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Research Article

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Arriving depleted after crossing of the Mediterranean: obligatory stopover patterns underline the importance of Mediterranean islands for migrating birds

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Abstract: Hundreds of millions of birds reach the Mediterranean islands or Mediterranean coast of Europe every spring after having crossed the Sahara Desert and the Mediterranean Sea. Using data from three small insular stopover sites, we calculated body mass without fuel for 18 trans-Saharan passerine migrants. We subsequently used arrival fuel loads coupled with potential flight range estimates to assess the percentage of birds that are forced to perform an obligatory stopover after crossing the Mediterranean Sea due to fuel depletion. Average arrival fuel loads were among the lowest ever recorded in the Mediterranean region and minimum body mass values recorded for several species were lower than any other individual value reported. The percentage of birds that needed to replenish their energy stores before resuming their northward migration journey varied from 0% to 50% depending on the species and locality studied. Based on conservative estimates at least 180 million birds of our study species are expected to migrate through Greece, 14% of which would not be able to resume their migration without refueling. The significance of small islands and coastal sites in the Mediterranean as obligatory refuelling sites is discussed and their conservation value for migratory birds is highlighted under the perspective of climate change.

Keywords: Stopover, Barrier crossing, Small islands, Fuel load, Conservation value

1 Introduction

Every year billions of birds, of thousands of species, cover enormous distances between their breeding and wintering grounds. Those seasonal movements regularly involve the crossing of vast ecological barriers such as deserts, mountain ranges and large water bodies. In the western Palaearctic migration system, most trans-Saharan passerine migrants have to cross the Sahara Desert and the Mediterranean Sea. In the central and eastern flyway, the desert and the sea can be considered as one ecological barrier as there are hardly any possibilities to refuel during crossing [1]. Thus, prior to the barrier crossing, birds should be energetically prepared for this demanding task [2-5].

Migration is indeed the most energy-demanding task in a bird's life cycle. When facing the Sahara Desert, a bird can cross it by intermittent flight, with stopovers to rest and refuel, whereas the Mediterranean Sea must be crossed in non-stop continued flight [6, 7]. Small and large islands scattered in the Mediterranean Sea are often the first available land that migratory birds encounter after crossing the Sea and the desert during their northward spring migration. Passerines arriving with depleted fuel reserves after crossing this large ecological barrier have

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been reported in central and eastern areas of the Mediterranean [8, 9]. A varying percentage of birds and species have enough energy reserves to resume their northward migration once reaching the Thyrrenian islands in the central Mediterranean [10], whereas cases of birds with no residual fat reserves or even dying from depletion are not uncommon [11]. Arrival energy reserves and environmental conditions at stopover sites could lead to increased stopover duration thus delay departure from sites [12, 13] and could even influence the breeding phenology and performance of birds [14]. Nevertheless, the importance of stopover sites such as islands just after the barrier crossing is not only limited to refuelling purposes as birds often need to rest or sleep after endurance flights [15, 16], settle until more favourable meteorological conditions occurs, or even gather information and/or socially interact with conspecifics to evaluate the progress of the migration journey [17]. Therefore, stopover site availability after barrier crossing and habitat suitability for fuelling are of particular importance for a successful migration.

According to optimal migration models [18], migrating birds should try to minimise either energy investment or duration of migration (i.e. time-minimizing scenario). It is therefore expected that birds arriving with high energy reserves will resume their journey as soon as possible while birds with low residual energy reserves have to restore them and remain at a stopover site. At this interplay between migratory decisions, insular stopover sites located after ecological barriers should be extremely important especially under the prospect of climate change; studies employing future projections have shown that responses of European birds include poleward shifts in their breeding and wintering distribution and such predicted changes will increase migration distances for some species rendering them susceptible to increased mortality risks [19].

Here, we aim to bring the significance of small islands in the Mediterranean into perspective and highlight their conservation value for migratory birds. To this aim, we use empirical data coupled with avian flight models to calculate the proportion of birds from different species that are not able to continue their migration (must perform an obligatory stopover) at three insular stopover sites in the eastern Mediterranean. Then, we use current data on breeding population sizes and calculated the number of birds that migrate through the region and therefore provide a quantitative estimate of birds that could potentially experience future changes to their migratory journeys.

