPLOTACIÓN DEL NÉCTAR POR PASERIFORMES EN LOCALIDADES DE ESCALA MEDITERRÁNEAS

Jacopo G. CECERE* [1], Costanza MATRICARDI**, Beatrice FRANK***, Simona IMPERIO****, Fernando SPINA*****, Gabriel GARGALLO******, Christos BARBOUTIS******* and Luigi BOITANI*

SUMMARY.—*Nectar exploitation by songbirds at Mediterranean stopover sites.*

The nectar use by songbirds in Europe is reported by many authors but several of them refer to local or occasional events on both introduced and native plants. A study carried out on Ventotene Island (Italy) shows that nectar could be an important food resource for migrants which land at stopover sites. In this study we investigated the distribution of nectar feeding behaviour at Mediterranean stopover sites in spring, checking 10 species for the presence of pollen on plumage during ringing activities carried out at 14 stopover sites placed in Spain, Italy and Greece. Moreover we investigated the possible relationship between nectar consumption by migrants and vegetation at three stopover sites, through the time budget analysis of 8 species during no-flight activities.

*Sylvia* and *Phylloscopus* species were often found to use nectar, the former more frequently than the latter. However, nectar exploitation results usual only at 2 Mediterranean sites out of 14, Ventotene and Antikythira (Greece), while it seems to be common at African stopover sites. The analysis of time budget and the pattern of nectar feeding distribution at stopover sites suggests that in the Mediterranean region nectar consumption is most likely related to the youngest phases of vegetation, these possibly being richer in flowering plants potentially usable by songbirds.

*Key words*: diet, habitat use, nectar, *Phylloscopus*, stopover, *Sylvia*, time-budget.

* Department of Animal and Human Biology, University of Rome "La Sapienza", Viale dell' Università 32, 00185 Roma, Italy.

** Piazza Cecco d'Ascoli 19, 60300 Ascoli Piceno, Italy.

*** Department of Geography Memorial University, St. John's, NL, A1B3X9, Canada.

**** RicercaFauna, Via del Felciaro snc, 00020 Ciciliano (RM), Italy.

***** Istituto Superiore per la Protezione e la Ricerca Ambientale, Via Cà Forcanetta 9, 40064 Ozzano Emilia (BO), Italy.

****** Catalan Ornithological Institute, Museu de Ciències Naturals, Passeig Picasso s/n, 08003 Barcelona, Spain.

******* Department of Biology & Natural History Museum of Crete, University of Crete, P.O. Box 2208, 71409 Heraklion, Crete, Greece

[1] Corresponding author: jacopo.cecere@uniroma1.it

RESUMEN.—*Explotación del néctar por paseriformes en localidades de escala mediterráneas.*

El uso de néctar por parte de los paseriformes en Europa ha sido citado por numerosos autores, sin embargo en muchas ocasiones se hace referencia a casos locales u ocasionales, tanto en relación a plantas introducidas como nativas. El estudio realizado en la isla de Ventotene (Italia) muestra que el néctar puede ser un importante recurso alimenticio para los migrantes cuando permanecen en lugares de escala migratoria. Se Investigó la distribución del comportamiento de alimentación de néctar en áreas de escala migratoria durante la primavera, muestreando la presencia de polen en el plumaje de 10 especies durante las actividades de anillamiento rutinarias realizadas en 14 áreas de escala situadas en España, Italia y Grecia. Se estudió la posible relación entre el consumo de néctar y la vegetación, en tres áreas distintas, mediante el análisis del uso del tiempo de 8 especies durante sus actividades diarias.

Las especies del género *Sylvia* y *Phylloscopus* fueron a menudo proclives a emplear néctar, las primeras con más frecuencia que las últimas. Sin embargo, la explotación del néctar sólo es usual en 2 de los 14 lugares estudiados en el Mediterráneo, Ventotene y Antikythira (Grecia), mientras que parece que es común en las áreas de escala africanas. El análisis del uso del tiempo y el patrón en la distribución del consumo de néctar sugieren que, en la región mediterránea, este consumo del néctar está vinculado con más frecuencia durante las fases iniciales de la vegetación, quizás más ricas en plantas florecientes, potencialmente utilizables por los paseriformes.

*Palabras clave*: dieta, escalas, néctar, *Phylloscopus, Sylvia*, uso de hábitat y de tiempo.

## INTRODUCTION

When migrating songbirds land at stopover sites, they need to acquire food in a short period of time, facing unfavourable weather conditions, predation risks, competition with resident birds which are on their familiar ground, and several other migrants too (e.g., Moore and Wang, 1991; Gauthreaux and Belser, 1999; Dierschke, 2003; Cimprich *et al.*, 2005).

A study carried out on Ventotene, a small island in the central Mediterranean Sea, highlights that the exploitation of nectar could play an important role for European warblers during spring migration, being an energy drink easy to obtain and assimilate (Schwilch *et al.*, 2001). Apart from Ventotene, the regular consumption of nectar by old-world migrants at stop-over sites, has been reported only from the oasis of Ouadâne, in the western Sahara (Salewski *et al.*, 2006). Other occurrences about the regular use of nectar by songbirds are known, but during the winter season: in southern Spain, chiffchaff *Phylloscopus collybita*, blackcap *Sylvia atricapilla* and sardinian warbler *S. melanocephala* habitually consume nectar of *Anagyris foetida* and consequently pollinate the plant (Ortega-Olivencia *et al.*, 2005), and the same bird species, together with blue tit *Cyanistes caeruleus*, feed on the nectar of an introduced plant *Eriobotrya japonica* in Madrid (Merino and Nogueras, 2003). Further observations of nectar feeding are reported for European birds, however they refer to circumstantial or occasional events on introduced plants, which often show typical bird-flower characteristics (Holm and Laursen, 1982; Prinzinger, 1988; Búrquez, 1989; Proctor *et al.*, 1996; Laursen *et al.* 1997; Harrup, 1998), and on native plants, such as *Rhamnus alaternus, Acer* sp.*, Crataegus* sp.*, Salix* sp.*, Ribes* sp.*,* etc. (reviewed by Ford, 1985; Kay, 1985; Calvario *et al.*, 1989). Despite several local reports, there has never been a previous assessment of the large-scale distribution of nectar feeding by migrating songbirds in Mediterranean region.

