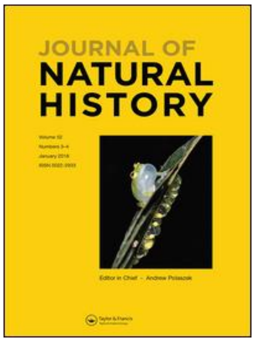

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# The diet of the Eleonora's falcon (*Falco eleonorae*) in the Aegean archipelago (Greece)

S. M. Xirouchakis[a,b], H. Alivizatos[c], E. Georgopoulou[a], A. Dimalexis[d], P. Latsoudis[c], D. Portolou[c], G. Karris[e], P. Georgiakakis[a], J. Fric[d], V. Saravia[c], C. Barboutis[c], S. Bourdakis[c], E. Kakalis[f], T. Kominos[c] and S. Simaiakis[b]

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**ABSTRACT**

In the present study we investigated the diet of Eleonora's falcons in Greece and assessed the regional dietary pattern of 16 breeding colonies of the Aegean. Overall 224 nests were visited and a total of 8067 prey items were collected which contained two mollusca classes, seven insect orders, one reptile family, two mammalian taxa and at least 54 avian species. Cicadas were the most common insects found in pellets (45.1%) followed by flying ants (34.8%) and beetles (15.8%) while just 20 species (33.3%) accounted for over 90% of the avian prey items identified in bird remains dominated (>50%) by the Willow Warbler (*Phylloscopus trochilus*), the Red-backed Shrike (*Lanius collurio*) and the Whitethroat (*Sylvia communis*). Insect feeding peaked in late August (39.8%) and late September (20.8%), whereas bird remains built up in falcon nests from mid-August onwards, culminating in late September (57.2%) and declined abruptly afterwards. Overall the falcons' diet diversity increased as the breeding season progressed and from the north towards the south Aegean. The avian prey species richness was negatively influenced by the distance of the colonies from the mainland and the weather conditions during September which coincides with the fledgling period of the young and the autumn peak of passerine migration.

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Diet diversity; Aegean Sea; *Falco eleonorae*; passerines; insects

## Introduction

The Eleonora's falcon is a medium-sized raptor and a long-distance migrant that overwinters mainly in Madagascar and breeds collonially on steep sea cliffs of unihabited islets and large islands (e.g. Cyprus) over the Mediterranean region and the eastern Atlantic, namely on the Canary Islands and the Moroccan coast (Walter 1979; Cramp and Perrins 1994). Its population numbers ca. 14,500 breeding pairs, with more than 85% of them concetrated on the Aegean archipelago in Greece (Dimalexis et al. 2008). The species is an aerial predator, feeding on insects in its wintering quarters and its breeding grounds till the egg-laying period and then upon bird migrants caught

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over the sea close to its colonies (Walter 1979). By this dietary shift the falcons take advantage of a plentiful food source i.e. the peak of the autumn migration (Cramp and Perrins 1994; Wink and Ristow 2000) at the price of their breeding cycle which is the most delayed among the birds of the northern hemisphere (Walter 1979; Spina et al. 1988; Ferguson-Lees and Christie 2001). The study of the Eleonora's falcon diet has been suggested as a valuable tool for assesing the temporal and spatial distribution of the migration flow and could provide even quantitative data on the abundace of migratoy passerines (Walter 1979; Ristow et al. 1986; Spina et al. 1987; Wink et al. 1993; De León et al. 2007).

Analysis of prey data of the Eleonora's falcon has been pursued across the species breeding and wintering range and relevant accounts on the composition of its diet are available (Araujo et al. 1977; Massa 1978; Walter 1979; Clark 1981; Mayol 1996; Thorstrom and Rene de Roland 2000; Ristow 2004; De León et al. 2007; Buij and Gschweng 2017 and references therein). The social life and evolutionary implications of the species insectivorus habits have also been highlighted (Ristow 2004) with significant conservation implications given the negative population trends in some Greek colonies due to secondary poisoning by pesticides, and food scarcity in Madagascar after locust-control campaigns in the 2000s (Tingle and McWilliam 1999; Thorstrom and Rene de Roland 2000; Ristow 2001; Tsatsakis et al. 2001; Peveling et al. 2003; Xirouchakis 2004; Sanderson et al. 2006). Furthermore the species breeding success rates are influenced by nesting habitat quality, parental care, intra-specific competition and rat predation but primarily by heat and food stress which are caused by adverse weather conditions i.e. low wind strength during autumn (Ristow and Wink 1985; Badami 1998; Xirouchakis et al. 2012).

Overall the species distribution pattern in both its breeding and wintering areas is strongly associated with climatic factors (i.e. wind, temperature, precipitation, solar radiation) which are most likely related to food availability (Kassara et al. 2012, 2017). This fact along with the species high degree of prey specialisation makes it most susceptible to climate change and in particular to fluctuation of atmospheric pressure systems which are regarded among the key-drivers of the migratory behaviour of passerines (Richardson 1990; Jenni and Kéry 2003; Gordo 2007; Jaffré et al. 2013; Kassara et al. 2017). In this context prey analysis at a regional scale would be most useful in detecting dietary patterns and identifying any mismatches between the Eleonora's falcon breeding activity and its food supply. In the present study we investigated the diet of the Eleonora's falcon in Greece aiming to provide an inventory on its prey species composition during the entire breeding season and assess any regional dietary discrepancies between colonies of different latitudes of the Aegean archipelago. Our aim was to provide a reference prey species list for future comparison of diet composition patterns among sub-populations, which could also be used in detecting variations in the prey species migration phenology and behaviour.

## Materials & methods

### *Data collection*

The study was carried out at 16 Eleonora's falcon colony-islets distributed over the north (north Sporades, $n$ = 4), central (Cyclades-Dodecanese, $n$ = 4), and south Aegean (Crete, $n$ = 8) at various distances from the mainland (0.4–46.5 km) and hosted a total of ca. 1,500 individual falcons or an estimated 540 breeding pairs (ca. 7.2% of the global population; Figure 1, Dimalexis et al. 2008). All islets were uninhabited, dominated by vegetation of coastal rocks namely halo-nitrophilous scrubs and received less than 300 mm of rainfall annually. The average temperature when falcons were present on them i.e. late spring to mid-autumn was 24 °C (range = 20–26). Excluding Dia island (north Crete, 11.2 km$^2$) the rest of the colony-islets were of tiny size (0.27 ± 0.95 km$^2$, range = 0.01–2.14) with the altitude of their highest point ranging between 10–200 m.a.s.l.