2 Methods

2.1 Ethical approval

This study was carried out in accordance with the European Convention for the Protection of Vertebrate Animals Used for Experimental and Other Scientific Purposes of the Council of Europe (http://conventions.coe.int/Treaty/EN/Treaties/Html/123.htm.). Ringing permits for each location were issued annually by the Hellenic Ministry of Environment and Energy.

2.2 Sampling area and data collection

Data was collected at three small Greek islands, situated in the Libyan, the Aegean and the Ionian Sea. From south to north these were, Gavdos (34°50′ N, 24°5′ E) lying in the Libyan Sea, 40 km south of the island of Crete, Antikythira (35° 51′ N, 23° 18′ E) between the Aegean and the Ionian Sea, 40 km south of the island of Kythera and the Strofades islands (37° 15’ N, 21° 00’ E) in the Ionian Sea, 50 km south of the island of Zakynthos (Fig. 1). Birds were captured using 16x16mm mesh, nylon, mist nets. Mist netting took place from dawn and thereafter for at least eight hours, except for days with adverse weather conditions. The total length of mist nets used were 150m, 90m and 60m for Antikythira, Strofades and Gavdos respectively. Mist netting took place for a total of 76 days between mid-April and mid-May of 2011-2013 at Gavdos, for a total of 736 days between the end of March/May of 2007-2019 at Antikythira and for a total of 44 days between end of April and beginning of May in 2009 -2010, 2012 -2015 and 2018 at Strofades islands (Table S1). Mist nets were checked for trapped birds every hour. Trapped birds in all sites were aged according to Svensson [20] and weighed to the nearest 0.1 g. Maximum-chord wing length [20] was recorded to the nearest 0.5mm as a measure of body size. Visible subcutaneous fat was classified in 9 score ordinal scale (fat score) according to Kaiser [21] and bird’s pectoral muscle mass was visually classified in 4 score ordinal scale (muscle score), based on its shape [22]. We considered data from species that are known to cross the Mediterranean Sea and the Sahara Desert before arriving in each area in the following analyses.

2.3 Estimating body mass without fuel and arrival fuel loads

We estimated body mass without fuel (m_0), i.e. the body mass of a bird with both a fat score and a muscle score of 0, according to the structural mass concept [23]. Thus, it should be noted that this is the most conservative estimation as it reflects a bird's mass with neither fat nor protein to use as fuel. We applied a regression function of the m0 (mass of all birds with both a fat score and a muscle score of 0) on their respective maximum wing chord (hereafter wing length):

$$m_0 = b_0 + b_1 \times \text{wing length} \qquad (1)$$

where b_0 is the intercept and b_1 a constant from the regression. This regression was applied separately to all species trapped at our study sites with a sample size larger than 10. In order to estimate the fuel load (f; bird's body components which can be used as fuel), the following equation was used:

$$f = (m - m_0) / m_0 \qquad (2)$$

where m, is the body mass at capture and m_0 is the birds' body mass without any fuel.

2.4 Estimating potential flight range

Assuming that flying birds lose mass at a constant rate of 1% per hour of flight [24, 25], potential flight ranges (Y; hereafter flight range) were estimated according to the flight range equation developed by Delingat et al. [26]:

$$Y = 100 \times U \times \ln(1 + f) \qquad (3)$$

where U is airspeed. Regarding U, the species-specific values reported in Bruderer and Boldt [27] were used. When the species-specific value was not available the equivalent value of a closely similar species was used. Specifically for the Wood warbler (*Phylloscopus sibilatrix*), the Collared flycatcher (*Ficedula albicollis*), the Sedge warbler (*Acrocephalus schoenobaenus*) and the Woodchat shrike (*Lanius senator*), we used the airspeeds measured for the Willow warbler (*Phylloscopus trochilus*), the Pied flycatcher (*Ficedula hypoleuca*, the Reed warbler (*Acrocephalus scirpaceus*) and the Red-backed shrike (*Lanius collurio*) respectively. For two species with no available airspeeds, the Golden oriole (*Oriolus oriolus*) and the Common nightingale (*Luscinia megarhynchos*), the overall mean value for passerines, 10 m/s, was used [27, 28]. Flight range was estimated under still air conditions