The first aim of the present study is to explore how the nectar feeding behaviour of

European warblers at stopovers sites is geographically spread across the Mediterranean during spring migration. Furthermore, for the better understanding of the role of different types of vegetation on the feeding behaviour, we analyse the time budget of eight species (two *Sylvia* warblers, three *Phylloscopus* warblers, two flycatchers and one chat) at three stop-over sites with Mediterranean vegetation characterised by different managements.

## Materials and methods

The assessment of nectar-feeding by birds was based on ringing activities carried out on 14 sites placed in 3 Mediterranean countries: 6 in eastern Spain (Cabrera, Illa de Colom, L'Alfacada, Estany de Mornau, Canal Vell, Llobregat), 7 in Italy (Cà Roman, Castelporziano, Ventotene, Ponza, Zannone, Capo Palinuro, Ustica) and 1 in Greece (Antikythira) (figure 1 and table 1). All data were collected during the spring 2008: from March to May in Llobregat; from mid March to mid May in Antikythira, Cabrera and Castelporziano; from the first April to mid May in Ventotene and Ponza and from mid April to late May in all other sites.

For this study, we analysed all the species which were mentioned in the past as feeding on nectar in Europe during spring migration (Laursen *et al.*, 1997; Schwilch *et al.*, 2001; Ortega-Olivencia *et al.*, 2005) and commonly

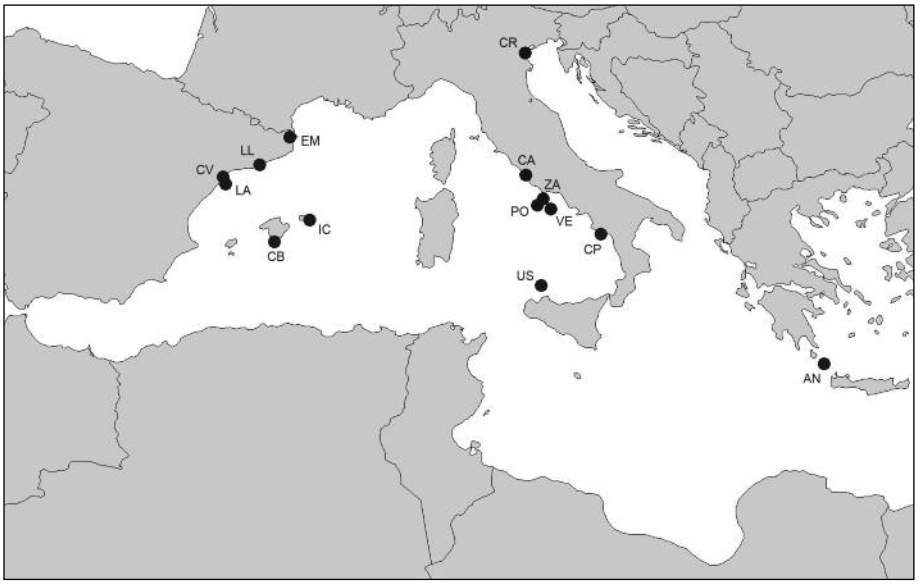


Fig. 1.—Geographical location of the 14 study sites. CB = Cabrera, IC = Illa de Colom, LA = L'Alfacada, EM = Estany de Mornau, CV = Canal Vell, LL = Llobregat, CR = Cà Roman, CA = Castelporziano, VE = Ventotene, PO = Ponza, ZA = Zannone, CP = Capo Palinuro, US = Ustica, AN = Antikythira.
*[Localización geográfica de las 14 localidades de estudio. CB = Cabrera, IC = Isla de Colom, LA = La Alfacada, EM = Estanque de Mornau, CV = Canal de Vell, LL = Llogregat, CR = Cà Román, CA = Castelporziano, VE = Ventotene, PO = Ponza, ZA = Zannone, CP = Capo Palinuro, US = Ustica, AN = Antikythira.]*

TABLE 1

Main habitats of the 14 study areas.
*[Principales hábitats de las 14 áreas de estudio.]*

| **Locality** | **Country** | **Habitat** |
|---|---|---|
| Cabrera | Spain | Maquis and few open areas |
| Illa de Colom, Menorca | Spain | Maquis and pine forest |
| L'Alfacada | Spain | Reed |
| Estany de Mornau | Spain | Reed and *tamarix* |
| Canal Vell | Spain | Reed, *tamarix* and *myoporum* bushes |
| Llobregat | Spain | Reed and mixed forest/bush |
| Ustica | Italy | Maquis |
| Capo Palinuro | Italy | Maquis and garrigue on rocky ground |
| Castelporziano | Italy | Maquis |
| Cà Roman | Italy | Garrigue and mixed forest/bush |
| Ventotene | Italy | Cultivated and set aside fields |
| Ponza | Italy | Maquis |
| Zannone | Italy | Maquis and holm-oak forest |
| Antikythira | Greece | Maquis and olive groves |

trapped at most of the 14 sites. In addition, all ringers were also requested to observe carefully the evidence of nectar feeding by other bird species. For every trapped bird of the 10 species analysed here (blackcap, garden warbler *S. borin*, subalpine warbler *S. cantillans*, whitethroat *S. communis*, sardinian warbler, icterine warbler *Hippolais icterina*, melodious warbler *H. polyglotta*, chiffchaff, wood warbler *P. sibilatrix*, willow warbler *P. trochilus*), presence/absence of pollen on the bill, forehead and breast feathers was assessed. As in previous studies (Ash, 1959; Ash *et al.,* 1961; Ford, 1985; Laursen *et al.*, 1997; Schwilch *et al.*, 2001; Salewski *et al.*, 2006), we considered the presence of pollen on the plumage as a proof of nectar consumption. Furthermore, the pollen on plumage was distinguished as fresh or dried: the latter is identifiable from agglutinations that are generally thicker than 1 mm and encrusted on the feathers. The frequency of captured individuals carrying fresh or dried pollen per species was calculated for each site.

