

Diet composition and diversity of the Peregrine Falcon *Falco peregrinus* over 30 years on coastal Mediterranean islands, France

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Abstract

We aimed to provide a long-term, comprehensive description of Peregrine Falcon *Falco peregrinus* diet composition and diversity on coastal Mediterranean islands, near a major urban area, at breeding and non-breeding seasons. We identified prey species from 87 remain samples of *F. peregrinus* preys year-round collected on six islands near Marseille, France (1995–2024). Prey relative abundance, biomass, and diversity indices were calculated. Seasonal, spatial, and temporal variations in diversity indices and prey taxa abundances were assessed using Kruskal–Wallis tests and generalized linear models. We identified 4,483 prey individuals across 180 species (*i.e.*, species richness), with birds <200 g dominating the diet. Shannon diversity index indicated high diversity, while Pielou's evenness suggested moderate dominance by a few species. The most consumed taxa were insectivorous passerines (19% abundance, 4% biomass), followed by Phasianidae (15%, 15%) (mainly Common Quail *Coturnix coturnix*), Apodidae (14%, 6%), Columbidae (11%, 25%), Turdidae (10%, 8%), and Sturnidae (8%, 6%) (Common Starling *Sturnus vulgaris*). During the breeding season, species richness and Shannon diversity were higher, while evenness was lower; Apodidae, Phasianidae and Columbidae were more consumed, and Turdidae and Sturnidae were more abundant in the non-breeding season. Urban vicinity islands showed higher richness and Shannon index but lower evenness than remote and uninhabited islands, with Apodidae and insectivorous passerines more abundant and Phasianidae and Columbidae less abundant. Temporal trends indicated declines in Common Quail remains over 30 years. Our 30-year study provides insights into Peregrine Falcon feeding ecology and highlights the high dietary diversity and trophic flexibility of Peregrine Falcons on Mediterranean coastal islands. Temporal, seasonal, and small-scale variations in the contribution of prey species to the diet may reflect factors related to prey ecology, including long-term trends in prey populations and their localised availability at or near nesting sites,

stopover areas, and along a coastal flyway.

Keywords: *Falco peregrinus*, diet composition, prey remains, Mediterranean, islands, Falconidae

INTRODUCTION

The Peregrine Falcon *Falco peregrinus* (hereafter referred to as “Peregrine”) is a cosmopolitan bird-eating raptor renowned for its exceptional aerial hunting skills and its ability to exploit diverse habitats (Negro & Galván, 2018; White *et al.*, 2024). Its diet has been thoroughly studied throughout the world (Uttendörfer, 1952; Fischer, 2004; Ratcliffe, 2010) and includes tens, if not hundreds of bird species captured, depending on the season and study areas. In fact, this last author believes that “it is easier to list [bird] species unlikely to be killed by Peregrines, for these are few and include only the largest forms”. In many areas Columbidae play a key role in the Peregrine’s diet (review in Valkama *et al.*, 2005) and for instance “in Britain the Peregrine is considered primarily a pigeon killer” (Ratcliffe 2010), as in other regions of Europe such as Germany (Sommer, 1989), Poland (Rejt, 2001), Spain (López-López *et al.*, 2008), or the Netherlands (Bijlsma *et al.*, 2018).

The Peregrine is widespread all around the Mediterranean Sea, where it breeds primarily on coastal cliffs. The rocky islets adjacent to Marseille have been documented as hosting a breeding population of Peregrines since at least the 17th century (Bouillon-Landais, 1859). The recently created (2012) Calanques National Park (which encompasses these islands) is actually considered a stronghold of the Peregrine on the French Mediterranean coast, with four pairs recorded on the mainland and islands in 1994 (Bayle, 1996), growing to seven in the 2020s (Bayle, 2015).

At the regional level, the Peregrine is classified as vulnerable, whereas its subspecies *brookei*, which breeds on the northern part of the Mediterranean basin (Wink, 2018) - and thus on the French Mediterranean coastline -, is classified as endangered (CEN PACA & LPO PACA, 2020). Studying the diet of a species of conservation interest such as the Peregrine can provide insights into its ecological role, its interactions with prey commu-

nities (such as, in the case of the present study, the impact of a possible predation on the insular seabird colonies), prey ecology (e.g., on the trans-Mediterranean migratory bird flow), and the effects of anthropization on prey availability and foraging behavior (e.g., proportion of “wild” and “urban” prey in the diet). Although Peregrine diets have been studied on Mediterranean islands such as Sardinia (Schenk *et al.*, 1982; Mocci Demartis & Murgia, 1986), Sicily (Falcone & Seminara, 1981; Leonardi & Mannino, 2007; Bondí *et al.*, 2023), and Crete (Pieper & Ristow, 2002), long-term assessments remain scarce. The archipelagos off Marseille, within the Calanques National Park, combine urban proximity, marine environments, and protected habitats along a major bird-flyway, spanning a gradient from uninhabited areas to sites near urban centers, making them an ideal setting to investigate Peregrine dietary patterns and long-term, seasonal, and small-scale spatial variation.

The primary objective of this study was to provide a comprehensive description of the trophic composition and diversity of the Peregrine diet based on prey remains collected over a 30-year period (1995–2024) across islands off the coast of Marseille. Specifically, the study aimed to: (i) establish a detailed inventory of prey species and quantify their contributions to overall abundance and biomass; (ii) assess dietary diversity; and (iii) examine the effects of urban proximity, seasonal variation, and long-term temporal trends on diet composition and diversity.

MATERIALS AND METHODS

Data collection

Study area

The islands of Marseille are located on the north-western coast of the Mediterranean Sea, at the eastern limit of the gulf of Lion, within the territory of the city of Marseille. They are grouped into two archipelagos: the Riou archipelago to the south of the Calanques massif and the Frioul archipelago to the west in the Marseille harbour, with an isolated islet off the coast, Planier (Fig. 1). The entire group of islands is part of the Calanques National Park. The Frioul is made up of two main islands, Pomègues and Ratonneau, and two smaller islets, If and Tiboulén de Ratonneau. Pomègues to the South and Ratonneau to the North are connected by a causeway built between 1822 and 1824, against which a small marina, Port-Frioul, is now located. The Frioul is 2 km from the mainland and stretches over 4 km along a northeast-southwest axis, thus separating the Marseille harbor into two parts. Its surface area is 191 ha, and its maximum altitude is 86 m. The Riou archipelago, composed of about 15 islands and islets, stretches over 7.5 km along a northwest/southeast axis and ranges from 80 m off the mainland at Maire to 3 km at the island of Riou. The total area of land is 158 ha, and the highest point reaches 191 m on Riou island. The archipelago is uninhabited. Planier is a 3-ha is-

let located offshore from the Calanques, 8.8 km west-southwest of the southwestern tip of the Calanques (cap Croisette). It is entirely occupied by a lighthouse and its associated buildings. The tower, at the top of which a Peregrine pair has nested since 2019, is 72 m tall. The automated lighthouse is still in operation, but the site has been uninhabited since 1992.