Overall 224 nests were visited from late May to mid-October during 2004, 2005 and 2006 and intact insect pellets ($n$ = 2,147) and bird remains i.e. complete body, wings, legs and feather pluckings were collected ($n$ = 252). On average seven nesting territories per colony were searched for prey leftovers by a team of 2–4 fieldworkers per visit (range = 2–-15). Fieldwork lasted from late morning (9:00–10:00 am) to early afternoon namely ca. 1 hr before dusk. Unexposed nests such as those located in potholes and rock cracks were

**Figure 1.** Map of the study area and sampling sites on Eleonora's falcon colony-islets: 1–4 (*north*), 5–8 (*central*) and 9–16 (*south*).

preferably sampled where feather pluckings had not been blown away by the wind. Insect pellets were usually found under prominent perching rocks near nests where they easily piled up. In each visit all prey items were collected and were kept in plastic bags with reference labels while relevant data were transferred into field protocols. Prey identification was made in the laboratory by comparison with reference collections of the Natural History Museum of Crete (e.g. exoskeleton fragments of invertebrates) and mammal and bird guides (Svensson and Grant 2001; Brown et al. 2003, 2004). The minimum number of individuals was estimated per pellet or avian remains and diet composition was assessed per two weeks period and per month in terms of prey frequency (i.e. number of items) and biomass. The latter was calculated for birds by the number of the different remains detected (e.g. wings, legs, skulls, feathers of the same body 'topography' etc.) multiplied by the mean weight of each prey species as this is reported in the literature (Snow and Perrins 1998). Insect prey was divided by taxa into dragonflies (Odonata), grasshoppers (Orthoptera), cicadas (Homoptera), beetles (Coleoptera), flies (Diptera), moths (Lepidoptera) and ants (Hymenoptera). Similarly bird prey were divided into 14 groups by families namely: raptors, waterbirds, game birds, pigeons, swifts and swallows, thrushes, pipits and wagtails, bee-eaters and hoopoes, nightjars, orioles and cuckoos, woodpeckers, warblers, flycatchers, shrikes, sparrows, finches and buntings.

### Statistical analysis

Apart from an initial prey list, total and average prey species richness and abundance were calculated for separate time periods (i.e. 2-weeks and months) and Aegean regions. The temporal and regional contribution of insects and birds to the falcons' diet was pursued in terms of both presence frequency (N% = number of prey items in each species/total number of species x100) and biomass calculated as averages (i.e. $B_i / N_{i,}$ $B_i$ = total biomass, $N_i$ = number of individuals) and respective comparisons were made by homogeneity G-tests (Zar 2009). Species rank-abundance (in a decreasing order of the numbers of individuals per prey species) and species accumulation curves (SAC) were calculated using the 'exact' method which computes the expected species richness and its standard deviation using a sample-based rarefaction process i.e. 100 permutations (Kindt et al. 2006; Chiarucci et al. 2008).

Diet diversity was investigated through prey species richness (i.e. the number of species) and species abundance (the number of individuals per species). In addition a number of indices were calculated such as the Shannon trophic diversity index $H' = -\sum_{\iota=1}^{R} p_i \ln p_i$, where $p_i$ is the proportion of individuals belonging to the $i^{th}$ species showing prey species richness and the evenness index $E = H'/\ln S$ (i.e. $S$ = total number of prey species) that ranges from 0 (i.e. presence of a dominant species) to 1 (i.e. all prey species are equally abundant and thus similarly significant in the diet) (May 1975; Washington 1984; Krebs 1989). As a measure of dominance, the Simpson index ($D = 1-\sum_{\iota=1}^{R} p_i^2$) was computed which gives more weight to the commonest prey species and takes values between 0 and 1 for generalist and specialist predators respectively. In the same sense the Berger index $d = N_{max}/N$ (where $N_{max}$ is the number of individuals in the most common prey species and N is the total number of individuals in the sample) was computed as a simple indicator of the numerical importance of the most abundant prey species. Differences in diet variability were analysed by Rényi diversity profiles (that unify the most common measures of species diversity) on the basis of equal sample sizes (e.g. numbers of falcon colonies) using a randomisation method aiming to achieve sample ordering (Kindt et al. 2001). Spatial and temporal prey composition similarities were explored by examining the fraction of species shared between sampling time periods and Aegean regions (i.e. Jaccard's index of similarity). For the same purpose the Morisita overlap index was also applied; $C_D = 2\sum_{\iota=1}^{S} x_i y_i/(D_x + D_y)\,XY$, where $x_i$ is the number of times species $i$ is represented in the total $X$ from one sample, $y_i$ is the number of times species $i$ is represented in the total $Y$ from another sample. $D_x$ and $D_y$ are the Simpson's index values for the $x$ and $y$ samples respectively and $S$ the number of unique species (0 for no overlap in terms of species, and 1 if the species occur in the same proportions in both samples) (Morisita 1959; Magurran 2004; Chao et al. 2005). Bird food niche breadth (FNB) per region and month was estimated by the Levin's index i.e. $L = 1/\sum_{i=1}^{R} pij^2$, where $p_{ij}$ is the fraction of prey items $i$ in the diet of food category $j$ (Levins 1968; Krebs 1989; Marti 2007). Non-parametric analyses were used in testing differences in the mean prey biomass and diet diversity among regions as well as between time periods (Zar 2009).

Nestedness metric based on overlap and decreasing fill (NODF; Almeida-Neto et al. 2008) was also used to measure nestedness among the Eleonora's falcon colony-islets (columns) and prey items (rows). A nested pattern is observed when assemblages of prey-items of sites with low species richness comprise non-random subsets of assemblages of richer sites. The software package NeD (Strona et al. 2014) was used to estimate NODF between 15-days interval sampling periods and within Aegean regions with Z-score values > 1.64 indicating significant nestedness at $p = 0.05$. To unveil diet preferences and express the relationship between species replacement (R), richness difference (D) and species similarity (S) the SDRsimplex approach was applied (Podani and Schmera 2011). The output scores were graphically reported using *ggtern* library (Hamilton 2017) in the open source R 3.4.2 programming language (R Development Core Team 2013).