*Time budget*

The time budget of 8 species (garden warbler, whitethroat, chiffchaff, willow warbler and wood warbler, pied flycatcher *Ficedula hypoleuca*, spotted flycatcher *Muscicapa striata*, whinchat *Saxicola rubetra*) was analysed at three stopover sites. Chiffchaff, willow warbler and wood warbler were considered as one taxon (*Phylloscopus* spp.) due to the difficulties in distinguishing the species in the field. The three study areas, Ventotene, Ponza and Zannone (figure 1), are small islands belonging to the Isole Pontine archipelago, located in the central Tyrrhenian Sea. Ventotene is a little island (1.3 $Km^2$) characterised by a small vi-

llage and several narrow fields which were all formerly cultivated. Nowadays, fields are cultivated and set aside cyclically. Therefore many abandoned fields, characterised by pioneer vegetation, are present every year in Ventotene. Moreover, natural Mediterranean maquis is scarce and confined to cliffs and few sites nearby. Ponza is the biggest island of the archipelago (7.5 $Km^2$). Despite the presence of two villages, the agriculture on this island is uncommon. Uninhabited areas are mostly covered by natural Mediterranean maquis, characterised by dense and medium-high shrubs (*Pistacia lentiscus, Spartium junceum, Erica arborea, Myrtus communis, Phyllirea* sp.). Zannone is the smallest of the three islands (0.9 $Km^2$) and is totally uninhabited. About half of the island is covered by natural holm-oak woods and the other half is characterized by impenetrable and high Mediterranean maquis.

The behaviour of migrants was filmed with a camera from several fixed points on each island. The recordings were carried out from the 25 April to the 10 May in 2006-08 on Ventotene, in 2007 on Zannone and in 2008 on Ponza island. Cameramen worked from 8:00 to 17:00 GMT+1. Thereafter, the resulting films were divided into three time bands (8:01-11:30; 11:31-15:00; 15:01-18:30 GMT+1). The distribution patterns of recorded films among the three time bands did not significantly differ between the three study areas ($\chi^2 = 6.14$; df = 4; n = 539; p = 0.19).

Every bird was followed during no-flight activity and the filming was stopped when it started to fly. For each recorded bird, the main behaviour was noted down every 10 seconds and assigned to one of the following six categories: (i) nectar feeding, when birds go directly to visit flowers without checking for presence of other resources on leaves and branches; they use to insert the bill inside many flowers belonging to the same plant (part of the behaviour is also described and drawn by Schwilch et al. 2001); (ii) insect feeding, when birds quickly check for presence of food on the whole plant (leaves, branches, flowers) and, in most of the cases, they do not insert the bill into the flowers; (iii) nectar or insect feeding, whenever it was not possible to distinguish the two behaviours for certain; (iv) perching, including resting and waiting; (v) plumage care; and (vi) other behaviour, such as social interactions. All the plants used for nectar feeding by birds were identified.

Individuals observed for less than 10 seconds were not considered. Despite birds not being individually recognisable, every place was surveyed for no more than 20 minutes, thus minimising the probability of observing the same individual at different times in the same day. Moreover, it must be considered that in spring migrants stay at stopover sites the shortest time possible (Alerstam and Lindström, 1990). On Ventotene Island, for instance, most migrants seem to stay at the most for two days during spring migration (Tenan and Spina, *pers. obs.*), and a similar result was obtained for willow warblers landing at western Mediterranean stopover sites in spring (Barriocanal and Robson, 2007).

In order to compare the time budget between the three different sites, we averaged the proportions of the same activity observed for all individuals belonging to the same species, thus obtaining a single value for each behaviour related to every species.

## RESULTS

A total of 14,844 birds were checked for presence or absence of pollen on their plumage during the ringing activities carried out in the 14 sites (702 in Cabrera; 566 in Illa de Colom; 569 in L'Alfacada; 420 in Estany de Mornau; 491 in Canal Vell; 997 in Llobregat; 229 in Cà Roman; 1,197 in Castelporziano; 2,707 in Ventotene; 3,749 in Ponza; 1,603 in Zannone; 264 in Capo Palinuro; 639 in Ustica; 711 in Antikythira). The differences in sam-

TABLE 2

Percentages of birds with fresh (%f) or dried (%d) pollen on beak or plumage, calculated on total checked birds (n) for each site. Percentages are calculated only for n > 10.