The islands of Marseille are primarily made up of limestone karstic formations from the Lower Cretaceous. They are in the driest region of France, corresponding to the semi-arid bioclimatic zone. The climate is characterized by very low rainfall, significant sunlight, high temperatures, and strong winds. This environment supports a flora characteristic of the transition zone between the thermo-Mediterranean and meso-Mediterranean climatic zones, adapted to the ecological constraints of the area (notably winds and sea spray).

Context and frequency of sampling

This study is based on an opportunistic sampling of prey remains collected over a 30-year period (1995–2024) from Peregrine territories on six islands off the coast of Marseille, with one breeding pair or nest monitored per island, as part of the scientific monitoring of Peregrine reproduction conducted by the Calanques National Park (Parc national des Calanques, 2025). A total of 87 prey samples were analyzed, each corresponding to a distinct sampling event conducted during a specific season and year. Of these, 36 samples were collected on Pomègues

in the Frioul archipelago; 12 on Riou, 4 on Plane, 4 on Maire, and 27 on Jarre in the Riou archipelago; and 4 on Planier islet (Appendix 1). Material corresponding to the breeding season (February to mid-June on the French Mediterranean coast (LPO PACA, 2022; Audevard, n. d.); $n=71$) was either collected beneath the nests, or in the nests after fledging. The average date of collection in the nests was June 25 (earliest date: May 12; latest date: August 27). In Pomègues, prey remains were also simultaneously collected from a nearby pluck site, likely used by the male. Outside the breeding season, from mid-June to January, samples were collected opportunistically from roosts or perches. Nest contents (including twigs and pebbles) were scraped and placed in a plastic bag. The material was sorted later in laboratory. Samples collected beneath the nests, on pluck sites and roosts or under perches were handpicked: each element found (feather, bone, or pellet) was picked up individually, but all remains gathered during the same site visit were placed together in a plastic bag.

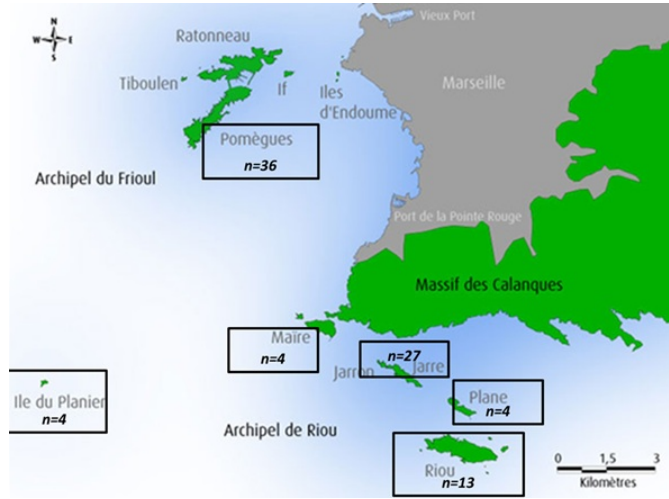


Figure 1. Map of the islands of Marseille with number of samples collected per island between 1995 and 2024 (n=87)

Prey identification and quantification

Numerous studies of predatory birds worldwide report dietary proportions based on analyses of large numbers of pellets or prey remains. Such analyses may be biased because some prey remains are more conspicuous or persistent than others (Rosenberg & Cooper, 1990). But Simmons *et al.* (1991) have shown that by combining pellets and prey remains (collected with equal effort), more accurate estimates of overall diet can be achieved. Thus, all types of prey items were looked for and collected during each sampling event and were sorted later in the laboratory into three categories: feathers, bones, and pellets. Nest contents represented an average of

35 pluckings, bones of a minimum of 17 birds, and 18 pellets, remains collected on the pluck site of Pomègues an average of 59 pluckings, bones of a minimum of 4 birds, and less than 1 pellet. Identification of this material was performed using reference collections. Species-level identification was pursued whenever possible; however, some individuals (particularly those recovered from pellets) could not be identified to species. Age class determination was possible for some larger species breeding on the islands (birds: Yellow-legged Gull *Larus michahellis*, Feral Pigeon *Columba livia* (dom.), and Eurasian Jackdaw *Coloeus monedula*; mammals: European Rabbit *Oryctolagus cuniculus*, and Black Rat *Rattus rattus*).

A minimum number of individuals (MNI) was determined for each sample by cross-checking remains. In certain genera (e.g., Swifts *Apus*, Thrushes *Turdus*, Pipits *Anthus*, Leaf Warblers *Phylloscopus*), a small number of individuals (most often extracted from pellets) could not be identified to the species level. For calculation purposes, these individuals were distributed proportionally among the identified species of the corresponding genus in each sample.

Prey classification

We classified preys into 21 functional or taxonomic groups: Turdidae, Phasianidae, Rallidae, Columbidae, Apodidae, Sturnidae, Oriolidae, *Coloeus monedula*, other Corvidae, *Larus michahellis*, other Laridae, shorebirds, seabirds, waterbirds, raptors, insectivorous passerines, granivorous passerine, various birds, unidentified birds, mammals, and insects (see Supplementary Material 2). *C. monedula* and *L. michahellis* were classified separately from other Corvidae and Laridae due to their status as breeders in the study area.

The average body mass of species *i* (W_i , in grams) was obtained from published data and estimates compiled from over 150 previous studies across 26 Western Palearctic countries, covering the diets of 30 raptor species (13 Accipitriformes, 8 Falconiformes, and 9 Strigiformes). Prey were categorized into size classes based on average weight (W_i) in 50 g intervals and grouped as follows: 1-50 g (small), 51-150 g (medium), 151-

400 g (large), 401-1,800 g (very large). Bird prey were also categorized according to their phenological status in the study area: migratory species (species occurring only during spring and/or autumn migration periods), summer breeders (species breeding in the study area during spring and summer but absent during winter), wintering species (migratory species also present during the winter period), and resident species (present year-round).

