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## Fuelling in front of the barrier - are there age based behavioral differences in Garden Warblers *Sylvia borin*?

Garden Warblers *Sylvia borin* were studied during autumn stopover in Crete before crossing the barrier of the Mediterranean Sea and the Sahara desert. Birds followed with transmitters show extensive stopover periods, which were longer in first-year birds, 16 days, compared with adult birds, 14 days. The distribution of body masses from birds trapped in fig trees were used to estimate the departure body mass and the results found indicate that both age categories on average depart with a fuel load close to 100% of lean body mass. The movement of transmitter birds shows differences between first-year and adult birds. Adult birds move further away from the release site and many also left the study area. Several were found settled outside the study area, up to 17 km away, indicating that they regularly make longer stopover movements. It is suggested that this might be a result of that they return to a place where they stayed during an earlier migration. It was shown that stopover site fidelity exists and nine garden warblers were recaptured in the area during a following autumn. The results found high-lights the importance of stopover areas close to the Sahara desert.

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Christos Barboutis<sup>1</sup>, Ian Henshaw<sup>2</sup>, Cecilia Kullberg<sup>2</sup>, Stamatina Nikolopoulou<sup>3</sup>, Thord Fransson<sup>4</sup>.

Corresponding author: Christos Barboutis, [barboutischr@gmail.com](mailto:barboutischr@gmail.com)

1: Natural History Museum of Crete, University of Crete, PO Box 2208, 71409, Iraklion, Greece . e-mail: [barboutischr@gmail.com](mailto:barboutischr@gmail.com), tel: +30 2810 393292 fax: + 30 2810 393281).

2: Department of Zoology, Stockholm University, 106 91 Stockholm, Sweden.

3: Institute of Marine Biology and Genetics, Hellenic Centre for Marine Research, PO Box 2214, Iraklion, 71003 Crete, Greece.

4: Department of Environmental Research and Monitoring, Swedish Museum of Natural History, Box 50 007, SE-104 05, Stockholm Sweden.

## 20 INTRODUCTION

21 About 2 billion songbirds breeding in the Western Palearctic cross the Saharan desert every  
22 autumn to reach their wintering grounds (*Hahn et al., 2009*). The area of Sahara has not always acted as  
23 an ecological barrier for migratory birds, and had expanded to a considerable size already a few million  
24 years ago (*Bruderer & Salewski, 2008*). Gradual variations in the extent of the desert has occurred over  
25 time, most recently from a humid period to a period of desertification in North Africa seem to have started  
26 about 6000 years ago (*Holmes, 2008; Kröpelin et al., 2008*). These conditions have probably resulted in  
27 fluctuations in the difficulty for birds to cross the barrier. Some long distance migrants that choose not to  
28 circumvent the Mediterranean Sea have nowadays to cross an ecological barrier that can reach up to 2200  
29 km (*Barboutis et al., 2011*). Most of the long distance migrants are not adapted to refuel in oases or in the  
30 surrounding vegetation (*Jenni-Eiermann et al., 2011*) and thus extensive fuel loads are stored in advance  
31 as can be seen from the very high body masses of birds close to the barrier (*e.g. Finlayson, 1981;*  
32 *Fransson et al., 2006; 2008*).

33 Migrants are expected to optimally modulate their travel costs in terms of time, energy and safety  
34 (*Alerstam & Lindström, 1990*) while crossing diverse geographic sectors, resulting in variation in body  
35 mass between different sectors along the migration route (*Yohannes et al., 2009*). Several species have  
36 been shown to be non-randomly distributed between areas close to the Sahara desert during autumn,  
37 indicating that species specific areas are used during preparation for the crossing (*Fransson et al., 2005*).  
38 In accordance with this, several species have been shown to exhibit stopover site fidelity close to the  
39 barrier (*e.g. Moreau, 1972; Cantos et al., 1994; Merom et al., 2000*). Information about spatio-temporal  
40 variation in stopover duration and body mass accumulation is crucial in order to understand the  
41 organization of the migratory journey of birds (*Alerstam & Lindström, 1990*). However, detailed  
42 information of stopover behavior in songbirds is rare and this is especially evident when it comes to  
43 preparation close of the Sahara desert.