| | | Cabrera (Spain) | Illa de Colom, Menorca (Spain) | L'Alfacada (Spain) | Estany de Mornau (Spain) | Canal Vell (Spain) | Llobregat (Spain) |
|---|---|---|---|---|---|---|---|
| ***Blackcap*** | % tot | 4.7 | 11.1 | 8.3 | 16.5 | 5.7 | 8.8 |
| | %f | 0 | 2.2 | 8.3 | 1.1 | 2.9 | 5.4 |
| | %d | 4.7 | 8.9 | 0 | 15.4 | 2.9 | 3.4 |
| | n | 43 | 45 | 12 | 91 | 35 | 148 |
| ***Garden W.*** | % tot | 1.2 | 1.8 | 2.0 | 2.6 | 0.9 | 2.4 |
| | %f | 0 | 0 | 0 | 0.9 | 0 | 2.4 |
| | %d | 1.2 | 1.8 | 2.0 | 1.8 | 0.9 | 0 |
| | n | 250 | 114 | 50 | 114 | 112 | 169 |
| ***Subalpine W.*** | % tot | 0 | 0 | 0 | 8.3 | – | 0 |
| | %f | 0 | 0 | 0 | 4.2 | – | 0 |
| | %d | 0 | 0 | 0 | 4.2 | – | 0 |
| | n | 11 | 13 | 12 | 24 | 3 | 23 |
| ***Whitethroat*** | % tot | 0 | 4.7 | 0 | 7.0 | 4.8 | 2.0 |
| | %f | 0 | 2.3 | 0 | 0 | 2.4 | 2.0 |
| | %d | 0 | 2.3 | 0 | 7.0 | 2.4 | 0 |
| | n | 112 | 43 | 58 | 43 | 42 | 99 |
| ***Sardinian W.*** | % tot | – | 0 | | – | | |
| | %f | – | 0 | | – | | |
| | %d | – | 0 | | – | | |
| | n | 5 | 39 | 0 | 5 | 0 | 0 |
| ***Icterin W.*** | % tot | 0 | 0 | – | 0 | 0 | 0 |
| | %f | 0 | 0 | – | 0 | 0 | 0 |
| | %d | 0 | 0 | – | 0 | 0 | 0 |
| | n | 20 | 34 | 4 | 19 | 13 | 43 |
| ***Melodious W.*** | % tot | – | | – | 0 | – | – |
| | %f | – | | – | 0 | – | – |
| | %d | – | | – | 0 | – | – |
| | n | 4 | 0 | 5 | 58 | 7 | 6 |

*[Porcentaje de aves con polen fresco (%f) o seco (%d) en el pico o plumaje, calculado sobre un total de aves muestreadas (n) por cada localidad. Estos porcentajes están calculados sólo para n > 10.]*

| Ustica (Italy) | Capo Palinuro (Italy) | Castelporziano (Italy) | Cà Roman (Italy) | Ventotene (Italy) | Ponza (Italy) | Zannone (Italy) | Antikythira (Greece) |
|---|---|---|---|---|---|---|---|
| 3.0 | – | 0.6 | 7.6 | 59.5 | 10.9 | 0 | 42.9 |
| 0 | – | 0 | 0 | 48.6 | 2.2 | 0 | 17.9 |
| 3.0 | – | 0.6 | 7.6 | 10.8 | 8.7 | 0 | 25.0 |
| 33 | 7 | 162 | 92 | 148 | 92 | 5 | 28 |
| 0.9 | | 0 | – | 27.4 | 1.7 | 3.3 | 5.2 |
| 0.9 | | 0 | – | 26.5 | 0.5 | 1.7 | 4.7 |
| 0 | | 0 | – | 0.9 | 1.2 | 1.7 | 0.4 |
| 212 | 0 | 57 | 8 | 1171 | 1532 | 543 | 445 |
| 3.5 | 8.3 | 0 | 0 | 39.5 | 2.3 | 2.2 | |
| 3.5 | 4.2 | 0 | 0 | 37.0 | 0 | 0 | |
| 0 | 4.2 | 0 | 0 | 2.5 | 2.3 | 2.2 | |
| 57 | 48 | 173 | 11 | 630 | 132 | 45 | 0 |
| 1.2 | 5.7 | 0 | – | 29.8 | 0.1 | 3.1 | 19.3 |
| 1.2 | 0 | 0 | – | 29.4 | 0 | 1.5 | 10.5 |
| 0 | 5.7 | 0 | – | 0.4 | 0.1 | 1.5 | 8.8 |
| 165 | 88 | 631 | 10 | 531 | 1348 | 647 | 57 |
| 0 | 4.8 | 0 | 0 | 48.5 | 0 | 0 | |
| 0 | 0 | 0 | 0 | 45.5 | 0 | 0 | |
| 0 | 4.8 | 0 | 0 | 3.0 | 0 | 0 | |
| 16 | 42 | 60 | 36 | 33 | 17 | 11 | 0 |
| 0 | | 0 | – | | | – | 6.6 |
| 0 | | 0 | – | | | – | 3.9 |
| 0 | | 0 | – | | | – | 2.6 |
| 55 | 0 | 49 | 4 | 0 | 0 | 4 | 76 |
| | 0 | – | – | | | | – |
| | 0 | – | – | | | | – |
| | 0 | – | – | | | | – |
| 0 | 16 | 7 | 5 | 0 | 0 | 0 | 1 |

TABLE 2 (cont.)

| | | Cabrera (Spain) | Illa de Colom, Menorca (Spain) | L'Alfacada (Spain) | Estany de Mornau (Spain) | Canal Vell (Spain) | Llobregat (Spain) |
|---|---|---|---|---|---|---|---|
| *Chiffchaff* | % tot | – | – | – | – | – | 8.7 |
| | %f | – | – | – | – | – | 4.3 |
| | %d | – | – | – | – | – | 4.3 |
| | n | 4 | 3 | 3 | 1 | 2 | 23 |
| *Wood W.* | % tot | 0 | 0 | – | 0 | 0 | 0 |
| | %f | 0 | 0 | – | 0 | 0 | 0 |
| | %d | 0 | 0 | – | 0 | 0 | 0 |
| | n | 59 | 40 | 5 | 21 | 48 | 30 |
| *Willow W.* | % tot | 0.5 | 1.3 | 0 | 2.3 | 0 | 0.7 |
| | %f | 0.5 | 0.9 | 0 | 2.3 | 0 | 0.7 |
| | %d | 0 | 0.4 | 0 | 0 | 0 | 0 |
| | n | 194 | 235 | 420 | 44 | 229 | 456 |

ple sizes depends mainly on the total number of birds trapped at each site and on the number of ringers present at each station. Sample sizes and the proportions of birds with fresh and dried pollen for all examined species at each site are given in table 2. Percentages are calculated only for $n > 10$.