Data Analysis

Indicators calculation and diet composition

Prey abundance (N_i) was derived from the minimum number of individuals (MNI) recorded per identified species or taxon *i* in each sample (i.e., each sample corresponds to a single site visit). **Prey biomass** (B_i) was calculated as $B_i = N_i \times W_i$. **Relative abundance** ($P_i = N_i / \sum N_i$) and **relative biomass** ($R_i = B_i / \sum B_i$) were computed for each prey species and functional taxonomic group, both overall and per sample. **Species richness** (S), defined as the total number of distinct species observed, was calculated for the entire dataset and for each sample. The **frequency of occurrence** (F_i) of each species was calculated as the proportion of samples in which that species was present.

Diversity indices were computed using the *vegan* package in R (R version 4.4.3):

- **Shannon diversity** index: $H' = -\sum P_i \times \ln(P_i)$, which captures both species richness and evenness by

assigning equal weight to all species. Ranges between 0 (only one prey category consumed) and $\ln(S)$ (Shannon et Weaver, 1963).

- **Pielou's evenness** index: $J' = H' / \log(S)$, which quantifies how evenly individuals are distributed among species. Values range from 0 (maximum dominance by a few species) to 1 (maximum evenness, where all species are equally abundant) (Pielou, 1966).

Effect of area, season, and year on diet composition and diversity

Non-parametric Kruskal–Wallis tests were used to evaluate whether diversity indices (species richness, Shannon index, and Pielou's evenness) varied between Pomègues (island in an urban vicinity, close to Marseille) and the other islands more distant from the big city, and season (breeding vs. non-breeding).

Generalised Linear Models (GLMs) were fitted using the *glmmTMB* package in R, with a binomial distribution and a logit link, to test the effects of area, season, and year on the relative abundance of the most frequently consumed prey taxa. For each taxon, the response variable was the number of prey items of that taxon versus all other taxa combined. The models included three fixed effects: area (2 levels: Pomègues [reference] and other islands), season (2 levels: non-breeding [reference] and breeding), and year (reference level = 1995). Model assump-

tions were validated using diagnostic tools from the *DHARMa* package, including tests that allowed for the exclusion of overdispersion and zero inflation in the data. All statistical tests were conducted using a significance threshold of $p < 0.05$.

RESULTS

Diet composition and diversity

The analysis of 87 samples (corresponding to 87 site visits) yielded a total of 4,483 prey individuals (Tab. 1). The median number of prey remains (collected during one site visit) was 34 [Interquartile: 8–86], and the median biomass was 3,431 g [702–9,037]. In the cases in which prey remains could not be identified to species level, these were classified respectively as unidentified small passerine ($N=47$), unidentified bird ($N=6$), and unidentified locust ($N=1$), together representing 1.2% of the total prey abundance. Prey species richness (S) was high, with 180 different species identified overall and a median of 21 [6–35] species per sample (Tab. 1). Considering all sites, periods and years, the Shannon diversity index ($H' = 3.8$) indicated substantial prey diversity, although with some dominance by a subset of species.

Pielou's evenness index ($J' = 0.74$) further suggested a relatively balanced distribution of individuals among prey species, albeit with moderate uneven-

ness due to the predominance of a few species.

The average weight of the prey was 100.9 g, ranging from 1 or 2 g (insects) to 1,800 g (single Mediterranean Shag *Gulosus desmarestii*). Most of the consumed prey biomass consisted of prey items weighing less than 350 g (Fig. 2). Small-size prey contributed the most in terms of abundance (40% out of 4,483 prey individuals), whereas medium-sized prey contributed the most in terms of relative biomass, accounting for 43% of the total estimated 452 kg of consumed biomass. The remainder of the diet consisted of large-sized prey (150–400 g classes), which represented 12% of total abundance and 33% of biomass, and very large prey items accounting for 2% of abundance and 14% of biomass.

Birds accounted for 99.58% of all collected prey items ($N = 4,465$), mammals for 0.29% ($N = 13$) and insects for 0.13% ($N = 6$) (Tab. 2). The 10 most consumed bird species were Common Quail *Coturnix coturnix* (relative abundance: 15% of total prey abundance), Common Swift *Apus apus* (10%), Common Starling *Sturnus vulgaris* (7%), Song Thrush *Turdus philomelos* (6%), European Turtle Dove *Streptopelia turtur* (5%), Pallid Swift *Apus pallidus* (4%), Feral Pigeon (3%), European Robin *Erithacus rubecula* (2%), Eurasian Collared Dove *Streptopelia decaocto* (2%), and Common Blackbird *Turdus merula* (2%), with these species occurring in 41% to 76% of samples. Together, they accounted for 56% of the total abundance and 54% of the total biomass.

The remainder of the diet was distributed among 173 other identified species, with relative abundances ranging from 1.4% for Tree Pipit *Anthus trivialis* down to 0.02%.

Using our functional classification, the most consumed prey groups by number were insectivorous passerines (19% of total prey), followed by Phasianidae (15%), Apodidae (14%), Columbidae (11%), Turdidae (10%), and Sturnidae (7%) (Fig. 3). In terms of biomass, Columbidae, Phasianidae, and Turdidae contributed the most, representing 25%, 15%, and 8% of the total biomass, respectively. Granivorous passerines, ‘various bird’, and shorebirds accounted for 6%, 4%, and 4% of the total prey abundance. Other bird taxa were only marginally consumed, each contributing less than 2% to the total prey abundance. Strictly migratory bird species accounted for half of relative abundance and biomass (Fig. 4), while wintering, breeder, and resident bird species accounted for 19%, 15% and 8% of relative abundance, respectively.