Last, a dataset of explanatory variables (Table 1) were analysed (for 27 colony-years) by applying a generalised linear mixed-effect model (GLMM) with a log-link function of species richness (i.e. response variable) and a negative binomial error structure due to overdispersion of the observed number of prey species (count data) (Venables and Ripley 2002). Topography and weather variables (Table 1) were set as fixed effects whereas region and year were fitted as random effects. The contribution of each explanatory variable was tested with a manual F-test stepwise backward procedure by removing each variable from the full model and then comparing them using a type II ANOVA. Explanatory variables were initially examined for multicollinearity by inspecting correlation pair-plots and finally selected in the regression analysis by a Variance Inflation Function for values below three (McCullagh and Nelder 1989; Lin et al. 2011). Descriptive results are presented as means with one standard deviation (x ± s.d.). All statistical analyses were made at a 0.05 level of significance and were carried out with the software Past 3.0, SPSS 19, and the open source R 3.4.2 programming language and its contributing libraries *BiodiveristyR, vegan* and *lme4* (Hammer et al. 2001; Bryman and Cramer 2011; R Development Core Team 2013; Oksanen 2015; Bates et al. 2015; Kindt 2017).

**Table 1.** Topography and monthly means of weather variables in the Eleonora's falcon colonies (islets) in the Aegean Sea where diet samples were collected during May-October (2004–2006).

| Variable | Description | Source |
|---|---|---|
| Dismain | Distance of the colony-islet from the mainland (km) | 'Measure line' Tool in QGIS 2.18.3 (2017) |
| Colar | Area of the colony-islet (km$^2$) | 'Field calculator' Area function in QGIS 2.18.3 (2017) |
| Popcol | Colony size (number of individuals) | BirdLife Hellas database (2007) |
| Solar | Ground solar radiation (Watts/m$^2$) on the colony-islet | MODIS satellite images at 16-day intervals and 250m resolution (https://lpdaac.usgs.gov/lpdaac/get_data/data_pool) |
| Veg | NDVI* (0–1) at 25km-radius around the colony-islet | |
| Temp** | Ground temperature (°C) on the colony-islet | National Observatory of Athens at 3-hrs intervals daily and 2m a.s.l. (http://cirrus.meteo.noa.gr/forecast/bolam/index.htm) |
| Windsp** | Wind speed (km/h) on the colony-islet | |
| Windir | Wind direction (0–360 degrees) on the colony-islet | |

* Normalised Difference Vegetation Index remotely sensed by a satellite and calculated from the visible and near-infrared light reflected by vegetation i.e. near-infrared radiation minus visible radiation divided by near-infrared radiation plus visible radiation (Shunlin 2004).

## Results

Over the study years a total of 8,067 prey items were collected (Table 2) between late May and the end of October. In all, two mollusc, seven insect, one reptile, two mammalian taxa and at least 54 avian species were identified. The most infrequent prey items were snails that accounted for 84.6% of the molluscs, lizards ($n = 4$) of the genus *Lacerta* and pipistrelles bats that formed 78.6% of the mammalian prey (Table 2). Noteworthy the majority (92.8%) of bat remains were detected in pellets originated from the colonies around Crete at distance ranging from 0.4–10 km while 46.4% of them were traced in pellets from the Dia Island 10 km north of the coast of the city of Heraklion. Cicadas were the most common insects found in pellets (44.7%) followed by ants (35.3%) and beetles (15.8%) with most numerous ones those of the Scarabaeidae family (9.2%). The contribution of dragonflies, grasshoppers, flies and moths was insignificant i.e. <5%. Similarly, 16 avian species (ca. 30%) accounted in total for 88.5% of the falcons' avian prey items by number. Three avian species dominated the diet namely the Willow Warbler (*Phylloscopus trochilus*), the Red-backed Shrike (*Lanius collurio*), and the Whitethroat (*Sylvia communis*) which accounted for ca. 60% of all the bird prey items. Besides, the bird prey species accumulation curves showed that the rate at which new species were found in falcon nests levelled off quickly after sampling about five colonies depicting a rather sufficient sampling effort (Figure 2). On a weight (biomass) basis, 12 identified species (i.e. 22.2%) made up 81.2% by weight of the diet and the remaining 42 adding only 18.8%. The Red-backed Shrike, the Whitethroat, the Moorhen (*Gallinula chloropus*), the Turtle Dove (*Streptopelia turtur*), the Willow Warbler and the Whinchat (*Saxicola rubetra*) were the most important prey species that accounted for 54% of the total biomass consumed by the falcons.

Pellets were accumulated from early June through late September and dropped afterwards showing a trimodal pattern of insect feeding namely in late July (19.7%), late August (38.4%) and late September (19.9%). Likewise, bird remains were collected from mid-June to late October building up substantially from mid-August onwards and culminating during the second half of September (57.6%). These differences were significant by testing if the observed frequency of insect and avian prey followed their actual availability i.e. number of pellets and pluckings collected in each time period and region respectively (G-tests, $P < 0.0001$). No significant spatial differences were found in the frequencies of

**Table 2.** Animal taxa and species identified in pellets and prey remains collected from Eleonora's falcon nests in colonies of the Aegean archipelago during May-October (2004–2006).