Ventotene and Anthikitira are the sites with the highest proportion of birds with fresh pollen on their plumage. At the former, all *Sylvia* warblers showed high proportions of fresh pollen (blackcap 59 %; sardinian warbler 48 %; subalpine warbler 40 %; whitethroat 30 % and garden warbler 27 %), while such relationship was lower in *Phylloscopus* species. The blackcap was also the species with the highest proportion of fresh pollen on plumage (43 %) on Anthikitira, and was followed by whitethroat (19 %), willow warbler (14 %) and wood warbler (13 %). At the remaining 12 sites, birds with fresh pollen on plumage are rare and the proportions of each single species are rather similar between the sites.

Individuals belonging to the genus *Sylvia* were observed with fresh pollen on their plumage at 11 sites out of 14. Ventotene is the site where *Sylvia* warblers show the highest proportions of birds with fresh pollen on the plumage (31 %), followed by Anthikitira (6 %), Llobregat (3 %), Zannone (2 %), Illa de Colom, L'Alfacada, Estany de Mornau, Canal Vell, Ustica and Capo Palinuro with 1 % and Ponza with 0.3 %. No *Sylvia* warblers with fresh pollen were observed on Cabrera, Castelporziano and Cà Roman. The pattern of *Sylvia* warblers with fresh pollen significantly differs between sites ($\chi^2 = 1{,}928.38$; df = 12; $n = 9{,}071$; $p < 0.0001$). Of the *Sylvia* warblers

| Ustica (Italy) | Capo Palinuro (Italy) | Castelporziano (Italy) | Cà Roman (Italy) | Ventotene (Italy) | Ponza (Italy) | Zannone (Italy) | Antikythira (Greece) |
|---|---|---|---|---|---|---|---|
| 0 | – | 0 | 23.1 | 12.5 | 0 | – | – |
| 0 | – | 0 | 0 | 9.4 | 0 | – | – |
| 0 | – | 0 | 23.1 | 3.1 | 0 | – | – |
| 13 | 4 | 34 | 13 | 32 | 40 | 5 | 1 |
| 0 | 13.3 | – | 3.4 | 3.1 | 0 | 0 | 13.3 |
| 0 | 0 | – | 0 | 0 | 0 | 0 | 13.3 |
| 0 | 13.3 | – | 3.4 | 3.1 | 0 | 0 | 0.0 |
| 45 | 15 | 1 | 29 | 32 | 357 | 127 | 75 |
| 0 | 0 | 0 | 0 | 5.4 | 0 | 2.4 | 14.3 |
| 0 | 0 | 0 | 0 | 5.4 | 0 | 0 | 14.3 |
| 0 | 0 | 0 | 0 | 0 | 0 | 2.4 | 0 |
| 43 | 44 | 23 | 21 | 130 | 231 | 216 | 28 |

considered in this study, the blackcap is the species with the highest degree of nectarivory.

In the case of *Phylloscopus* species, fresh pollen on plumage was observed for wood warblers only at Anthikitira, for willow warblers at Anthikitira, Ventotene (5 %) and some Spanish sites, but with percentages of 2 % or lower, and for chiffchaff at Ventotene (9 %) and Llobregat (4 %).

Icterine warblers with fresh pollen were observed only in Anthikitira, while no melodious warblers were observed with pollen on plumage. Such event could be due to very rare captures of melodious warblers in all research sites.

Unfortunately, the low frequency of positive events (birds with fresh pollen) at various sites did not allowed us to perform analysis at species level or for the genus *Phylloscopus* and *Hippolais*.

Individuals with dried pollen on plumage were observed for various species at many sites, but the proportions were generally very low (table 2). Only the blackcap distinguishes itself with high proportions of individuals with dried pollen at several sites.

*Time budget*

A total of 539 individuals of the six species reported above were filmed for 8 hours, 14 minutes and 18 seconds. However, only 438 of them were observed for more then 10 seconds, and their behaviour was recorded 2,915 times (average 6.65 ± 0.41 observations per bird) (table 3). Table 3 also gives the proportions of the different behaviour adopted by each species on all three islands.

TABLE 3

Results of time-budget study. Ind. = total individuals analysed; records = times when a behaviour was recorded.
*[Resultados en la inversión de tiempo. Ind. = total de individuos analizados; registros = número de ocasiones en las que fue registrado un comportamiento.]*

| species | Island | % nectar feeding | % insect feeding | % nec/ins feeding | % plumage care | % perching | % other behav. | ind. | records |
|---|---|---|---|---|---|---|---|---|---|
| Garden warbler | *Ponza* | 0 | 27.3 | 0 | 9.1 | 63.6 | 0 | 22 | 102 |
| | *Ventotene* | 84.5 | 0 | 8.8 | 1.8 | 4.9 | 0 | 57 | 545 |
| | *Zannone* | 0 | 73.9 | 4.3 | 8.7 | 13.0 | 0 | 23 | 165 |
| Whitethroat | *Ponza* | 0 | 83.3 | 0 | 8.3 | 8.3 | 0 | 12 | 65 |
| | *Ventotene* | 91.1 | 2.8 | 0 | 0 | 6.1 | 0 | 30 | 291 |
| | *Zannone* | 0 | 81.8 | 0 | 0 | 15.9 | 2.3 | 11 | 85 |
| *Phylloscopus* spp. | *Ponza* | 0 | 100.0 | 0 | 0 | 0 | 0 | 20 | 100 |
| | *Ventotene* | 9.1 | 63.6 | 18.2 | 4.5 | 4.5 | 0 | 22 | 109 |
| | *Zannone* | 0 | 94.7 | 0 | 0 | 5.3 | 0 | 38 | 277 |
| Pied flycatcher | *Ponza* | 0 | 32.5 | 0 | 0 | 67.5 | 0 | 10 | 51 |
| | *Ventotene* | 0 | 0 | 0 | 5.3 | 94.7 | 0 | 19 | 45 |
| | *Zannone* | 0 | 0 | 0 | 5.3 | 94.7 | 0 | 19 | 42 |
| Spotted flycatcher | *Ponza* | 0 | 23.9 | 0 | 0 | 76.1 | 0 | 62 | 376 |
| | *ventotene* | 0 | 20.2 | 0 | 10.9 | 68.8 | 0 | 21 | 98 |
| | *zannone* | 0 | 0 | 0 | 0 | 100.0 | 0 | 25 | 289 |
| Whinchat | *ponza* | 0 | 0 | 0 | 0 | 100.0 | 0 | 13 | 117 |
| | *ventotene* | 0 | 0 | 0 | 5.6 | 94.4 | 0 | 18 | 41 |
| | *zannone* | 0 | 18.8 | 0 | 0 | 81.3 | 0 | 16 | 117 |