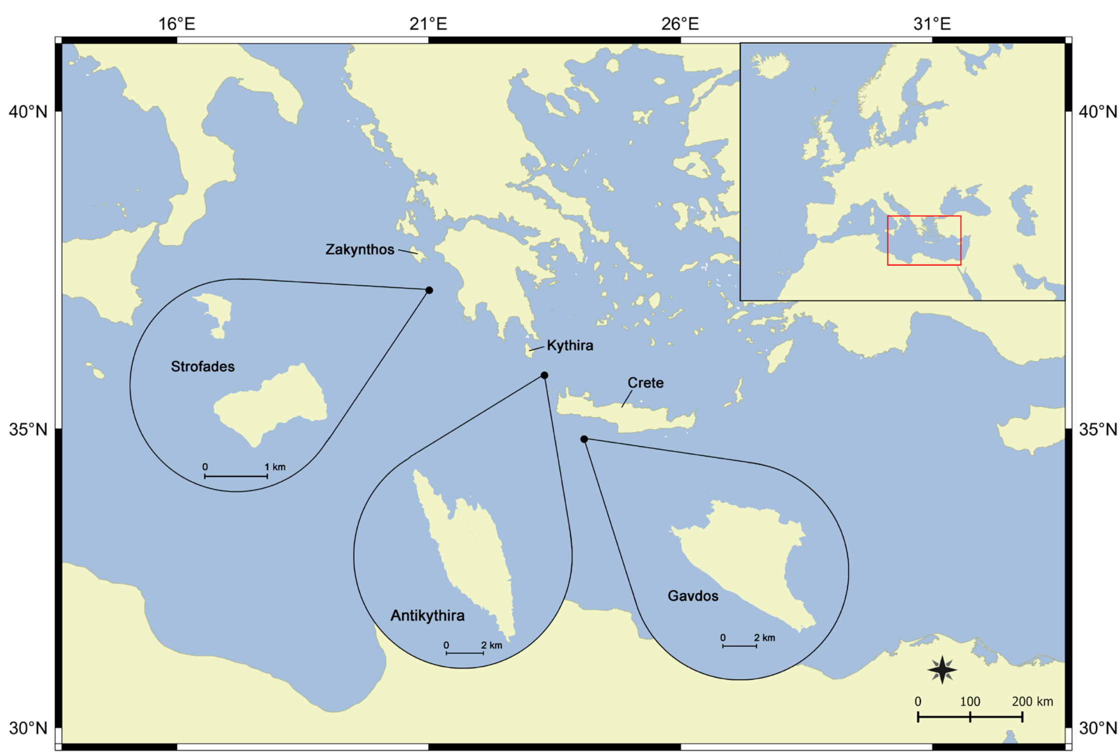

Figure 1. Map of our study area in eastern Mediterranean. Dots and zoomed insets show our study sites (Strofades, Antikythira, Gavdos), whereas the nearest to them larger islands are also noted (Zakynthos, Kythira and Crete respectively).

as wind direction is highly varying in the wider study area and the average tailwind component during the peak of the spring migration period is close to zero [29]. To estimate the percentage of birds that had the necessary fuel to reach the next larger island, where more refuelling opportunities are expected to exist (Fig. 1), the flight range equation was calculated for every individual bird trapped and we examined if they could continue their flight for 40 km in the case of birds trapped in Gavdos and in Antikythira and 50 Km in the case of birds trapped in Strofades. Due to the uneven sample size between the three study sites, the overall percentage of birds per species that could not continue their migration was estimated as the average of the estimated percentage of all sites.