| | No. of individuals | % occurrence frequency | % biomass |
|---|---|---|---|
| **AEGEAN** | | | |
| Pellet (n) | 2147 | | |
| Pluckings (n) | 252 | | |
| **MOLLUSCA** | 39 | | |
| Gastropoda indet. | 33 | 84.6 | |
| Bivalvia indet. | 6 | 15.4 | |
| **INSECTA** | 5317 | | |
| **Odonata** | 6 | 0.1 | |
| Aeschnidae | 6 | 0.1 | |
| **Orthoptera** | 49 | 0.9 | |
| Acrididae | 49 | 0.9 | |
| **Homoptera** | 2399 | 45.1 | |
| Cicadidae | 2399 | 45.1 | |
| **Coleoptera** | 841 | 15.8 | |
| Carabidae | 81 | 1.5 | |
| Scarabaeidae | 497 | 9.3 | |
| Buprestidae | 66 | 1.2 | |
| Alleculidae | 141 | 2.7 | |
| Coleoptera indet. | 62 | 1.2 | |
| **Diptera** | 151 | 2.8 | |
| Tipulidae | 10 | 0.2 | |
| Tabanidae | 4 | 0.1 | |
| Diptera indet. | 137 | 2.6 | |
| **Lepidoptera** | 21 | 0.4 | |
| Nymphalidae | 4 | 0.1 | |
| Noctudidae | 8 | 0.2 | |
| Sphingidae | 8 | 0.2 | |
| Lepidoptera indet. | 1 | 0.0 | |
| **Hymenoptera** | 1850 | 34.8 | |
| Formicidae | 1850 | 34.8 | |
| **REPTILIA** | 4 | | |
| Lacerta spp. | 4 | 100 | |
| **AVES** | 2826 | | |
| *Coturnix coturnix* | 35 | 1.2 | 4.7 |
| *Ixobrychus minutus* | 4 | 0.1 | 0.8 |
| *Falco tinnunculus* | 1 | 0.03 | 0.3 |
| *Crex crex* | 3 | 0.1 | 0.7 |
| *Porzana parva* | 6 | 0.2 | 0.4 |
| *Gallinula chloropus* | 19 | 0.7 | 8.3 |
| *Calidris alpina* | 1 | 0.03 | 0.1 |
| *Tringa glareola* | 3 | 0.1 | 0.3 |
| *Columba livia* | 4 | 0.1 | 1.4 |
| *Streptopelia turtur* | 18 | 0.6 | 7.0 |
| *Caprimulgus europaeus* | 4 | 0.1 | 0.5 |
| *Otus scops* | 1 | 0.03 | 0.2 |
| *Apus apus* | 22 | 0.8 | 1.2 |
| *Cuculus canorus* | 9 | 0.3 | 1.4 |
| *Clamator glandarius* | 1 | 0.03 | 0.2 |
| *Merops apiaster* | 27 | 1 | 2.1 |
| *Upupa epops* | 40 | 1.4 | 3.5 |
| *Jynx torquilla* | 37 | 1.3 | 1.8 |
| *Hirundo rustica* | 30 | 1.1 | 0.8 |
| *Anthus trivialis* | 12 | 0.4 | 0.3 |
| *Motacilla flava* | 24 | 0.8 | 0.6 |
| *Erithacus rubecula* | 8 | 0.3 | 0.2 |
| *Phoenicurus phoenicurus* | 29 | 1 | 0.6 |
| *Saxicola rubetra* | 255 | 9 | 6.6 |
| *Luscinia megarhynchos* | 110 | 3.9 | 3.2 |

(*Continued*)

**Table 2.** (Continued).

| | No. of individuals | % occurrence frequency | % biomass |
|---|---|---|---|
| *Oenanthe oenanthe* | 25 | 0.9 | 0.8 |
| *Oenanthe hispanica* | 5 | 0.2 | 0.1 |
| *Locustella lusciniodes* | 6 | 0.2 | 0.1 |
| *Acrocephalus schoenobaenus* | 15 | 0.5 | 0.2 |
| *Acrocephalus scirpaceus* | 16 | 0.6 | 0.3 |
| *Acrocephalus arundinaceus* | 12 | 0.4 | 0.5 |
| *Acrocephalus* spp. | 7 | 0.2 | 0.2 |
| *Hippolais icterina* | 11 | 0.4 | 0.2 |
| *Hippolais pallida* | 3 | 0.1 | 0.0 |
| *Sylvia melanocephala* | 1 | 0.03 | 0.0 |
| *Sylvia cantillans* | 4 | 0.1 | 0.1 |
| *Sylvia communis* | 458 | 16.2 | 8.9 |
| *Sylvia atricapilla* | 67 | 2.4 | 1.5 |
| *Sylvia borin* | 17 | 0.6 | 0.4 |
| *Sylvia* spp. | 28 | 1 | 0.6 |
| *Phylloscopus sibilatrix* | 13 | 0.5 | 0.2 |
| *Phylloscopus collybita* | 5 | 0.2 | 0.0 |
| *Phylloscopus trochilus* | 646 | 22.9 | 6.7 |
| *Phylloscopus* spp. | 7 | 0.2 | 0.1 |
| *Muscicapa striata* | 52 | 1.8 | 1.1 |
| *Ficedula albicollis* | 3 | 0.1 | 0.0 |
| *Ficedula parva* | 5 | 0.2 | 0.1 |
| *Lanius collurio* | 464 | 16.4 | 16.5 |
| *Lanius senator* | 11 | 0.4 | 0.4 |
| *Lanius minor* | 6 | 0.2 | 0.2 |
| *Lanius* spp. | 3 | 0.1 | 0.1 |
| *Oriolus oriolus* | 50 | 1.8 | 4.3 |
| *Carduelis carduelis* | 4 | 0.1 | 0.1 |
| *Passer hispaniolensis* | 5 | 0.2 | 0.2 |
| *Emberiza* spp. | 5 | 0.2 | 0.1 |
| Passeriformes indet. | 161 | 5.7 | 8.4 |
| Aves indet. | 8 | 0.3 | 0.6 |
| **MAMMALIA** | 28 | | |
| *Pipistrellus* spp. | 22 | 78.6 | |
| Vespertilionidae indet. | 6 | 21.4 | |
| **Total** | **8067** | | |

birds preyed between north, central and south Aegean colonies (G-test, $X^2 = 2.7$, d.f. = 3, $P = 0.26$) or between those of west, central and east Crete which are quite distant apart (G-test $X^2 = 5.9$, d.f. = 3, $P = 0.052$). The latter pattern was also detected for insect prey between west and east falcon colonies of Crete (G-test $X^2 = 3.8$, d.f. = 3, $P = 0.05$). Regarding the temporal composition of separate insect taxa in the diet, beetles predominated from mid-June to mid-July, cicadas from mid-July onwards peaking in early September while ant consumption culminated in early August (Figure 3(a)). In October the insect prey consisted exclusively of ants and grasshoppers, but the sample size was unreliable (n = 4). Warblers were the main prey species of the falcon's bird diet throughout the breeding season followed by shrikes and thrushes (G-test, $P < 0.0001$, Figure 3(b)). The narrowest bird food spectrum was observed from the beginning of the breeding season until mid-July where warblers, thrushes, flycatchers and wagtails (16–31 June) as well as robins and chats (1–15 July) were the main species identified in bird remains collected at falcon nests (G-test, $P < 0.0001$, Figure 3(b)).