44 One of the most numerous long-distance migrating passerines in the Palearctic to perform this  
45 barrier crossing is the Garden Warbler *Sylvia borin* (*Hahn et al., 2009*). Garden Warblers seem to increase  
46 their average body mass during the migration from their breeding grounds to the edge of the barrier in

47 autumn, and this increase was found to be larger in eastern birds (*Bairlein, 1991; Schaub & Jenni, 2000*).  
48 Most of the fuel needed for the barrier crossing, however, is accumulated at their last stopover before the  
49 passage (*Fransson et al., 2008*). The Garden Warbler is known for its seasonal frugivory (*Bairlein, 2002*)  
50 where figs *Ficus carica* provide an important food source when fuelling in autumn in the Mediterranean  
51 region (*Thomas, 1979; Fransson et al., 2008*). Garden Warblers show an age-related difference in timing  
52 of autumn migration, where adult birds depart ahead of first-year birds (*Fransson, 1995; Barboutis, 2010;*  
53 *Iwajomo et al., 2012*).

54 In this study we investigate if there are age-related differences in stopover behavior between first-  
55 year and adult Garden Warblers in Crete when preparing for the crossing of the Mediterranean Sea and the  
56 Sahara desert in autumn.

57

## 58 **METHODS**

### 59 **The study site**

60 Garden Warblers were studied in south central Crete (Fig. 1a,b) during periods of autumn migration  
61 between 2004 and 2012 (with exception of 2005). The study area is situated in the neighborhood of the  
62 village Kalivia (35°03' N 25°13' E) in the eastern part of the Mesara plains about 20 km from the southern  
63 coastline of Crete. The area consists of agricultural landscapes and riverine vegetation along seasonal  
64 rivers. Fieldwork was carried out during 2 – 4 weeks every year and the dates for fieldwork visits varied  
65 between years to cover the passage period of the different age-groups in the region according to Barboutis  
66 (2010). The earliest start date was on the 20<sup>th</sup> August and the latest ending on the 29<sup>th</sup> September.

67

### 68 **Trapping and radio-tracking**

69 Garden Warblers were trapped with mist nets either with tape lures started at dawn at one site close to  
70 the village of Kalivia or without luring at different fig trees within the valley. Trapped birds were aged  
71 according to Svensson (1992) and weighed to the nearest 0.1 gram. Maximum wing length (*Svensson,*  
72 *1992*) was recorded as a measurement of body size. In total 1113 Garden Warblers were trapped using tape

73 lures, 658 first-year and 445 adult birds, while another 618 were trapped at fig trees without luring, 369  
74 first-year and 249 adult birds.

75 Light-weight radio transmitters (model BD-2N, Holohil Company Ltd. in Canada) were used on  
76 77 Garden Warblers, out of which 29 were first-years (2004 and 2009) and 48 were adult birds (2006–  
77 2009). The radio transmitters were attached with Cyanoacrylate glue to trimmed feathers on the back or by  
78 leg-loop harness (*Rappole & Tipton, 1991*) and weighed approximately 0.5 g with a minimum life-span of  
79 21 days. All the birds equipped with radio transmitters were trapped using tape lures at the site close to the  
80 village of Kalivia (Fig 1 c). It has been shown that a great proportion of birds trapped with tape lures early  
81 in the morning are birds that have performed a migratory flight the night before (*Schaub et al., 1999,*  
82 *Fransson et al., 2008*) and combined with the fact that we only equipped lean birds with radio  
83 transmitters, we believe that the majority of birds studied were newly arrived at the study site. First-year  
84 birds were given transmitters between 29<sup>th</sup> August and 14<sup>th</sup> September while adults between 21<sup>st</sup> August  
85 and 8<sup>th</sup> September. Only Garden Warblers with a small amount of visible fat were chosen and the body  
86 mass of the transmitter birds varied between 16.2g and 19.8g (mean 18.17g ± 1.01) in first-years and 16.2  
87 g and 19.9 g (mean 17.98 g ± 1.03) in adult birds. Radio-tagged birds were searched for every day in an  
88 area of approximately 7 x 10 km (Fig. 1c) using hand held three and four element Yagi antennas or by an  
89 antenna attached to the roof of a car. The area outside the study area was sometimes searched for birds that  
90 disappeared, but this was for practical reasons not possible to perform regularly. Transmitters were  
91 normally detected up to a distance of about 3-4 km. Birds carried the transmitters until they disappeared,  
92 but four transmitters fell off (three that were glued and one with leg-harness) and one other had its antenna  
93 broken and these were not included in the analysis. Trapping and attachment of radio transmitters were  
94 carried out under a licence issued from the Greek Ministry Agriculture and the Hellenic Bird Ringing  
95 Centre.