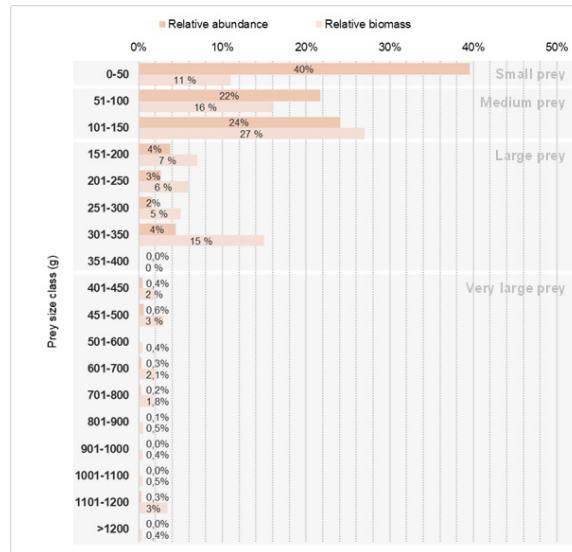


Figure 2. Relative abundance and biomass of prey, by prey size class (n=4,483 prey)

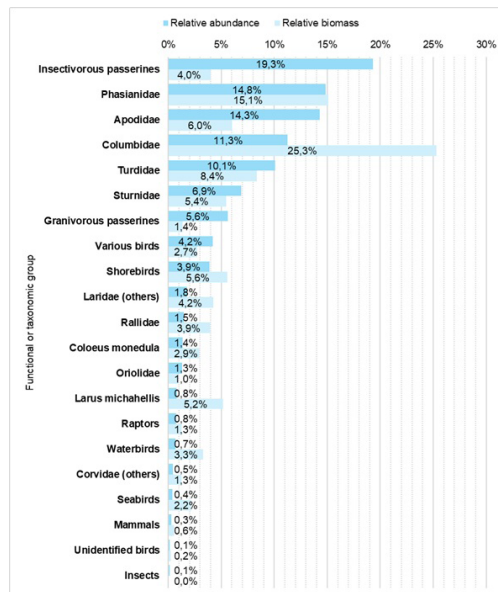


Figure 3. Relative abundance and biomass of prey, by taxa (n=4,483 prey)

Table 1. Summary of dietary and diversity indices

		All samples combined (n=87)	Median [IQR] per sample
Abundance (number of preys)	<i>N</i>	4483	34 [8-86]
Biomass (g)	<i>B</i>	452166	3431 [702-9037]
Species richness	<i>S</i>	180	21 [6-35]
Shannon index	<i>H'</i>	3.83	2.67 [1.79-3.08]
Pielou's evenness	<i>J'</i>	0.74	0.91 [0.85-0.96]

IQR : interquartile

Note: Theoretical maximum values: $H' = \ln(S) = 5.2$ (i.e., maximum diversity); $J' = 1$ (i.e., maximum evenness between species).

Spatial, seasonal, and temporal variation in dietary diversity and composition

Dietary diversity indices differed significantly across both seasons and areas (Tab. 3). Compared to the uninhabited islands far from the city, Pomègues (the island in the urban vicinity) exhibited significantly higher species richness and Shannon index (species richness: $\chi^2 = 25.38$, $p < 0.001$; Shannon: $\chi^2 = 24.46$, $p < 0.001$), along with significantly lower Pielou's evenness index (Pielou: $\chi^2 = 5.79$, $p = 0.016$). This suggests that while prey diversity was higher in Pomègues, prey consumption was more uneven, with a few dominant species contributing disproportionately. Species richness and Shannon index were also significantly higher during the breeding season than in the non-breeding season (species richness: $\chi^2 = 19.44$, $p < 0.001$; Shannon: $\chi^2 = 18.91$, p

< 0.001), whereas the Pielou's evenness index was significantly lower (Pielou: $\chi^2 = 11.52$, $p < 0.001$). This indicates that a greater variety of prey was consumed during the breeding season, but that prey use was less evenly distributed across species, reflecting a higher dominance by certain prey types.

The results of our generalized linear models, which simultaneously assess the effects of spatial, seasonal, and temporal factors on the relative abundance of most consumed prey taxa in the Peregrine diet, are presented in Supplementary Material 3.

Relative abundances of several prey taxa differed between Pomègues (urban vicinity) and the other islands. Phasianidae (estimate $0.44 \pm \text{SE } 0.11$) and Columbidae (0.29 ± 0.12) were significantly more abundant whereas Apodidae

Table 2. Characteristics of prey species and contribution to the diet of Falco peregrinus (n=4,483 prey)

Species characteristics						Contribution to diet				
Scientific name	Common name	Status*	Age class**	Mean weight (g)		Abundance (n)	Relative abundance (%)	Biomass (g)	Relative biomass (%)	Frequency of occurrence (%)
Functional taxonomic group				Wi		Ni	Pi	Bi	Ri	F
Phasianidae						665	14.83 %	68305	15.11 %	
<i>Coturnix coturnix</i>	Common Quail	M	ad.	100		662	14.77 %	66200	14.64 %	73 %
<i>Alectoris rufa</i>	Red-legged Partridge	R	ad.	485		2	0.04 %	970	0.21 %	2 %
<i>Phasianus colchicus</i>	Common Pheasant	R	ad.	1135		1	0.02 %	1135	0.25 %	1 %
Apodidae						641	14.30 %	27200	6.02 %	
<i>Apus apus</i>	Common Swift	B	ad.	40		447	9.97 %	17880	3.95 %	66 %
<i>Apus pallidus</i>	Pallid Swift	B	ad.	40		168	3.75 %	6720	1.49 %	52 %
<i>Tachymarptis melba</i>	Alpine Swift	B	ad.	100		26	0.58 %	2600	0.58 %	27 %
Columbidae						505	11.26 %	114485	25.32 %	
<i>Streptopelia turtur</i>	European Turtle Dove	M	ad.	145		229	5.11 %	33205	7.34 %	66 %
<i>Streptopelia decaocto</i>	Eurasian Collared Dove	R	ad.	190		101	2.25 %	19190	4.24 %	41 %
<i>Columba livia (dom.)</i>	Feral Pigeon	R	juv. ad	240 345		141	3.15 %	48330	10.69 %	51 %
<i>Columba palumbus</i>	Common Wood Pigeon	M	ad.	485		20	0.45 %	9700	2.15 %	19 %
<i>Columba oenas</i>	Stock Dove	M	ad.	290		14	0.31 %	4060	0.90 %	15 %
Turdidae						453	10.10 %	37845	8.37 %	
<i>Turdus philomelos</i>	Song Thrush	W	ad.	75		255	5.69 %	19125	4.23 %	76 %
<i>Turdus merula</i>	Common Blackbird	W	ad.	95		92	2.05 %	8740	1.93 %	47 %
<i>Turdus viscivorus</i>	Mistle Thrush	M	ad.	115		48	1.07 %	5520	1.22 %	40 %