2.5 Species and number of birds using the migration corridor

In order to provide a quantitative estimate of the number of birds belonging to our study species that use Greek islands and coastal sites as a migration corridor during spring, we used the most recent breeding bird population estimates included in the European Red List of Birds [30], following the approach of Hahn et al. [31]. More specifically, we used all ring recovery data for our study species that included birds ringed in Greece and recovered elsewhere during the spring migration and vice versa (data provided by the Hellenic Bird Ringing Center). Then, for each species we drew a minimum convex polygon around the recoveries and used the breeding population estimates for each country that was included in the polygon as an estimate of the number of birds that would migrate through Greece (Fig. S1). We did not consider non-breeders that could account for 15% within a population [31, 32] thus keeping our estimates rather conservative.

Furthermore, we assessed the number of species of trans-Saharan migratory birds belonging to passerines and near passerines (i.e. belonging to the orders Apodiformes, Caprimulgiformes, Cuculiformes, Coraciiformes, Piciformes, Columbiformes and Bucerotiformes) arriving to Greek islands and coastal areas in south Greece. For estimating the number of species, we used eBird's (www.ebird.org) bar chart tool [33] to retrieve records of species at the Peloponnese, the island of Crete, South Aegean and the Ionian islands, from March to May. Additionally, the daily ornithological species list of the Antikythira Bird Observatory held since 2008 on daily bases during spring migration period was used. Only species that winter south of the desert of the Sahara and are expected to reach Greece after having crossed the ecological barriers of the

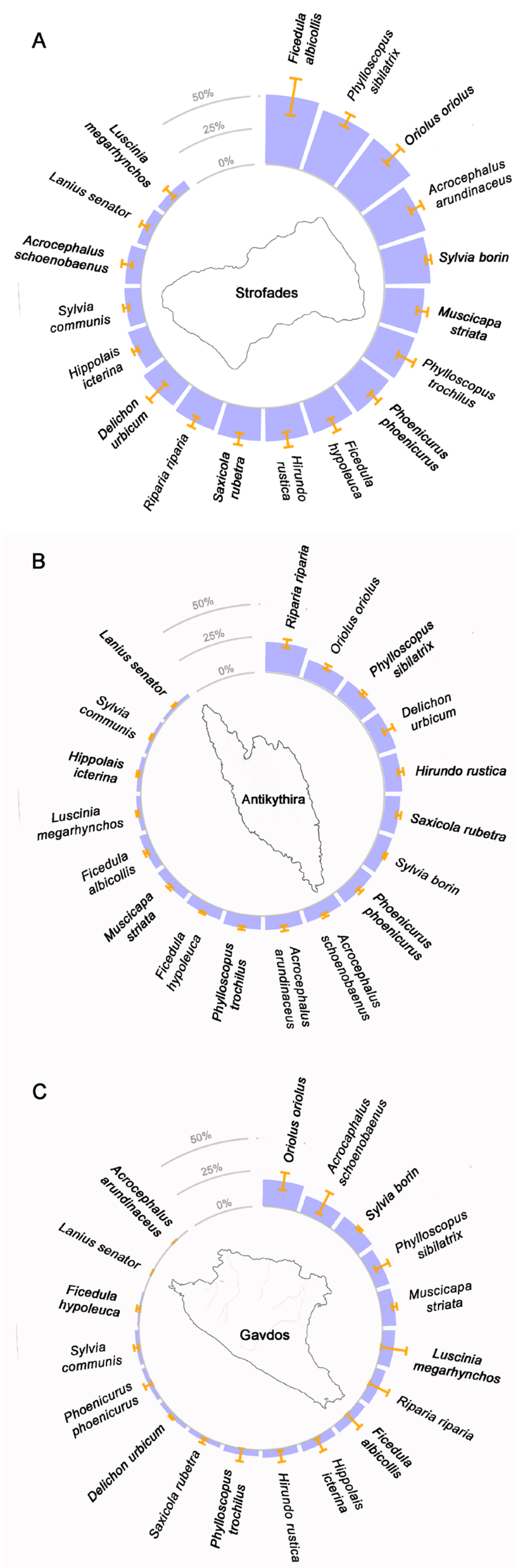

Figure 2. Percentage of birds per species that must perform an obligatory stopover in: a) Strofades, b) Antikythira and c) Gavdos. Orange bars depict standard error.