96

### 97 **Departure body mass**

98 When estimating the departure body mass, we have used the median stopover period of birds with  
99 transmitters that we have classified to have stayed in the study area until they departed for sub-Saharan

100 Africa (see results), and body mass of birds trapped at fig trees. The method used assumes that birds in fig  
101 trees are equally likely to be captured during any given day, and birds trapped at fig trees represent those  
102 that have established in the study area (*Fransson et al., 2008*) and that their body mass is increasing  
103 during their stopover. If the mean stopover duration at our site is  $\chi$ , then the mean body mass of the  $(1/\chi$   
104  $\times 100)$  % of the heaviest birds represent the departure morning body mass (see *Alerstam & Lindström,*  
105 *1990* for the logic behind this). When calculating the heaviest fraction of birds at fig trees we have  
106 included also body mass values from recaptures, which means that a small number of birds are involved  
107 with body masses from different days.

108

## 109 RESULTS

110 Mean body mass of birds trapped using tape lures on southern Crete was lower for first-year birds  
111 compared to adult birds (first-year birds:  $19.73 \pm 2.38$  g, 14.2 – 29.0, n= 636; adult birds:  $20.45 \pm 2.61$  g,  
112  $16.2 - 29.5$ , n=444; Mann-Whitney:  $Z=-4.277$ ,  $p<0.001$ ). First-year birds had shorter wings than adult  
113 birds (mean wing length of first year birds:  $79.9 \pm 1.6$  mm, n=640 and adult birds:  $81.1 \pm 1.7$  mm, n=445;  
114 Mann-Whitney:  $Z=-11.24$ ,  $p<0.001$ ). Adult birds trapped by means of luring show an increasing body  
115 mass against date (Spearman correlation;  $R_s= 0.15$ ,  $p= 0.001$ , n=450) while no such correlation was found  
116 in first year birds ( $R_s= 0.03$ ,  $p= 0.437$ , n=658).

117 Mean body mass of first-year birds trapped for the first time at fig trees was  $21.81 \pm 3.56$  g (14.6-34.0  
118 g, n=470) and was lower compared with adult birds  $23.47 \pm 3.26$  g (16.1-31.6 g, n=296; Mann-Whitney:  
119  $Z=-6.519$ ,  $p<0.001$ ).

120 More than half of the adult birds (54%) disappeared from the study area during the first nine days  
121 while the same figure for first-year birds was much less, 24% (Mann-Whitney:  $Z=3.509$ ,  $p<0.001$ ; Fig 2)  
122 and only a few individuals disappeared in the interval 7-9 d. Due to the bi-modal distribution of number of  
123 days transmitter birds were present in the area (Fig 2) and flight range estimates indicating that garden  
124 warblers have to make a considerable stopover and fuelling to be able to cross the desert (*Fransson, et al.*  
125 *2008; Barboutis, et al. 2011*), we have assumed that those that stayed longer than 9 d made a complete  
126 stopover in the study area. The median stopover duration for birds that stayed longer than 9 d was longer