On Ventotene island, whitethroat and garden warbler spent most of the time feeding on nectar, 91 % and 85 % respectively. On the contrary, the whitethroat spent more than 80 % of its time feeding on insects on both Zannone and Ponza, while garden warbler spent 74 % of its time feeding on insects on Zannone and more than 60 % of time in perching activity on Ponza.

*Phylloscopus* warblers spent almost all their time in insect feeding activity, such as searching and catching, both on Ponza (100 %) and Zannone (95 %). On Ventotene, insect feeding is the most frequent behaviour for these species (64 %), taking into account that not always it is possible to distinguish nectar feeding behaviour from insect eating.

For pied flycatcher, spotted flycatcher and whinchat there are no evident differences in behaviour between the three sites. Perching was the most frequent activity at each site for all the three species, followed by insect feeding for pied flycatcher on Ponza (32.5 %), for spotted flycatcher on Ponza (23.9 %) and Ventotene (20 %) and for whinchat on Zannone (19 %).

Nectar feeding by birds was observed and filmed only on Ventotene where exploited plants were almost exclusively *Ferula communis* and *Brassica oleracea*-group species. Some plants of the latter taxon were identified as *B. montana*, recognised in the past as *Brassica oleracea robentiana* (Gladis and Hammer, 2001), but we do not exclude the possibility of hybridisation with cultivated cabbage *Brassica olereacea* ssp., thus we prefer to refer to these plants as *Brassica oleracea* –group sp. Finally, only one garden warbler was observed feeding on nectar of *Lavatera arborea.*

## Discussion

In our study we present a large-scale view of nectar feeding by songbirds at stop-over sites during spring migration. In accordance with previous studies (Schwilch *et al.*, 2001; Salewski *et al.*, 2006), *Sylvia* warblers are the species with the highest degree of nectarivory and, between them, blackcap is the species which feed on nectar more frequently. Individuals belonging to the genus *Sylvia*, with fresh or dried pollen on plumage, were observed in all sites. Nevertheless, the proportion of birds with pollen were very low, except on Ventotene island where many birds regularly feed on nectar. *Phylloscopus* species feed on nectar mainly on Antikythira, but individuals with fresh or dried pollen on plumage were observed at many other sites, both in Spain and Italy (table 2). *Hippolais* species do not habitually use nectar as nourishment: only on Antikythira, some icterine warblers and one individual of eastern olivaceous warbler *H. pallida* were observed with pollen on plumage. The use of nectar by icterine warbler is also recorded from Ventotene (Schwilch *et al.*, 2001), while in the western Sahara nectar consumption is described for eastern and western olivaceous warblers *H. opaca* (Salewski *et al.*, 2006). The fact that the *Sylvia* species feed on nectar more frequently than *Phylloscopus* and *Hippolais* species, is possibly due to their ability to exploit several trophic resources (for a review: Shirihai *et al.*, 2001; Alström *et al.*, 2006). Analysing the nectar feeding behaviour, we have to take into consideration that, in general, the proportions of birds with pollen recorded in the present study could be underestimated. Some of the birds, in fact, are likely trapped just after their arrival at a stop-over site, when they have not yet had the possibility of feeding on nectar. Moreover, the probability of maintaining pollen on the beak could depend on the form and size of the beak, which differ among bird species, but also on the characteristics of the pollen.

During spring migration, songbirds spend as short time as possible at stopover sites (Alerstam and Lindström, 1990), thus it is reasonable to think that dried and agglutina-

ted pollens may originate from feeding on nectar at stopover sites visited prior to the trapping site. Laursen *et al.* (1997) found pollens coming from the Mediterranean region on migrants trapped in Denmark. In the case of Mediterranean trapping sites, pollens could come directly from Africa. From our results, nectar exploitation appears to take place at different African stopover sites, since the proportion of trapped birds with dried pollen on plumage is very similar among several sites throughout the Mediterranean region, from Spain to Greece, particularly for blackcap and garden warbler (table 2). Such results are also partially similar for chiffchaff, whitethroat and subalpine warbler. On the contrary, the nectar exploitation *in situ* is not uniformly distributed in the Mediterranean region. It occurs almost exclusively on two islands, Ventotene and Antikythira, and is rare or totally absent at the other 12 stopover sites analysed. This is probably due to different resource availabilities, namely large quantities of plants in flower during the migration period. Ventotene and Antikythira stand out from the other sites since they are strongly characterised by the presence of pioneer vegetation. At the first site, fields abandoned for three or four years are common. The main habitats present in Antikythira are a mix of natural maquis and olive groves, lightly managed to avoid the growth of bushes and trees for the olive harvesting. Sheep grazing is also common on the island. On Cabrera as well, despite the main vegetation being maquis, there are fields which were abandoned many years ago. These fields were then grazed by domestic animals until approximately 5 years ago and since grazing stopped, the open areas have been rapidly returning towards typical maquis-like vegetation. The remaining 11 sites are covered with less managed or unmanaged vegetation, characterised by reed, garrigue, maquis or forests (table 1). It could be possible that the youngest phases of vegetational successions in Mediterranean regions are richer in plants which are potentially usable by songbirds for nectar feeding than the following phases. This occurrence is probably not enough to induce a large nectar exploitation by songbirds. Other variables are possibly necessary, especially a flowering period matching with migrant passage, thus also latitude and exposure could be important undirected variables for nectar use.