Sahara Desert and the Mediterranean Sea were included in this assessment.

3 Results

Mean arrival fuel loads were estimated for 18 trans-Saharan migratory passerine species (Table 1; Table S2; regressions calculated for species that had more than 10 birds with recorded wing length, body mass and fat and muscle score of 0). Fuel load of birds arriving to our study sites varied from 23.3% of their structural mass in the Icterine warbler (*Hippolais icterina*), to 8.7% in the case of Sand martin (*Riparia riparia*) across the three small islands (Table 1). The lowest average arrival fuel load was recorded for the Wood warbler (*Phylloscopus sibilatrix*) at Strofades islands (2% ± 7.9 % of structural mass) and the largest fuel load was recorded for the Woodchat shrike (*Lanius senator*) at Gavdos (31.7± 16.4 %). Potential flight range estimates were calculated for 38,253 birds arriving at our three study sites. The percentage of birds that could not resume their migratory flight to the nearest more suitable fuelling localities, varied from 50.6% in the case of the Collared flycatcher (*Ficedula albicollis*) arriving at Stofades islands, to 0% (all individuals could continue their migration) in the case of the Great reed warblers (*Acrocephalus arundinaceus*) and the Woodchat shrike arriving to Gavdos (Fig. 2; Table S3). Across all islands, a mean of more than 14% of the birds belonging to our study species were not able to resume their migration.

A conservative estimate of almost 184.9 million birds belonging to our study species migrate through Greece during spring, with the Willow warbler (*Phylloscopus trochilus*), the Barn swallow (*Hirundo rustica*), the Common whitethroat (*Sylvia communis*) and the Wood warbler being the most abundant ones, altogether accounting for almost 60% of all birds (Table S4). Of those

Table 1. Arrival fuel load (% of structural mass) per species for all birds and for each study site and minimum body mass recorded per species.

Species	Fuel load (% ± SD)	n	Min body mass	Antikythira Fuel load (% ± SD)	n	Gavdos Fuel load (% ± SD)	n	Strofades Fuel load (% ± SD)	n
Riparia riparia	8.3 ± 8.4	1592	8.1	7.5 ±8.0	1147	12.0 ± 9.4	240	8.7 ± 9.5	205
Oriolus oriolus	11.2± 10.8	1624	33.6	12.0 ± 11.0	1390	11.9 ± 11.4	87	2.8 ± 8.7	147
Delichon urbicum	11.6± 9.9	703	9.3	9.3 ± 9.9	386	17.2 ± 9.7	224	7.9 ± 10.4	93
Phylloscopus sibilatrix	12.3± 12.7	2768	5.5	13.2 ± 13.1	2466	15.4 ± 12.6	68	2.0 ± 7.9	234
Acrocephalus arundinaceus	14.3± 12.4	901	18.2	16.0 ± 12.9	692	19.8 ± 11.0	28	6.9 ± 10.8	181
Sylvia borin	14.9± 12.7	9030	9.5	17.0 ± 13.6	7116	13.1 ± 11.3	403	5.6 ± 8.8	1511
Ficedula hypoleuca	15.0± 12.5	3574	7.6	15.6 ± 12.8	3208	20.3 ± 10.7	80	6.4 ± 9.2	286
Acrocephalus schoenobaenus	15.3± 32.5	2314	6.3	15.9 ± 35.7	2000	15.5 ± 13.6	78	10.2 ± 10.9	236
Phoenicurus phoenicurus	15.6± 13.9	1304	9.0	16.2 ± 14.0	1131	18.0 ± 18.7	24	10.9 ± 11.8	149
Muscicapa striata	15.6± 12.4	3356	8.8	16.9 ± 12.6	2659	15.7 ± 12.5	230	8.2 ± 11.0	467
Hirundo rustica	16.0± 13.9	813	11.3	15.7± 13.6	598	18.0 ± 15.0	151	13.8 ± 14.3	64
Saxicola rubetra	16.5± 13.9	1379	9.5	15.9 ± 13.5	751	23.9 ± 15.6	293	11.2 ± 13.5	335
Ficedula albicollis	18.1± 13.0	1385	7.1	18.7 ± 13.1	1262	23.7 ± 12.5	41	6.7 ± 12.4	82
Phylloscopus trochilus	19.7± 17.2	1067	5.4	19.8 ± 17.1	986	21.7 ± 14.8	18	17.7± 18.6	63
Lanius senator	20.8± 11.9	1060	21.2	21.4 ± 11.8	829	31.9 ± 16.4	56	14.5 ± 11.0	175
Luscinia megarhynchos	21.5± 13.5	1328	11.3	21.9 ± 13.6	1261	20.3 ± 15.3	17	12.6 ± 10.7	50
Sylvia communis	22.5± 14.6	2515	9.3	25.1 ± 15.4	1730	24.6 ± 15.4	135	14.9 ± 12.5	650
Hippolais icterina	23.3± 14.3	1570	8.9	24.7 ± 14.8	1327	24.8 ± 14.5	67	12.3 ± 10.4	176