Peregrine Falcon diet on Mediterranean islands

Species characteristics					
Scientific name	Common name	Status*	Age class**	Mean weight (g)	
<i>Turdus iliacus</i>	Redwing	M	ad.	65	
<i>Turdus pilaris</i>	Fieldfare	M	ad.	105	
<i>Turdus torquatus</i>	Ring Ouzel	M	ad.	100	
Sturnidae					
<i>Sturnus vulgaris</i>	Common Starling	W	ad.	80	
Oriolidae					
<i>Oriolus oriolus</i>	Eurasian Golden Oriole	M	ad.	75	
<i>Coloeus monedula</i>***					
<i>Coloeus monedula</i>	Eurasian Jackdaw	R	pul.	120	
		R	juv.	160	
		R	ad.	230	
Corvidae (others)					
<i>Pica pica</i>	Eurasian Magpie	R	ad.	205	
<i>Corvus corone</i>	Carion Crow	R	ad.	505	
<i>Pyrrhonorax pyrrhonorax</i>	Red-billed Chough	W	ad.	305	
insectivorous passerines					
<i>Hirundo rustica</i>	Barn Swallow	M	ad.	19	
<i>Cecropis rufula</i>	Red-rumped Swallow	M	ad.	22	
<i>Ptyonoprogne rupestris</i>	Eurasian Crag Martin	R	ad.	22	
<i>Delichon urbicum</i>	House Martin	M	ad.	20	
<i>Riparia riparia</i>	Sand Martin	M	ad.	14	
<i>Alauda arvensis</i>	Eurasian Skylark	M	ad.	38	

Contribution to diet					
Abundance (n)	Relative abundance (%)	Biomass (g)	Relative biomass (%)	Frequency of occurrence (%)	
40	0.89 %	2600	0.58 %	35 %	
12	0.27 %	1260	0.28 %	11 %	
6	0.13 %	600	0.13 %	7 %	
308	6.87 %	24640	5.45 %	73 %	
58	1.29 %	4350	0.96 %	36 %	
61	1.36 %	13280	2.94 %	41 %	
3					
6					
52					
21	0.47 %	5705	1.26 %		
15	0.33 %	3075	0.68 %	15 %	
4	0.09 %	2020	0.45 %	3 %	
2	0.04 %	610	0.13 %	2 %	
866	19.32 %	17987	3.98 %		
32	0.71 %	608	0.13 %	25 %	
1	0.02 %	22	0.00 %	1 %	
1	0.02 %	22	0.00 %	1 %	
13	0.29 %	260	0.06 %	14 %	
4	0.09 %	56	0.01 %	5 %	
56	1.25 %	2128	0.47 %	40 %	

Species characteristics					
Scientific name	Common name	Status*	Age class**	Mean weight (g)	
<i>Lullula arborea</i>	Wood Lark	M	ad.	30	
<i>Galerida cristata</i>	Crested Lark	M	ad.	45	
<i>Motacilla alba</i>	White Wagtail	W	ad.	21	
<i>Motacilla cinerea</i>	Grey Wagtail	M	ad.	18	
<i>Motacilla flava</i>	Yellow Wagtail	M	ad.	18	
<i>Anthus trivialis</i>	Tree Pipit	M	ad.	21	
<i>Anthus spinoletta</i>	Water Pipit	M	ad.	25	
<i>Anthus pratensis</i>	Meadow Pipit	W	ad.	19	
<i>Anthus campestris</i>	Tawny Pipit	M	ad.	25	
<i>Prunella modularis</i>	Duncock	M	ad.	20	
<i>Prunella collaris</i>	Alpine Accentor	W	ad.	40	
<i>Lanius collurio</i>	Red-backed Shrike	M	ad.	30	
<i>Lanius senator</i>	Woodchat Shrike	M	ad.	35	
<i>Lanius minor</i>	Lesser Grey Shrike	M	ad.	45	
<i>Lanius meridionalis</i>	Southern Grey Shrike	M	ad.	65	
<i>Sylvia atricapilla</i>	Eurasian Blackcap	M	ad.	19	
<i>Sylvia borin</i>	Garden Warbler	M	ad.	20	
<i>Curruca communis</i>	Common Whitethroat	M	ad.	15	
<i>Curruca hortensis</i>	Western Orphean Warbler	M	ad.	23	
<i>Curruca melanocephala</i>	Sardinian Warbler	R	ad.	14	
<i>Curruca undata</i>	Dartford Warbler	W	ad.	10	

Contribution to diet				
Abundance (n)	Relative abundance (%)	Biomass (g)	Relative biomass (%)	Frequency of occurrence (%)
2	0.04 %	60	0.01 %	2 %
5	0.11 %	225	0.05 %	6 %
5	0.11 %	105	0.02 %	6 %
7	0.16 %	126	0.03 %	8 %
43	0.96 %	774	0.17 %	31 %
64	1.43 %	1344	0.30 %	38 %
2	0.04 %	50	0.01 %	2 %
5	0.11 %	95	0.02 %	6 %
4	0.09 %	100	0.02 %	5 %
6	0.13 %	120	0.03 %	7 %
1	0.02 %	40	0.01 %	1 %
9	0.20 %	270	0.06 %	8 %
19	0.42 %	665	0.15 %	18 %
1	0.02 %	45	0.01 %	1 %
1	0.02 %	65	0.01 %	1 %
58	1.29 %	1102	0.24 %	35 %
51	1.14 %	1020	0.23 %	38 %
19	0.42 %	285	0.06 %	17 %
2	0.04 %	46	0.01 %	2 %
7	0.16 %	98	0.02 %	8 %
2	0.04 %	20	0.00 %	2 %

Species characteristics					
Scientific name	Common name	Status*	Age class**	Mean weight (g)	
<i>Curruca iberiae</i>	Western Subalpine Warbler	M	ad.	11	
<i>Acrocephalus scirpaceus</i>	Common Reed Warbler	M	ad.	12	
<i>Acrocephalus schoenobaenus</i>	Sedge Warbler	M	ad.	12	
<i>Acrocephalus arundinaceus</i>	Great Reed Warbler	M	ad.	32	
<i>Locustella naevia</i>	Common Grasshopper Warbler	M	ad.	15	
<i>Hippolais polyglotta</i>	Melodious Warbler	M	ad.	12	
<i>Phylloscopus collybita</i>	Common Chiffchaff	W	ad.	8	
<i>Phylloscopus trochilus</i>	Willow Warbler	M	ad.	9	
<i>Phylloscopus sibilatrix</i>	Wood Warbler	M	ad.	10	
<i>Phylloscopus bonelli</i>	Western Bonelli's Warbler	M	ad.	8	
<i>Regulus regulus / ignicapillus</i>	Goldcrest or Firecrest	M	ad.	6	
<i>Ficedula hypoleuca</i>	European Pied Flycatcher	M	ad.	13	
<i>Ficedula albicollis</i>	Collared Flycatcher	M	ad.	14	
<i>Muscicapa striata</i>	Spotted Flycatcher	M	ad.	16	
<i>Oenanthe oenanthe</i>	Northern Wheatear	M	ad.	26	
<i>Oenanthe hispanica</i>	Black-eared Wheatear	M	ad.	23	
<i>Saxicola rubetra</i>	Whinchat	M	ad.	16	
<i>Saxicola rubicola</i>	European Stonechat	M	ad.	15	
<i>Monticola solitarius</i>	Blue Rock Thrush	R	ad.	75	