127 for first-years (16 d, n=22) than adults (14 d  $\pm$  0.6, n=22; Mann-Whitney:  $Z=-1.993$ ,  $p=0.046$ ). The  
128 median distance from the trapping site to the place where birds spent their last day (Fig 1c) was shorter for  
129 first-years (0.8 km) compared to adults (2.1 km; Mann-Whitney:  $Z=-2.47$ ,  $p=0.018$ , Fig. 3). Out of the  
130 birds that disappeared from the study area three adult birds were eventually found at 8.5, 10.0 and 16.9 km  
131 from the trapping site (Fig 1b). All of them were recorded in the study area during the day of trapping only  
132 and were not found the following morning. They were relocated after three, six and eight days  
133 respectively and remained at those places until at least 10-12 days after the initial capture. One of them  
134 was followed in detail and left after 12 days and is included in the above calculations of stopover duration.

135 The morning body mass of the departure day in birds staying longer than 9 d is calculated as the  
136 average body mass out of the 1/16 and the 1/14 heaviest fractions of first-year and adult birds trapped at  
137 fig trees, respectively. In both cases the estimated average morning body mass during the last day of  
138 stopover was 29.5 g (range in first-year birds: 28.1 - 34.0 g and in adult birds: 28.6 - 31.6 g). To get body  
139 mass conditions in evening, prior to departure, we add one gram giving the estimated evening departure  
140 body mass of both first-year and adult Garden Warblers is 30.5 g.

141 From trapping at fig trees, it is clear that stopover site fidelity between years exists in garden warblers  
142 at this stage and nine birds were recaptured during a later autumn in the same area, in several cases in the  
143 same fig tree as they were initially ringed. Only two of those were ringed as first-year birds and one of  
144 them, ringed in 2009, was recaptured in both 2010 and 2011. Transmitters were attached to four of those  
145 during the year of ringing and two were followed in the area for more than ten days.

146

## 147 **DISCUSSION**

148 The results found in this study show that both first-year and adult Garden Warblers make an extensive  
149 stopover in autumn before crossing the Mediterranean Sea and the Sahara desert. The median stopover  
150 periods of about two weeks are approximately twice as long as found in Garden Warblers by using  
151 capture-recapture methods further north and west in Europe (*Schaub & Jenni, 2001*). It has, however, been  
152 shown when comparing telemetry and mark-recapture methods for estimating stopover duration that the  
153 telemetry method could result in much longer stopover durations (*Bächler & Schaub, 2007*). Adult birds



154 had an estimated stopover period significantly shorter than the one found in first-year birds and such age-  
155 related differences have also been found in other species during autumn migration (*c.f. Ellegren, 1991;*  
156 *Rguibi-Idrissi et al., 2003*). Both first-year and adult birds seem to make local movements during the first  
157 period of time after arrival, in adult birds this regularly involved leaving the study area while first-year  
158 birds, as shown by Fransson et al. (2008), normally stayed within the study area. This means that some  
159 birds included in the study might have arrived from other sites on Crete and thus had a longer stopover  
160 duration than estimated. Birds chosen for transmitters were however lean, indicating that they were  
161 trapped early during their stop over.

162 Both first-year and adult birds made a considerable fuelling gain during stopover and the estimated  
163 departure body mass is close to 100% fuel load compared with the body mass without fat (*Ellegren &*  
164 *Fransson, 1992*). The method used assumes that birds are equally likely to be captured during any day of  
165 stopover when settled at fig trees and that the heaviest birds are found on the departure day (*Alerstam &*  
166 *Lindström, 1990*). However, Bibby et al. (1976) found that the probability of trapping Sedge Warblers  
167 *Acrocephalus schoenobaenus* decreased with increasing body mass. We do not know if this is true also for  
168 Garden Warblers, but since they practically only feed on figs (based on analysis of faecal samples;  
169 Barboutis et al. unpubl. data) we believe the probability of trapping at fig trees should not change with  
170 body mass. Additionally As a portion of birds leave the study area, as shown by telemetry, this assumption  
171 is violated. The estimated departure body mass though, is probable not affected as the assumption stands  
172 true for birds staying over for more than 9 days which are the birds that show high body mass.  
173 Interestingly, the calculated departure body mass found in this study (30.5g) is very close to the one found  
174 using an average calculated fuel deposition rate from re-trapped birds in combination with stopover length  
175 on partly the same dataset of first-year Garden Warblers in Crete (30.3g; *Fransson et al., 2008*).