species the Willow warbler, Barn swallow and the Wood warbler were also estimated to be among the species with the largest number of birds that need to undertake an obligatory stopover at an island or a coastal locality when reaching Greece after the Mediterranean crossing (Fig. 3). Overall, an average of 30 million birds are estimated to perform an obligatory stopover. Additionally, it was assessed that 48 more passerines and close to passerines (66 species in total) reach Greece every spring after crossing the desert and the sea (Table S5).

4 Discussion

Birds arriving at Greek islands have either just crossed the Sahara Desert and the Mediterranean Sea thus experience relatively low average fuel loads or stop in the islands in good condition after refueling in North Africa. Fuel loads of species caught in our study sites such as the Spotted Flycatcher (*Muscicapa striata*), the Garden Warbler (*Sylvia borin*), and the Common Nightingale (*Luscinia megarhynchos*) are among the lowest values reported from other Mediterranean sites [34-37]. Additionally, minimum body mass values recorded for several species (*Acrocephalus schoenobaenus, Muscicapa striata, Phoenicurus phoenicurus, Riparia riparia, Saxicola rubetra, Sylvia borin*) were lower than any other minimum individual value reported [35, 37-40]. These results complement previous reports of birds with depleted fuel reserves reaching insular Greece during the northward migration [9, 41, 42].

The low arriving fuel loads at our study sites are probably a result of the vast length of the combined ecological barrier of the Sahara Desert and Mediterranean Sea that can reach or even exceed 2800 km [29], with hardly any possibilities to refuel. Surely refueling opportunities exist in North Africa [37] and that is reflected in the high percentage of individuals of some species that do not arrive depleted (e.g *Lanius senator*). However, there is evidence that species adapted to mesophilic and moist habitats show difficulties in successfully refuelling during migration in dry regions [43] like those of North Africa. Therefore, the low arrival fuel loads we recorded in this study indicate that there are probably not any widespread refuelling possibilities close to the African coast of the Mediterranean Sea before reaching the Greek islands.

Whether the fuel depleted birds arriving at Greek islands during spring are “fall-outs”, i.e. not capable of further migration [44], cannot be fully assessed based on this study. Our data suggest that some individuals perform