Contribution to diet					
Abundance (n)	Relative abundance (%)	Biomass (g)	Relative biomass (%)	Frequency of occurrence (%)	
15	0.33 %	165	0.04 %	14 %	
3	0.07 %	36	0.01 %	3 %	
2	0.04 %	24	0.01 %	2 %	
1	0.02 %	32	0.01 %	1 %	
6	0.13 %	90	0.02 %	7 %	
9	0.20 %	108	0.02 %	9 %	
5	0.11 %	40	0.01 %	5 %	
17	0.38 %	153	0.03 %	15 %	
16	0.36 %	160	0.04 %	16 %	
1	0.02 %	8	0.00 %	1 %	
3	0.07 %	18	0.00 %	3 %	
42	0.94 %	546	0.12 %	24 %	
1	0.02 %	14	0.00 %	1 %	
42	0.94 %	672	0.15 %	26 %	
48	1.07 %	1248	0.28 %	32 %	
5	0.11 %	115	0.03 %	6 %	
17	0.38 %	272	0.06 %	13 %	
5	0.11 %	75	0.02 %	6 %	
12	0.27 %	900	0.20 %	13 %	

Species characteristics					
Scientific name	Common name	Status*	Age class**	Mean weight (g)	
<i>Monticola saxatilis</i>	Rufous-tailed Rock Thrush	M	ad.	55	
<i>Phoenicurus phoenicurus</i>	Common Redstart	M	ad.	16	
<i>Phoenicurus ochruros</i>	Black Redstart	R	ad.	16	
<i>Erithacus rubecula</i>	European Robin	W	ad.	17	
<i>Luscinia megarhynchos</i>	Common Nightingale	M	ad.	21	
<i>Luscinia svecia</i>	Bluethroat	M	ad.	19	
<i>Parus major</i>	Great Tit	M	ad.	19	
<i>Pariparus ater</i>	Coal Tit	M	ad.	10	
<i>Troglodytes troglodytes</i>	Eurasian Wren	W	ad.	9	
Granivorous passerines					
<i>Emberiza calandra</i>	Corn Bunting	M	ad.	47	
<i>Emberiza cirius</i>	Cirl Bunting	M	ad.	24	
<i>Emberiza citrinella</i>	Yellowhammer	M	ad.	28	
<i>Emberiza schoeniclus</i>	Common Reed Bunting	M	ad.	19	
<i>Fringilla coelebs</i>	Common Chaffinch	M	ad.	23	
<i>Fringilla montifringilla</i>	Brambling	M	ad.	24	
<i>Linaria cannabina</i>	Common Linnet	M	ad.	18	
<i>Carduelis carduelis</i>	European Goldfinch	M	ad.	17	
<i>Chloris chloris</i>	European Greenfinch	M	ad.	28	
<i>Serinus serinus</i>	European Serin	M	ad.	12	
<i>Spinus spinus</i>	Eurasian Siskin	M	ad.	13	

Contribution to diet					
Abundance (n)	Relative abundance (%)	Biomass (g)	Relative biomass (%)	Frequency of occurrence (%)	
3	0.07 %	165	0.04 %	3 %	
30	0.67 %	480	0.11 %	22 %	
13	0.29 %	208	0.05 %	14 %	
104	2.32 %	1768	0.39 %	48 %	
42	0.94 %	882	0.20 %	31 %	
1	0.02 %	19	0.00 %	1 %	
1	0.02 %	19	0.00 %	1 %	
1	0.02 %	10	0.00 %	1 %	
1	0.02 %	9	0.00 %	1 %	
251	5.60 %	6281	1.39 %		
27	0.60 %	1269	0.28 %	24 %	
5	0.11 %	120	0.03 %	6 %	
1	0.02 %	28	0.01 %	1 %	
26	0.58 %	494	0.11 %	23 %	
38	0.85 %	874	0.19 %	35 %	
1	0.02 %	24	0.01 %	1 %	
23	0.51 %	414	0.09 %	25 %	
18	0.40 %	306	0.07 %	19 %	
13	0.29 %	364	0.08 %	13 %	
42	0.94 %	504	0.11 %	33 %	
7	0.16 %	91	0.02 %	8 %	

Species characteristics					
Scientific name	Common name	Status*	Age class**	Mean weight (g)	
<i>Pyrrhula pyrrhula</i>	Eurasian Bullfinch	M	ad.	28	
<i>Coccothraustes coccothraustes</i>	Hawfinch	M	ad.	55	
<i>Passer domesticus</i>	House Sparrow	R	ad.	28	
<i>Passer montanus</i>	Eurasian Tree Sparrow	M	ad.	22	
Various bird species					
<i>Cuculus canorus</i>	Common Cuckoo	M	ad.	110	
<i>Clamator glandarius</i>	Great Spotted Cuckoo	M	ad.	165	
<i>Caprimulgus europaeus</i>	European Nightjar	M	ad.	75	
<i>Coracias garrulus</i>	European Roller	M	ad.	140	
<i>Merops apiaster</i>	European Bee-eater	M	ad.	55	
<i>Upupa epops</i>	Eurasian Hoopoe	M	ad.	65	
<i>Psittacula krameri</i>	Rose-ringed Parakeet	R	ad.	130	
<i>Melopsittacus undulatus</i>	Budgerigar	R	ad.	30	
<i>Pionus sp.</i>	Pionus Parrot	R	ad.	250	
<i>Dendrocopos major</i>	Great Spotted Woodpecker	M	ad.	80	
<i>Jynx torquilla</i>	Eurasian Wryneck	M	ad.	40	
<i>Passeriformes</i>	unidentified small passerine		ad.	24	
Raptors					
<i>Otus scops</i>	Eurasian Scops Owl	M	ad.	85	
<i>Accipiter nisus</i>	Eurasian Sparrowhawk	M	ad.	210	