Species richness of insect prey reached its maximum in late August while for bird prey increased progressively with the onset of the breeding season and peaked in late

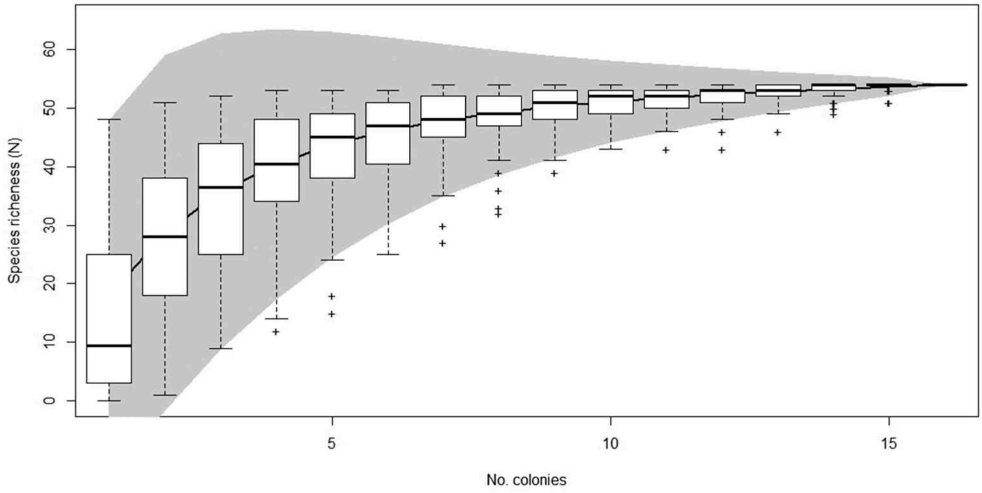

**Figure 2.** Expected *(shaded area of average Species Accumulation Curve and standard deviation)* and observed *(boxplots with mean and confidence intervals)* avian prey species richness of the Eleonora's falcon based on the number of the colonies sampled (n = 16).

September. The highest number of prey species for both taxa was recorded in the south Aegean colonies. Nevertheless, the Shannon diversity index which associates species abundance and relative richness among species showed that insect prey was more diverse in early July and in central Aegean colonies, whereas avian prey composition was most diverse during late August and in south Aegean colonies (Table 3). Dominance indices showed a diverse insect diet along the breeding season with the highest values observed in early July where in the meantime a 'monoculture' of avian prey was recorded. At a spatial scale a rather even distribution in prey items among all Aegean colonies was noted (Table 3). Noteworthy the E-evenness index indicated that the falcons' diet was enhanced in both insect and avian prey species as the breeding season progressed and from the north to the south Aegean colonies (Table 3). The Rényi average diversity profiles advocated this spatial tendency for prey species richness but with an even distribution of diet composition in central and south colonies (Figure 4).

The Levin's index of bird food niche breadth was similar among Aegean regions (i.e. 0.96) but temporally it increased till its first peak in August, dropped considerably in September and peaked again in October. The Jaccard's index indicated no spatiotemporal dissimilarities in the falcons' diet apart from a rather low percentage (ca. 30%) of common insect prey among July and September. On the contrary the Morisita overlap index showed a low similarity in space and time in diet composition with a downward trend from mid-July onwards, although bird diet among July and September was found quite similar ($C_d$ = 0.75). Furthermore a significant degree of nestedness was detected between the two weeks sampling periods for bird (NODF = 71.67, $p < 0.001$) and insect (NODF = 78.19, $p < 0.001$) prey species. Only prey bird (NODF = 74.79, $p < 0.001$) and insect species (NODF = 77.44, $p < 0.001$) in the South Aegean region were significantly nested. Regarding the Central and North Aegean islet groups, no nested patterns in the diet preferences of the Eleonora's falcons were observed (Table 4). Based on the SDRsimplex approach high