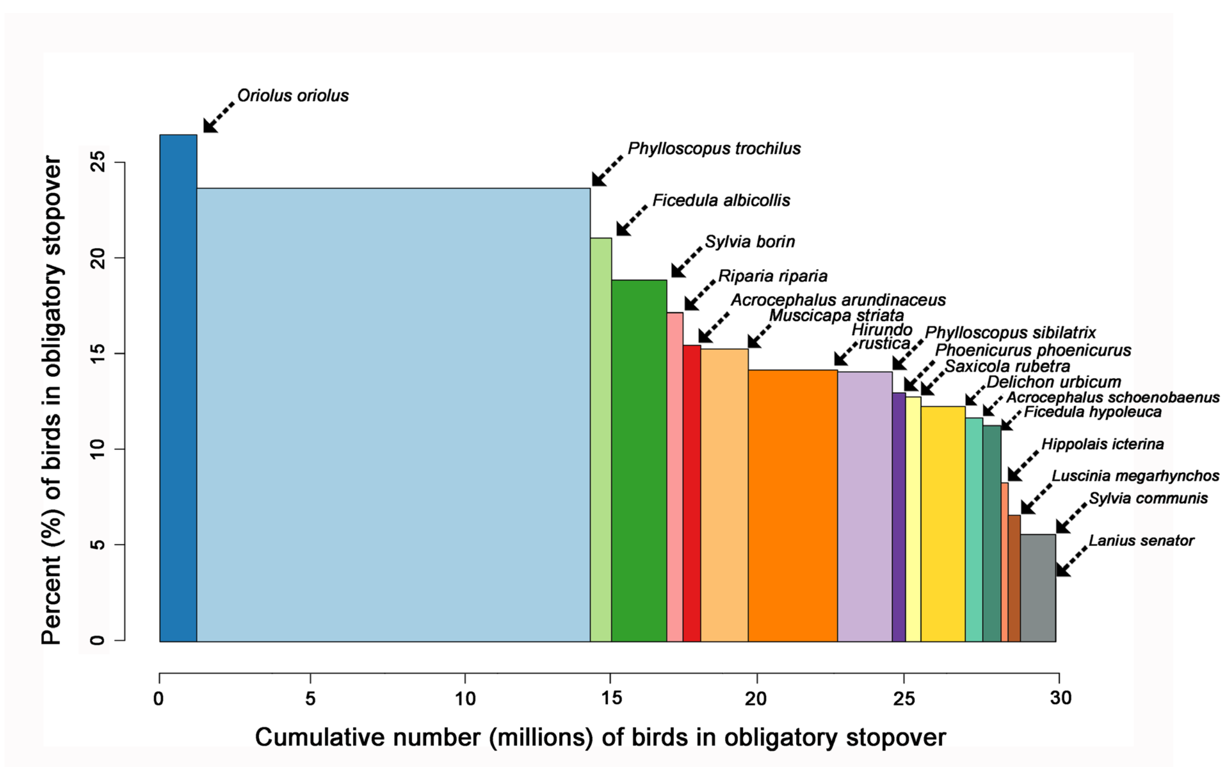

Figure 3. Overall percentage of birds that have to undertake a stopover in Greek islands and coastal sites and the respective cumulative estimate per species in millions of individuals.

an obligatory stopover being unable to continue their migration, however, other birds seem to actively decide to land depending on their fuel loads and species-specific habitat requirements [40]. Future assessment of the abundance of birds in the larger islands next to our study sites could shed some light on the fall-out hypothesis in the eastern Mediterranean region; if lean birds are more abundant in the "low-quality" small islands (that inherently offer fewer refuelling opportunities) it would seem that birds would have no option but land at the first available site after sea crossing [37]. Regarding the fate of the extremely lean birds we encountered, some preliminary data indicate that at least some extremely lean birds of some species could manage to recover during their stopover and resume their migration; having depleted a large amount of protein, mainly from the breast muscle [41] and the digestive organs [45] along with the fat reserves which are the main fuel [46], they are actively seeking and consuming nectar [47], an energy source readily obtained during spring time on north Mediterranean and easy to assimilate after their long-distance flight [48]. Additionally, evidence from Mauritania indicates that individual birds with fuel loads much below average are capable of recovering and refueling even in dire environments [39]. On the other hand, extended incidents of birds dying from depletion at our study sites are not unusual and have been observed during the course of this study with mortality rates being highest in Strofades islands. That could possibly result due to Strofades geographical position coupled with the general northern – northeastern spring migration direction, so birds have to undertake a longer barrier crossing and therefore more often reach the island depleted.