176 Birds trapped with tape lures show that adult Garden Warblers were significantly heavier than first-  
177 year birds and if a majority of them are newly arrived (*Schaub et al., 1999*), adult birds seem to arrive to  
178 Crete with larger energy stores than first-year birds. A pattern with heavier adults at sites close to  
179 ecological barriers during autumn migration has been described several times both in the Eurasian-African  
180 and the American bird migration system (*Veiga, 1986; Spina & Bezzi, 1990; Woodrey & Moore, 1997;*

181 *Yosef & Chernetsov, 2004*). This indicates that, at least in some species, age-related migration strategies  
182 exist in front of large ecological barriers. The difference found in body mass between adult and first-year  
183 birds trapped for the first time at fig trees might also be a result of adult birds arriving to Crete with larger  
184 energy stores.

185 The period of stopover is shorter in adult birds but no difference seems to exist in the departure body  
186 mass. Attaining a fuel load that ensures crossing from Crete to the southern edge of the Sahara is most  
187 certainly critical and might explain the pattern found in departure body mass. Since carrying fuel loads of  
188 the magnitude found in our study entails costs (*Alerstam & Lindström, 1990; Kullberg et al., 1996*), we  
189 can not expect birds to have much of a security margin at this point, unlike has been suggested for first-  
190 year Magnolia Warblers *Dendroica magnolia*, crossing the much shorter ecological barrier of the Gulf of  
191 Mexico (*Woodrey & Moore, 1997*). The distance to pass the Saharan desert includes stretches of about  
192 2200 km with few or no possibilities for a Garden Warbler to refuel. *Barboutis et al. (2011)* simulated the  
193 desert crossing and found that only one out of 14 transmitter birds with estimated departure fuel loads was  
194 unable to reach the southern edge of the desert due to low energy reserves. The bird that did not manage  
195 the crossing had an estimated departure body mass of 27.3 g, which is clearly below the range of body  
196 masses estimated for birds during their last day of stopover in this study.

197 Movements of radio-tracked birds during the stopover show differences in stopover behavior between  
198 first-year and adult Garden Warblers and a larger proportion of adult birds disappeared from the study area  
199 during the first 9 d. Among those that stayed longer and that we believed made a complete stopover in the  
200 study area, adult birds spent the last day before departure further away from the initial trapping site than  
201 first-year birds. Birds that left the study area shortly after ringing did not carry sufficient fuel loads to  
202 cross the Mediterranean Sea and the Sahara, thus it is more likely that they made stopover movements to  
203 places outside our study area. The fact that three adult birds were found away from the study area at places  
204 where they stayed for more than ten days support this. In several cases this movement was clearly done by  
205 nocturnal flights. This is in line with recent findings that birds during stopover often make nocturnal  
206 flights that include several km (*Mills et al., 2011; Taylor et al., 2011*)

207 Why are adult birds leaving the study area much more often than first-year birds? The fact that we have  
208 recaptured nine Garden Warblers in the same area as they were ringed during a preceding year clearly  
209 indicates that some of them are faithful to stopover sites. It might be that some birds are not able to locate  
210 the exact stopover site used the previous year but land at another place on Crete. If the new place is not  
211 satisfactory (fuel deposition rate, competition etc) based on expectation from previous years, they may  
212 later on relocate to the place where they stayed the previous year. This place might be some distance away,  
213 as shown by one adult bird found 17 km north of the release site. First-year birds on their first migration  
214 have no prior experience of suitable stopover sites and they also moved shorter distances than adults to  
215 find a site where they stayed. Even if many adults left the area after one day, there are still some that leave  
216 after a few days. Why this pattern exists we cannot explain at this stage. Stopover site fidelity seems not to  
217 be very common in songbirds, but it is interesting that it has been described several times close to the  
218 Sahara desert crossing and the crossing of the Mexican Gulf (*Moreau, 1972; Cantos & Telleria, 1994;*  
219 *Merom et al., 2000; Catry et al., 2004; Jubete et al., 2006; Somershoes et al., 2009; Vogt et al., 2012*).  
220 Since good stopover sites close to large ecological barriers could be of decisive importance for a  
221 successful passage (*cf. Fransson et al., 2008*) it might be that fidelity at those stopover sites has been  
222 advantages and thus specially favored/evolved in front of large ecological barriers.