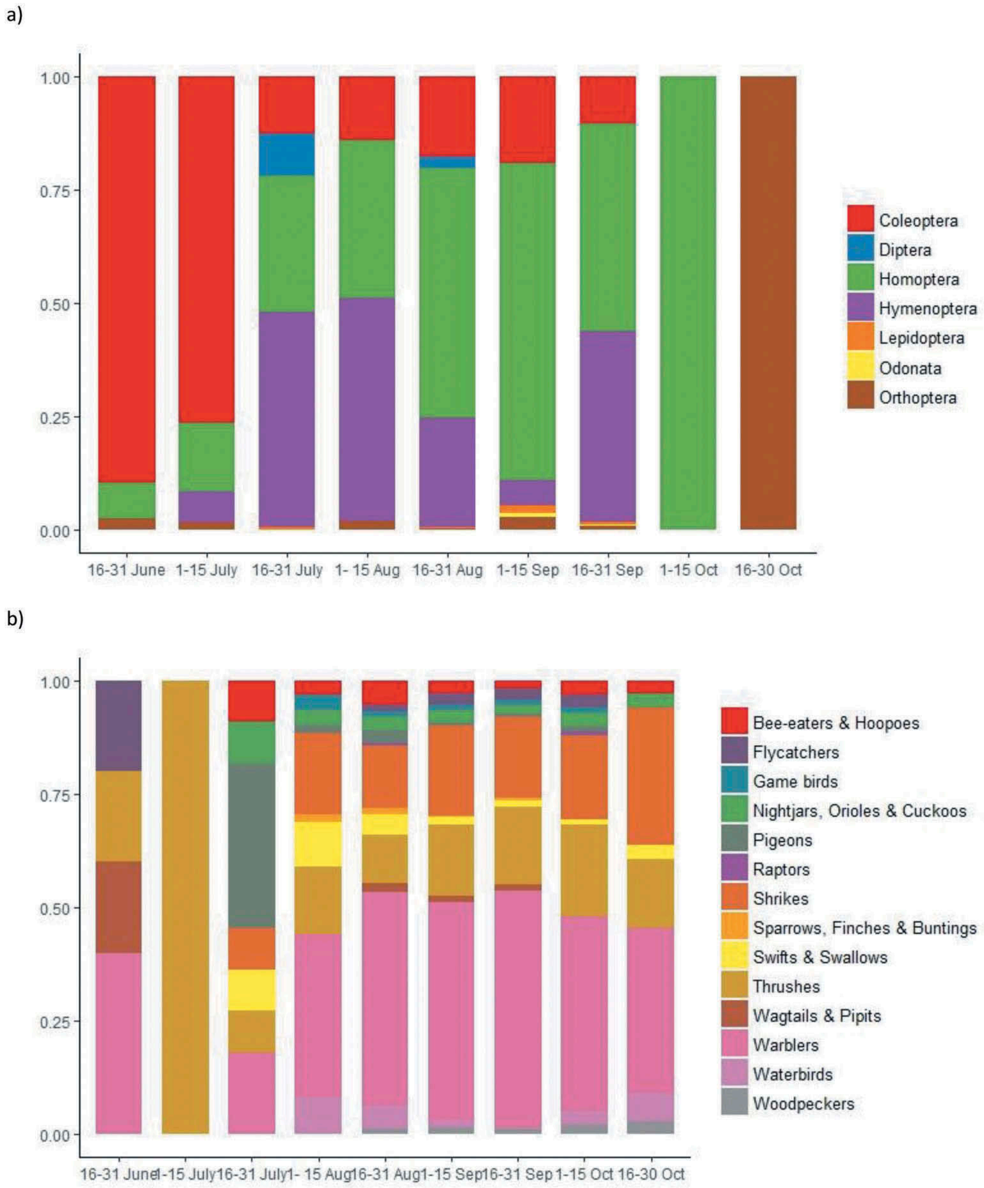

**Figure 3.** Temporal variation in the (a) insect and (b) bird diet of the Eleonora's falcon during the breeding season in the Aegean archipelago.

richness differences are observed for bird (D = 59.43%) and insect (D = 48.93%) prey species with a moderate to high degree of similarity (S = 24.10% and R = 39.76% for bird and insect prey species respectively) and low species replacement (R = 16.46% and R = 11.31% for bird and insect prey species respectively) at the temporal scale. At the spatial scale, only the South Aegean region was considered because the North and Central Aegean regions had a small (unreliable) sample size. In the South Aegean region high richness differences and species similarity were reported for bird and insect prey species

**Table 3.** Diversity of insect and bird prey species of Eleonora's falcon diet in the Aegean. (*r = Species richness, H´ = Shannon diversity Index; D = Simpson dominance index, B = Berger dominance index, E = Evenness. Left column: Insects, Right column: Birds*).

| Time period/Aegean Regions | *r* | | *H′* | | *S* | | *B* | | *E* | |
|---|---|---|---|---|---|---|---|---|---|---|
| 16–31 June | 6 | 5 | 1.44 | 1.61 | 0.29 | 0.20 | 0.45 | 0.20 | 0.71 | 1.00 |
| 1–15 July | 7 | 1 | 1.74 | 0.00 | 0.20 | 1.00 | 0.31 | 1.00 | 0.81 | 1.00 |
| 16–31 July | 11 | 10 | 1.37 | 1.90 | 0.33 | 0.22 | 0.48 | 0.42 | 0.36 | 0.67 |
| 1–15 August | 10 | 24 | 1.29 | 2.71 | 0.37 | 0.09 | 0.49 | 0.14 | 0.36 | 0.62 |
| 16–31 August | 13 | 38 | 1.32 | 2.76 | 0.37 | 0.10 | 0.55 | 0.20 | 0.29 | 0.42 |
| 1–15 September | 10 | 46 | 1.15 | 2.57 | 0.51 | 0.13 | 0.70 | 0.25 | 0.32 | 0.28 |
| 16–31 September | 11 | 50 | 1.16 | 2.58 | 0.39 | 0.13 | 0.46 | 0.24 | 0.29 | 0.26 |
| North | 6 | 24 | 1.67 | 2.59 | 0.21 | 0.12 | 0.26 | 0.22 | 0.89 | 0.56 |
| Central | 8 | 41 | 1.88 | 2.47 | 0.18 | 0.14 | 0.27 | 0.27 | 0.82 | 0.29 |
| South | 16 | 53 | 1.29 | 2.63 | 0.37 | 0.13 | 0.51 | 0.22 | 0.23 | 0.26 |