The pooled data from our three study sites indicate that the percentage of birds that are forced to undergo an obligatory stopover before leaving the islands varied from 25.5% in the case of the Golden Orioles (*Oriolus oriolus*) down to 3.3% in the case of Woodchat Shrike. Strikingly, in the case of the Collared flycatcher arriving to the island of Strofades, up to half of the individuals must refuel before resuming their migration. Based on our estimations approximately 30 million of birds belonging to the 18 study species perform an obligatory stopover at insular or coastal sites in Greece every spring. However, the estimates reported here should be treated with caution; the fact that we used a conservative method of estimating body mass without fuel has subsequently led to an underestimation of the number of birds that perform an obligatory stopover. Having in mind that as fat storage gets depleted, the portion of protein involved in active migratory flight increased [49], proteins produce eight time less energy compared to fat [46] and the low physiological stated of birds arriving to our study sites, a good proportion of birds that have been estimated to just being able to overpass our study sites might not actually not make it. Our calculations therefore, represent the minimum number of birds whereas the true number could in fact be much higher. At least 48 more species of trans-Saharan migratory passerines and non-passerines are also migrating through Greece every spring, and probably some individuals also reach the stopover sites energy depleted. Therefore, the amount of birds that need to undertake an obligatory stopover at insular or coastal sites in Greece could reach up to several hundreds of millions, making these stopover sites of outmost importance for the survival of migratory birds.

Although replenishing of energy reserves is considered the main aim of stopover events, birds do not stopover at insular sites in the Mediterranean only to refuel as shown by the large species variety of migrating birds recorded, of which many birds have enough fuel reserves to continue their norward journey [15]. Many birds, the numbers of which cannot yet be estimated sufficiently, need the stopover sites for non-fuelling purposes and will continue migration the following night. After long endurance flights over the Mediterranean Sea, birds seem to need to recover from sleep deprivation [50-52], whereas others might be forced to use stopover sites to avoid adverse weather conditions which are not rare during spring in the Mediterranean region [53]. Furthermore, local environmental conditions at stopover sites might be necessary for some species to evaluate and predict condition at final destinations further north [54].

The importance of Mediterranean islands is further brought into perspective if we consider the estimated obligatory stopover of hundreds of millions of birds under future changes in climate. Besides, migration is an adaptive strategy for organisms to exploit the seasonality in resource availability. There is so far plenty of evidence for the modification of migratory routes as a result of climate change in several avian species, including longer migratory journeys [19, 55, 56]. Longer flight ranges need increased energy demands which subsequently lead to more stopovers needed and ultimately can lead to a mismatch between time arrival and breeding [57]. Specifically for the Western Palearctic migration system, threats are even more ominous; increased drought events especially in areas adjacent to the Sahara Desert will effectively lead to the elongation of the barrier and could pose serious direct threats to migrating birds such as increased mortality rates. [58]. Considering our results, showing that at least 30 million of birds must perform stopover in insular or coastal sites in Greece regardless of habitat quality, even the smallest decrease of resources in these habitats could lead to extreme consequences; phenological mismatch between migratory birds and seasonal resources due to climate change has already resulted in population declines in some regions [59, 60]. However, behavioural flexibility of birds and the overall adaptive potential of populations to respond to changing conditions could alleviate the effects of these threats [61, 62]. It is possible for example that some refueling opportunities in Africa could partly mitigate further large-scale energy depletion. Conservation strategies could certainly benefit from a mitigation approach thus facilitating adaptation of birds in the new conditions though maintenance or restoration of a heterogeneous mosaic of resources. The ability to inform such conservation strategies though relies on the availability of knowledge from monitoring projects to perform vulnerability assessments [63] and further understanding of the evolutionary mechanisms through which climate change will affect individuals and populations [64, 65]. An ongoing monitoring of how migratory birds manage to cross the Sahara desert and the Mediterranean Sea is therefore of utmost importance.

Author contributions: C.B. conceived the idea. C.B., E.N., G.K., S.X. and T.F. collected the data. C.B. and A.B. analysed the data. C.B. and A.B. wrote the manuscript. All authors have read and approved the manuscript.

Data Availability: The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

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