Contribution to diet					
Abundance (n)	Relative abundance (%)	Biomass (g)	Relative biomass (%)	Frequency of occurrence (%)	
1	0.02 %	28	0.01 %	1 %	
15	0.33 %	825	0.18 %	11 %	
32	0.71 %	896	0.20 %	24 %	
2	0.04 %	44	0.01 %	2 %	
189	4.22 %	12318	2.72 %		
13	0.29 %	1430	0.32 %	14 %	
5	0.11 %	825	0.18 %	6 %	
33	0.74 %	2475	0.55 %	27 %	
5	0.11 %	700	0.15 %	5 %	
7	0.16 %	385	0.09 %	7 %	
57	1.27 %	3705	0.82 %	33 %	
6	0.13 %	780	0.17 %	3 %	
4	0.09 %	120	0.03 %	5 %	
1	0.02 %	250	0.06 %	1 %	
2	0.04 %	160	0.04 %	2 %	
9	0.20 %	360	0.08 %	10 %	
47	1.05 %	1128	0.25 %	25 %	
34	0.76 %	5665	1.25 %		
19	0.42 %	1615	0.36 %	16 %	
2	0.04 %	420	0.09 %	2 %	

Species characteristics				
Scientific name	Common name	Status*	Age class**	Mean weight (g)
<i>Circus pygargus</i>	Montagu's Harrier	M	ad.	310
<i>Falco peregrinus</i>	Peregrine Falcon	R	pul.	600
<i>Falco subbuteo</i>	Eurasian Hobby	M	ad.	210
<i>Falco tinnunculus</i>	Common Kestrel	R	ad.	200
<i>Falco columbarius</i>	Merlin	M	ad.	180
<i>Athene noctua</i>	Little Owl	R	ad.	170
<i>Asio flammeus</i>	Short-eared Owl	M	ad.	305
Larus michahellis***				
<i>Larus michahellis</i>	Yellow-legged Gull			
		R	juv. cl. I	120
		R	juv. cl. II	315
		R	juv. cl. III	630
		R	juv. cl. IV	800
		R	ad.	1100
Laridae (others)				
<i>Larus canus</i>	Common Gull	M	ad.	410
<i>Chroicocephalus ridibundus</i>	Black-headed Gull	W	ad.	280
<i>Ichthyaeetus melanocephalus</i>	Mediterranean Gull	M	ad.	300
<i>Hydrocolaeus minutus</i>	Little Gull	M	ad.	125
<i>Sterna hirundo</i>	Common Tern	M	ad.	125
<i>Thalasseus sandvicensis</i>	Sandwich Tern	W	ad.	235
<i>Sternula albifrons</i>	Little Tern	M	ad.	50

Contribution to diet				
Abundance (n)	Relative abundance (%)	Biomass (g)	Relative biomass (%)	Frequency of occurrence (%)
1	0.02 %	310	0.07 %	1 %
2	0.04 %	1200	0.27 %	2 %
1	0.02 %	210	0.05 %	1 %
3	0.07 %	600	0.13 %	3 %
2	0.04 %	360	0.08 %	2 %
2	0.04 %	340	0.08 %	2 %
2	0.04 %	610	0.13 %	2 %
37	0.83 %	23445	5.19 %	20 %
5				
11				
6				
3				
12				
79	1.76 %	19210	4.25 %	
1	0.02 %	410	0.09 %	1 %
44	0.98 %	12320	2.72 %	36 %
5	0.11 %	1500	0.33 %	6 %
1	0.02 %	125	0.03 %	1 %
8	0.18 %	1000	0.22 %	7 %
15	0.33 %	3525	0.78 %	14 %
1	0.02 %	50	0.01 %	1 %

Species characteristics					Contribution to diet				
Scientific name	Common name	Status*	Age class**	Mean weight (g)	Abundance (n)	Relative abundance (%)	Biomass (g)	Relative biomass (%)	Frequency of occurrence (%)
<i>Chlidonias niger</i>	Black Tern	M	ad.	65	3	0.07 %	195	0.04 %	1 %
<i>Chlidonias hybrida</i>	Whiskered Tern	M	ad.	85	1	0.02 %	85	0.02 %	1 %
Shorebirds					174	3.88 %	25295	5.59 %	
<i>Himantopus himantopus</i>	Black-winged Stilt	M	ad.	170	27	0.60 %	4590	1.02 %	19 %
<i>Recurvirostra avosetta</i>	Pied Avocet	M	ad.	290	4	0.09 %	1160	0.26 %	5 %
<i>Burhinus oedicnemus</i>	Eurasian Stone-curlew	M	ad.	430	1	0.02 %	430	0.10 %	1 %
<i>Vanellus vanellus</i>	Northern Lapwing	M	ad.	215	13	0.29 %	2795	0.62 %	14 %
<i>Pluvialis apricaria</i>	European Golden Plover	M	ad.	200	3	0.07 %	600	0.13 %	3 %
<i>Pluvialis squatarola</i>	Grey Plover	M	ad.	220	5	0.11 %	1100	0.24 %	5 %
<i>Charadrius alexandrinus</i>	Kentish Plover	M	ad.	40	1	0.02 %	40	0.01 %	1 %
<i>Tringa totanus</i>	Common Redshank	M	ad.	125	8	0.18 %	1000	0.22 %	7 %
<i>Tringa glaurola</i>	Wood Sandpiper	M	ad.	65	20	0.45 %	1300	0.29 %	20 %
<i>Tringa ochropus</i>	Green Sandpiper	M	ad.	85	8	0.18 %	680	0.15 %	8 %
<i>Tringa erythropus</i>	Spotted Redshank	M	ad.	155	10	0.22 %	1550	0.34 %	8 %
<i>Tringa nebularia</i>	Common Greenshank	M	ad.	180	3	0.07 %	540	0.12 %	3 %
<i>Actitis hypoleucos</i>	Common Sandpiper	M	ad.	55	3	0.07 %	165	0.04 %	3 %
<i>Calidris pugnax</i>	Ruff	M	ad.	145	3	0.07 %	435	0.10 %	3 %
<i>Calidris alba</i>	Sanderling	M	ad.	60	12	0.27 %	720	0.16 %	11 %
<i>Calidris alpina</i>	Dunlin	M	ad.	50	11	0.25 %	550	0.12 %	9 %
<i>Calidris ferruginea</i>	Curlew Sandpiper	M	ad.	60	1	0.02 %	60	0.01 %	1 %
<i>Calidris canutus</i>	Red Knot	M	ad.	140	10	0.22 %	1400	0.31 %	11 %