## 223 CONCLUSION

224 In summary our study present evidence for age based behavioral differences in Garden Warblers  
225 regarding the strategies adopted in preparation for the crossing of a large ecological barrier. Differences  
226 found involve stopover duration as well as stopover movements, but in spite of those differences the  
227 estimated departure body mass of first-year and adult birds was very similar. Areas close to ecological  
228 barriers are critical for many birds to be able to make a successful crossing and as such those areas must  
229 be of high conservation interest in the near future. This is especially evident since the ongoing climate  
230 change might affect some of those areas very much (*Watson et al., 2013*).

231

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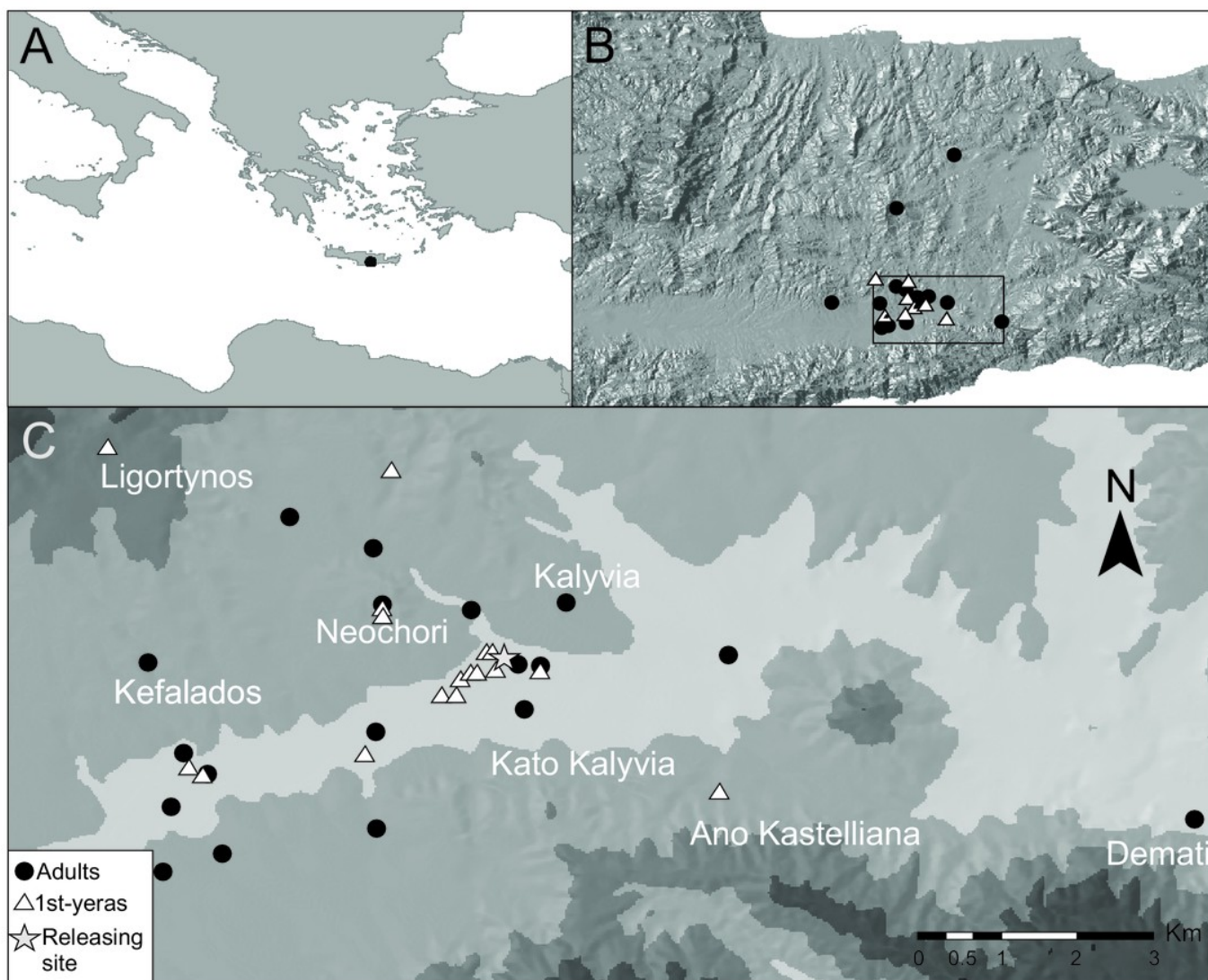
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# Figure 1