The hypothesis of the young phases of vegetation also appears to be confirmed by the time budget results. The three islands, placed in the same archipelago and analysed here, are characterised by three different stages of the Mediterranean vegetation: holm-oak woods and high maquis on Zannone, mainly medium-high maquis on Ponza and habitats heavily affected by human activities (fires, agriculture, grass cutting) on Ventotene. Only on the latter island, nectar feeding was observed, and from the data of the two *Sylvia* warblers analysed here, garden warbler and whitethroat, we discovered that they use more than 80 % of their time spent on the ground consuming nectar. On the two neighbouring islands, the same species were never observed feeding on nectar. It is known that the total time taken for migration is strongly influenced by how efficiently a migrant can use available stopover sites for refuelling (Alerstam and Lindström, 1990). The time budget analysis shows that whitethroats spend a large part of their time feeding on insects on Zannone and Ponza and on nectar on Ventotene; also garden warblers principally feed on nectar on Ventotene and on insects on Ponza but less in Zannone. We can assert that these two species manage to feed on all the three islands but, considering that at this stage they have reduced digestive traits (Hume and Biebach, 1996; Schwilch *et al.*, 2002), they may need to spend more time to refuel at the two sites where they are unable to feed on nectar. This could be due to two reasons: (i) nectar is very easy to obtain and, as opposed to insects, birds do not need to spend time finding it. (ii) At this

stage migrating songbirds need several hours to rebuild the gut for protein digestion (Hume and Biebach, 1996), while monosaccharides do not need to be digested since they are directly absorbed. A clear preference for nectar, when available, by migrating birds was experimentally demonstrated by Schwilch *et al.* (2001), who offered unlimited nectar, mealworms and water to caged birds (whitethroats and garden warblers). However, we lack data about the different contribution, on physiological or ecological grounds, that insect and nectar diets give to migrating *Sylvia* warblers at stopover sites in order to continue their migration.

The pattern for pied flycatcher, spotted flycatcher and whinchat is different from *Sylvia* warblers as these species do not feed on nectar and consequently the time budget of no-flight activities is similar at the three stopover sites. According to their feeding behaviour (for a review: Taylor, 2006a; Taylor, 2006b; Cramp, 1988), perching is the main behaviour for all three species at each site (table 2). *Phylloscopus* species spend most of their time looking for and feeding on insects on Ponza and Zannone. While on Ventotene insect feeding is also the main behaviour, such activity differs from the other two sites due to the presence of a small amount of nectar feeding. This result is in agreement with the low degree of nectarivory of *Phylloscopus* species (table 1).

The time of the day could influence the results obtained by filming but, considering that the distribution of films used for analyses among the three time bands is similar between the three study areas, we can conclude that the possible biases are equally distributed among sites. This allowed us to compare effectively the behaviour frequencies between the three study areas, despite some behaviour could be underestimated.

The category "other behaviour", which includes interaction with other birds, results as equal or close to zero for all species at the three sites. This suggests that in this study territorial behaviour and direct competition seem to be negligible among migrants, as in the case of nectar feeding.

During time budget activity, we identified three plant species used by birds for nectar feeding on Ventotene. In according with Schwilch *et al.* (2001), *Ferula communis* and *Brassica oleracea*-group sp. are the two most used plant taxa; in addition, just one individual was observed feeding on *Lavatera arborea*. All these plants are typical of abandoned fields on Ventotene. Unfortunately, we have no data about plants used by birds at the other study sites.

This study shows that the exploitation of nectar during spring migration is rather common among *Sylvia* warblers but less so among *Phylloscopus* species. The presence of birds with dried pollen on their plumage at all the Mediterranean stopover sites analysed here, suggest that warblers commonly use this resource in Africa, as already described for Mauritania (Salewski *et al.*, 2006). On the contrary, this behaviour is rare in the Mediterranean region and seems to be mainly related to few sites characterised by pioneer vegetation. Management plans of areas important for songbird migration must take into consideration that this type of vegetation could play a relevant role for the refuelling of *Sylvia* warblers during spring migration.

ACKNOWLEDGEMENTS.—We are extremely grateful to all ringers who participated at the field work on the 14 sites. In particular, we thank the coordinators of the ringing stations: B. Massa and E. Canale for Ustica, V. Cavaliere for Capo Palinuro; G. Landucci and P. Ruda for Castelporziano; L. Sattin for Cà Roman; A. Ferri for Ventotene; M. Cardinale for Ponza; M. Sacchi for Zannone; J. Castelló, O. Clarabuch, J. Feliu, M. A. Fuentes and M. Olivé for Aiguamolls, Estany de Mornau, l'Alfacada and Llobregat; R. Escandell for Illa de Colom; M. Suárez for Cabrera; and A. Evangelidis, observatory's coordinator of Antikythira. We

also thank the Corpo Forestale dello Stato and the National Park of Circeo for the permit to work on Zannone for the time-budget study, and S. Tenan for his useful information. Thanks to the reviewers for useful comments on previous draft. Result from Progetto Piccole Isole (ISPRA) paper nº. 44.

## BIBLIOGRAPHY

ALERSTAM, T. and LINDSTRÖM, A. 1990. Optimal bird migration: the relative importance of time, energy, and safety. In, E. Gwinner (Ed): *Bird Migration: Physiology and Ecophysiology*, pp. 331-351. Springer-Verlag. Berlin.