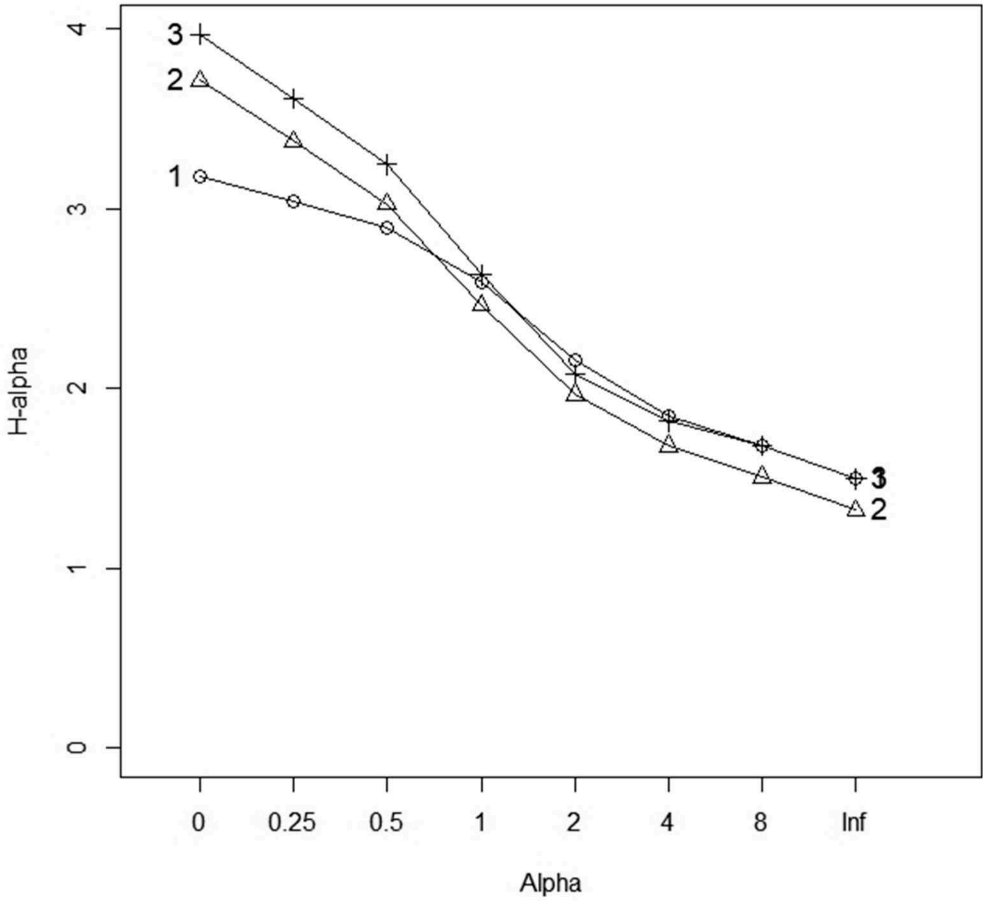

**Figure 4.** Rényi diversity profile of the Eleonora's falcon avian prey in north (1), central (2) and south (3) Aegean colonies. (*Profile values at scale parameter Alpha = 0, 1, 2 and infinite corresponding to Shannon diversity index, Simpson diversity index and Berger–Parker dominance index, respectively*).

**Table 4.** Summary results of nestedness (NODF) and percentage contributions from the SDRSIMPLEX analyses between sampling periods (i.e. 2-wks from mid-June to late September) and within Aegean regions.

| GROUPS | NODF | | SD | | Z-value | | S | | D | | R | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Between sampling periods | 71.67* | 78.19* | 3.52 | 6.10 | 5.99 | 3.20 | 24.10 | 39.76 | 59.43 | 48.93 | 16.46 | 11.31 |
| North | 48.43$^{\text{n.s.}}$ | 43.59$^{\text{n.s.}}$ | 6.14 | 13.63 | 0.04 | −0.75 | 15.90 | 37.57 | 55.17 | 8.47 | 28.93 | 53.97 |
| Central | 26.16$^{\text{n.s.}}$ | 53.76$^{\text{n.s.}}$ | 5.61 | 9.37 | −3.16 | −0.41 | 10.71 | 58.33 | 79.33 | 8.33 | 9.96 | 33.33 |
| South | 74.79* | 77.44* | 2.96 | 6.44 | 5.59 | 2.04 | 38.46 | 56.61 | 44.30 | 34.20 | 17.24 | 9.19 |

NODF, total matrix nestedness; SD, standard deviation; Z-value, S, relativized species similarity %; D, relativized richness difference %; R, relativized species replacement %. *P < 0.001, n.s.: not statistically significant.

**Table 5.** Results of the GLMM investigating the variation of the falcons' avian prey species richness in relation to topographic characteristics and weather variables falcon colonies (islets) in the Aegean Sea during August-September (2004–2006).

| Variable | Estimated coefficients | z value | *P* |
|---|---|---|---|
| Intercept | 8.46755 | 3.948 | 7.9e-05 *** |
| Distance of the colony-islet from the mainland (km) | −0.01777 | −1.752 | 0.07981 . |
| Area of the colony-islet (km$^2$) | −0.07724 | −2.681 | 0.00735 ** |
| Ground temperature (° C) on the colony-islet | −0.22236 | −2.573 | 0.01007 * |

(Table 4). Moderate to low were the richness differences of insect prey species in the three regions (Table 4). In the final glmm model three explanatory variables were retained (Table 5) namely the proximity of the islet-colony to continental areas (which was marginally significant), the islet area and the temperature. In specific prey species richness was expected to increase with decreasing distance of the falcons' colonies from the mainland, the islet size and the temperature during the peak of autumn migration (i.e. August-September).

## Discussion

Raptor dietary habits are investigated by numerous techniques that include pellet and stomach-content analysis, examination of prey remains collected at nests, direct observation of prey deliveries to nests and constant photographic or video monitoring (Marti 2007). Comparison of prey remains, pellet contents, and prey delivery videography showed that the latter was the most cost-effective method producing the least biased data (Booms and Fuller 2003; Lewis et al. 2004). Direct observations result in biases towards easily identified species (Sharp et al. 2002) while pellets frequently fail to detect several species found in prey remains. Nevertheless, depending on the species studied, pellet analysis and prey deliveries to nests recorded by visual monitoring may provide similar results (Taylor 1994). In the present study we performed prey remain and pellet analysis which offered a realistic picture of the Eleonora's falcon diet and is recommended as the best procedure if direct observations are not feasible (Pavez et al. 1992; Real 1996; Sequin et al. 1998).

The diet of the Eleonora's falcon in the Aegean archipelago consists primarily of small birds and insects. Some other taxa are occasionally consumed but they should not be considered as regular food items. For instance, snail shells were frequently found in falcon pellets as well as bats, which seem to be easily captured if readily available near the colonies. On the other hand, Lacertidae were the only reptile species found in pellets, but lizards should be regarded as unintentional kills rather than common prey items (Walter 1979). Considering that lizards are found in very high densities in the islets of the Aegean (Pafilis et al. 2013) they should aggregate in prey remains as a significant food source. However, lizards live commensally in falcon nests exploiting scraps of prey (Walter 1979; Fadda and Medda 2001; Delaugerre et al. 2012) and the falcons may kill them accidentally or deliberately as pests and not for consumption purposes. Regarding non-bird prey items these were primarily to cicadas, flying ants and beetles and to a lesser extent to moths, dragonflies and grasshoppers. The temporal consumption of these taxa followed their annual life cycle coinciding with their local abundance after their emergence period (Boer 1970; Patterson et al. 1997; Hedin et al. 2008). However, given that insect pellets were largely collected in colony-islets close to Crete (400 m), we suspect some insect taxa were selected by the falcons due to their availability in rural habitats (i.e. vineyards and olive groves). In this sense insect prey resources could not be classified as ephemeral and consequently the Eleonora’s falcon should be regarded as an insectivorous specialist. Moreover in contrast to other studies insect pellets did not decrease in numbers as the falcons turned to birds during the chick-rearing period (Ristow 2004). In the current study insect predation took place from mid-July throughout September probably depicting temporary diet shifts and optimal foraging strategies. This could be especially so during windless days when flying insects on the mainland become the only alternative food source and could additionally explain the highly nested temporal pattern of prey consumption.