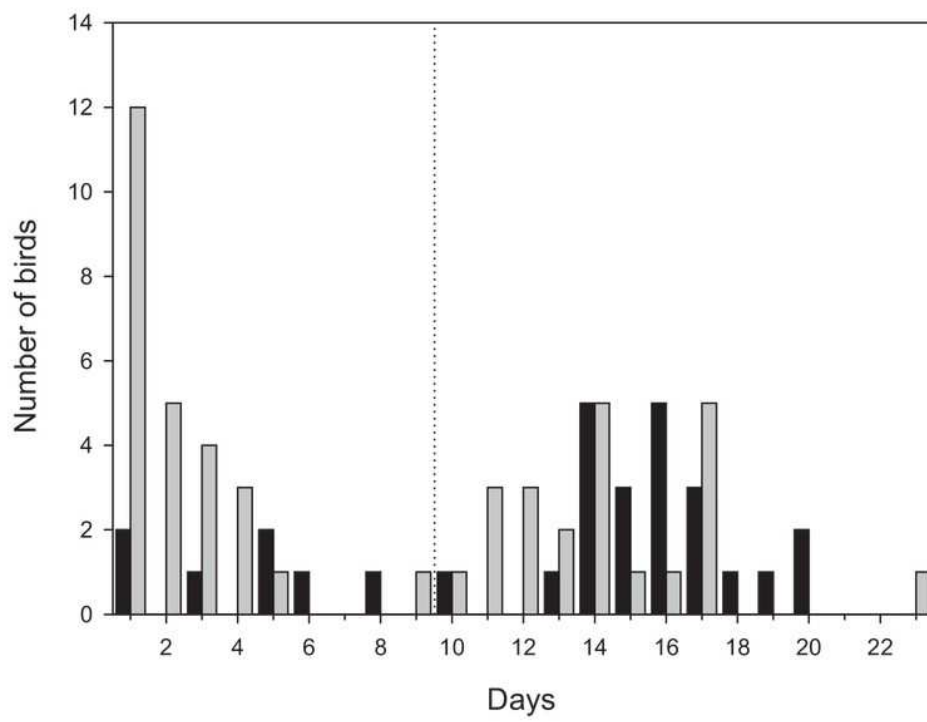
The study site.



## Figure 2

Number of days radio-tagged birds stayed within the study area.

Birds that stayed more than 9 days were classified as staying in the area for a full stopover (to the right of the dashed line). Black bars denotes first-year birds (n=29) and grey bars adult birds (n=48). One adult bird that moved outside the study area, but followed until it left after 12 days is included as well.



## Figure 3

Distribution of distances from the trapping site to the position where the bird spent the last day before take-off, for birds followed for a full stopover within the study area.

Black bars: first-year birds, n=22; grey bars: adult birds, n=21.