ALSTRÖM, P., AYMÍ, R., CLEMENT, P., DYRCZ, A., GARGALLO, G., HAWKINS, A. F. A., MADGE, S. C., PEARSON, D. J. and SVENSSON L. 2006. Family Silvidae (old world warblers). In, J. Del Hoyo, A. Elliott and D. A. Cristie (Eds): *Handbook of the birds of the world. Vol 11. Old world Flycatchers to old world Warblers*, pp. 492-712. Lynx Edicions. Barcellona.

ASH, J. S. 1959. Pollen contamination by birds. *British Birds*, 52: 421-426.

ASH, J. S., JONES P. H. and MELVILLE R. 1961. The contamination of birds with pollen and other substances. *B*riish *Birds*, 54: 93-100.

BARRIOCANAL, C. and ROBSON, D. 2007. Spring passage of Willow Warbler *Phylloscopus trochilus* across the western Mediterranean: comparing islands with the mainland. *Ardea*, 95: 91-96.

BÚRQUEZ, A. 1989. Blue Tits, *Parus caeruleus*, as pollinators of the crown imperial, *Fritillaria imperialis*, in Britain. *Oikos*, 55: 335-340.

CALVARIO, E., FRATICELLI, F., GUSTIN, M., SARROCCO, S. and SORACE, A. 1989. The Blackcap *Sylvia atricapilla* and the Garden Warbler *Sylvia borin* as pollinator of *Rhamnus alaternus* (Rhamnaceae). *Avocetta*, 13: 53-55.

CIMPRICH, D. A, WOODREY, M. S. and MOORE, F. R. 2005. Passerine migrants respond to variation in predation risk during stopover. *Animal Behaviour*, 69: 1173-1179.

CRAMP, S. (Ed.) 1988. *The Birds of Western Paleartic*, vol V, pp. 726-729. Oxford University Press. Oxford.

DIERSCHKE, V. 2003. Predation hazard during migratory stopover: are light or heavy birds under risk? *Journal of Avian Biology*, 34: 24-29.

FORD, H. A. 1985. Nectarivory and pollination by birds in southern Australia and Europe. *Oikos*, 44: 127-131.

GAUTHREAUX, S. A. and BELSER, C. G. 1999. Bird migration in the region of the Gulf of Mexico. In, N. J. Adams and R. H. Slotow (Eds). *Proceedings of the 22nd International Ornithological Congress, Durban, South Africa*, pp. 1931-1947. Birdlife South Africa. Johannesburg. South Africa.

GLADIS, TH. and HAMMER, K. 2001. Nomenclatural notes on the *Brassica oleracea-group. Genetic Resources and Crop Evolution*, 48: 7-11.

HARRUP, B. 1998. Wintering blackcaps taking nectar from, and probably pollinating, *Mahonia*. *British Birds*, 91: 201.

HOLM, E. and LAURSEN, K. 1982. Observation and experiments on the oral apparatus and its function in some warblers species (Sylviidae). *Zoologischer Anzeiger Jena*, 209: 224-246.

HUME, I. D. and BIEBACH, H. 1996. Digestive tract function in the long-distance migratory Garden Warbler, *Sylvia borin. Journal of Comparative Physiology B: Biochemical, Systematics and Environmental Physiology*, 166: 38- 395.

KAY, Q. O. N. 1985. Nectar from willow catkins as a food source for blue tits. *Bird Study*, 32: 40-44.

LAURSEN, K., HOLM, E. and SØRENSEN, I. 1997. Pollen as a marker in migratory warblers, sylviidae. *Ardea*, 85: 223-231.

MERINO, S. and NOGUERAS, I. 2003. Loquat *Eriobotrya japonica* as a winter nectar source for birds in central Spain. *Ardeola*, 50: 265-267.

MOORE, F. R. and WANG, Y. 1991. Evidence of food-based competition among passerine migrants during stopover. *Behavioral Ecology and Sociobiology*, 28: 85-90.

ORTEGA-OLIVENCIA, A., RODRÍGUEZ-RIAÑO, T., VALTUEÑA, F. J., LÓPEZ, J. and DEVESA, J. A. 2005. First confirmation of a native bird-pollinated plant in Europe. *Oikos*, 110: 578-590.

PRINZINGER, R. 1988. Nektar als regelmäßige Zugnahrung bei Grasmücken? *Journal of Ornithology*, 129: 475-478.

PROCTOR, M., YEO, P. and LACK, A. 1996. *The Natural history of pollination*. Timber Press: Portland. OR.

SHIRIHAI, H., GARGALLO, G., HELBIG, A. J., HARRIS, A. and COTTRIDGE, D. 2001. *Sylvia warblers – Identification, taxonomy and phylogeny of genus Sylvia*. Christopher Helm Ltd. London.

SALEWSKI, V., ALMASI, B. and SCHLAGETER, A. 2006. Nectarivory of Palearctic migrants at a stopover site in the Sahara. *British Bird*, 99: 299-305.

SCHWILCH, R., MANTOVANI, R., SPINA, F. and JENNI, L. 2001. Nectar consumption of warblers after long-distance flights during spring migration. *Ibis*, 143: 24-32.

SCHWILCH, R., GRATTAROLA, A., SPINA, F. and JENNI, L. 2002. Protein loss during long-distance migratory flight in passerine birds: adaptation and constraint. *The Journal of Experimental Biology*, 205: 687-695.

TAYLOR, P. B. 2006a. Spotted Flycatcher. In, J. del Hoyo, A. Elliott and D.A. Cristie (Eds): *Handbook of the birds of the world. Vol 11. Old world Flycatchers to old world Warblers*, pp. 492-712. Lynx Edicions Barcellona.

TAYLOR, P. B. 2006b. European Pied Flycatcher. In, J. del Hoyo, A. Elliott and D.A. Cristie (Eds). *Handbook of the birds of the world. Vol 11. Old world Flycatchers to old world Warblers*, pp. 492-712. Lynx Edicions. Barcelona.

*[Recibido: 15-12-2009]*
*[Aceptado: 25-02-2010]*