As far as the species avian prey is concerned the study confirms that the Eleonora’s falcon has synchronised its breeding season with the peak autumn migration over the Mediterranean (Walter 1979; Clark 1981; Badami 1998). Up to date the species bird prey list numbers 122 species (Buij and Gschweng 2017 and references there in) the bulk of which constitute long-distance trans-Saharan migrants (Ristow et al. 1986). In the present study the falcons’ prey selection varied in time which is in agreement with the high species richness differences observed in the temporal consumption of prey items from May to October (Table 4, D = 59.43% birds and 48.93% insects). However the spatial composition of the bird diet was rather homogeneous with a few dominant prey species (i.e. Willow Warbler, Red-backed Shrike, Whitethroat) which exhibit a prolonged migration period in the Mediterranean basin from August to October (Hedenström and Pettersson 1987; Shirihai et al. 2001; Tryjanowski and Yosef 2002; Didrickson et al. 2007; Korner-Nievergelt et al. 2012). Furthermore, the Willow Warbler and the Whitethroat are two of the most numerous species in the Western Palaearctic – Africa migration system (Hahn et al. 2009) whereas the Red-backed Shrike is very numerous in the Aegean as it migrates in autumn via Greece all the way through its entire range (Korner-Nievergelt et al. 2012). Likewise, in terms of weight, 52.5% of the prey biomass consumed consisted of five species namely the three most abundant ones plus the Whinchat and the Common moorhen. Furthermore, considering that the asymptotic value in Figure 2 as a measure of the total species completeness, indicate a rather sufficient sampling effort, one could assume that all the samples came from a rather qualitative homogeneous migration flow over the Aegean.

Both diversity and similarity indices suggest that the Eleonora's falcon feeds on insects during the pre-laying period and a wide spectrum of avian prey during the breeding season, which increases as the latter develops in correspondence with the intensity of the autumn migration of passerines. When the migration flow is weak (e.g. July) falcons feed on a diverse insect prey and specialise on a few resident bird species (e.g. thrushes, Figure 3(b)), which are most likely taken in continental regions. The wide diet preferences on bird and insect prey also explain the high richness differences observed in the temporal consumption of prey items from May to October. Similar results are produced by the Rényi diversity profiles that provide better ordering information than just diversity indices. Although there are regional differences in prey species richness (*H-alpha* in Figure 4), south colonies exhibit a higher prey diversity than the central ones while both their curves (Figure 4) drop abruptly at high alpha values indicating some effects of dominance in the species bird diet. High prey species richness could be viewed as a function of environmental stability (e.g. the arid rocky islets of Cyclades and Crete) and spatial homogeneity of the foraging habitat (e.g. vineyards, olive groves or orchards in nearby mainland). Besides bird hunting could be profitable in coastal areas of the large inhabited islands where artificial light conditions aggregates nocturnal migrants and might facilitate visibility for nocturnal foraging (Buij and Gschweng 2017). In contrast prey species in north Aegean colonies seem more evenly distributed as shown by their smoother Rényi diversity profile which implies a high availability of regional resources (Legendre and Legendre 1998). The North Aegean colonies belong to the Sporades island complex near a variety of bird habitats in continental Greece (e.g. wetlands, orchards, woodland, arable land etc.) all of which within the foraging range of falcons when the migration flow drops. The south region is highly nested and this is probably explained by the proximity of the islets to the island of Crete, which acts as a source for a diversity of prey species, however common for all islets. Although the north and central regions are close to the mainland (Greece and Asia Minor respectively), the variety of habitats offers a much wider diversity of prey species and explains the absence of a nested pattern in their diet. The influence of this factor might be more crucial than it was initially thought, although always mentioned in past studies on the species diet (Walter 1979; Ristow et al. 1986). Similar results were also produced by the general linear mixed-effect model, which showed that prey species richness is expected to be higher in tiny islets close to the mainland. This pattern implies that falcons prey upon a broader avian food spectrum in the nearest continental mass or over small islets in the open sea where escape opportunities for migratory passerines diminish. Meanwhile the significance of temperature on prey species richness should be viewed as a wind-related environmental effect. High ground temperatures occur during windless days in the Aegean and migratory passerines become scarce in the vicinity of the falcon colonies.

Although the qualitative evaluation of our study is valuable, any quantitative deductions for prey composition should be viewed with caution. Prey data were collected from 16 colony-islets with some methodological constrains (e.g. islet topography, climatic factors) all of which affect the sampling rate. For instance, the optimum wind conditions (i.e. direction and speed) that offer ample foraging opportunities for the falcons are unsuitable for field visits and prey collection. Seasonal winds might also carry away bird pluckings or insect pellets. Besides windless days (appropriate for visiting the colony islets) interrupt the migration flow and the build-up rate of bird remains at nests and in the meantime they alter the plucking behaviour of the adult falcons which is influenced by the number of feathers already accumulated at nests (Ristow et al. 1986). Last the fieldworkers' tendency to collect the pluckings of the most conspicuous and easily recognisable species may constitute additional bias. Taking these facts into account it is rather spurious to deduce that the present bird prey analysis can depict the density of the migration flow over the Aegean. Nevertheless, compared to other dietary data gathered within the species breeding range, quantitative differences were found in the present study, feasibly produced by deviations in the migration routes of certain passerine taxa (Walter 1979; Ristow et al. 1984; Spina et al. 1987; Wink et al. 1993; De León et al. 2007). However, the current work pinpoints the significance of insect feeding throughout the species breeding season and the influence of mainland regions on its diet composition. Both aspects have noteworthy conservation and research implications. Land use changes or agricultural practises in continental Greece may affect the species breeding success (Ristow 2001; Xirouchakis 2004), which is not safe just because it dwells uninhabited islets of the Aegean. Moreover, considering that the species is a specialist avian predator with a narrow bird food breadth during September, it could be used as a surrogate for the study of the migratory behaviour of certain passerine species and alterations resulting from effects of climate change (Wernham et al. 2002; Newton 2008). Migratory species are expected to winter at higher altitudes and depart later from their breeding grounds as local temperature has risen. In both cases the structure and phenology of the migration flow (Bairlein and Winkel 2001) could be achieved by monitoring specific Eleonora's falcon colonies and collect dietary data. This task would be a suitable alternative to long-term, time consuming, constant effort birding ringing campaigns of migratory passerines.

## Disclosure statement

No potential conflict of interest was reported by the authors.

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