Species characteristics					Contribution to diet				
Scientific name	Common name	Status*	Age class**	Mean weight (g)	Abundance (n)	Relative abundance (%)	Biomass (g)	Relative biomass (%)	Frequency of occurrence (%)
<i>Chlidonias niger</i>	Black Tern	M	ad.	65	3	0.07 %	195	0.04 %	1 %
<i>Chlidonias hybrida</i>	Whiskered Tern	M	ad.	85	1	0.02 %	85	0.02 %	1 %
Shorebirds					174	3.88 %	25295	5.59 %	
<i>Himantopus himantopus</i>	Black-winged Stilt	M	ad.	170	27	0.60 %	4590	1.02 %	19 %
<i>Recurvirostra avosetta</i>	Pied Avocet	M	ad.	290	4	0.09 %	1160	0.26 %	5 %
<i>Burhinus oedicnemus</i>	Eurasian Stone-curlew	M	ad.	430	1	0.02 %	430	0.10 %	1 %
<i>Vanellus vanellus</i>	Northern Lapwing	M	ad.	215	13	0.29 %	2795	0.62 %	14 %
<i>Pluvialis apricaria</i>	European Golden Plover	M	ad.	200	3	0.07 %	600	0.13 %	3 %
<i>Pluvialis squatarola</i>	Grey Plover	M	ad.	220	5	0.11 %	1100	0.24 %	5 %
<i>Charadrius alexandrinus</i>	Kentish Plover	M	ad.	40	1	0.02 %	40	0.01 %	1 %
<i>Tringa totanus</i>	Common Redshank	M	ad.	125	8	0.18 %	1000	0.22 %	7 %
<i>Tringa glaurola</i>	Wood Sandpiper	M	ad.	65	20	0.45 %	1300	0.29 %	20 %
<i>Tringa ochropus</i>	Green Sandpiper	M	ad.	85	8	0.18 %	680	0.15 %	8 %
<i>Tringa erythropus</i>	Spotted Redshank	M	ad.	155	10	0.22 %	1550	0.34 %	8 %
<i>Tringa nebularia</i>	Common Greenshank	M	ad.	180	3	0.07 %	540	0.12 %	3 %
<i>Actitis hypoleucos</i>	Common Sandpiper	M	ad.	55	3	0.07 %	165	0.04 %	3 %
<i>Calidris pugnax</i>	Ruff	M	ad.	145	3	0.07 %	435	0.10 %	3 %
<i>Calidris alba</i>	Sanderling	M	ad.	60	12	0.27 %	720	0.16 %	11 %
<i>Calidris alpina</i>	Dunlin	M	ad.	50	11	0.25 %	550	0.12 %	9 %
<i>Calidris ferruginea</i>	Curlew Sandpiper	M	ad.	60	1	0.02 %	60	0.01 %	1 %
<i>Calidris canutus</i>	Red Knot	M	ad.	140	10	0.22 %	1400	0.31 %	11 %

Species characteristics					
Scientific name	Common name	Status*	Age class**	Mean weight (g)	
<i>Calidris minuta</i>	Little Stint	M	ad.	25	
<i>Limosa limosa</i>	Black-tailed Godwit	M	ad.	300	
<i>Limosa lapponica</i>	Bar-tailed Godwit	M	ad.	330	
<i>Numenius phaeopus</i>	Whimbrel	M	ad.	415	
<i>Numenius arquata</i>	Eurasian Curlew	M	ad.	780	
<i>Gallinago gallinago</i>	Common Snipe	M	ad.	106	
<i>Lymnocyrtes minimus</i>	Jack Snipe	M	ad.	60	
<i>Scolopax rusticola</i>	Eurasian Woodcock	M	ad.	295	
Rallidae					
<i>Gallinula chloropus</i>	Common Moorhen	M	ad.	300	
<i>Rallus aquaticus</i>	Water Rail	M	ad.	125	
<i>Fulica atra</i>	Eurasian Coot	M	ad.	730	
<i>Porzana porzana</i>	Spotted Crane	M	ad.	90	
<i>Crex crex</i>	Corn Crane	M	ad.	150	
<i>Zapornia parva</i>	Little Crane	M	ad.	60	
Seabirds					
<i>Puffinus yelkouan</i>	Yelkouan Shearwater	B	ad.	410	
<i>Calonectris diomedea</i>	Scopoli's Shearwater	B	ad.	675	
<i>Hydrobates pelagicus</i>	European Storm Petrel	B	ad.	26	
<i>Gulosus desmaresti</i>	Mediterranean Shag	R	ad.	1800	
<i>Stercorarius parasiticus</i>	Parasitic Jaeger	M	ad.	440	

Contribution to diet					
Abundance (n)	Relative abundance (%)	Biomass (g)	Relative biomass (%)	Frequency of occurrence (%)	
2	0.04 %	50	0.01 %	2 %	
1	0.02 %	300	0.07 %	1 %	
1	0.02 %	330	0.07 %	1 %	
1	0.02 %	415	0.09 %	1 %	
1	0.02 %	780	0.17 %	1 %	
15	0.33 %	1590	0.35 %	15 %	
1	0.02 %	60	0.01 %	1 %	
9	0.20 %	2655	0.59 %	9 %	
65	1.45 %	17830	3.94 %		
26	0.58 %	7800	1.73 %	23 %	
14	0.31 %	1750	0.39 %	11 %	
9	0.20 %	6570	1.45 %	10 %	
7	0.16 %	630	0.14 %	8 %	
6	0.13 %	900	0.20 %	6 %	
3	0.07 %	180	0.04 %	3 %	
19	0.42 %	9931	2.20 %		
10	0.22 %	4100	0.91 %	11 %	
2	0.04 %	1350	0.30 %	2 %	
1	0.02 %	26	0.01 %	1 %	
1	0.02 %	1800	0.40 %	1 %	
3	0.07 %	1320	0.29 %	3 %	

Species characteristics					
Scientific name	Common name	Status*	Age class**	Mean weight (g)	
<i>Stercorarius cf. pomarinus</i>	Pomarine (?) Jaeger	M	ad.	700	
<i>Alca torda</i>	Razorbill	M	ad.	635	
Waterbirds					
<i>Podiceps cristatus</i>	Great Crested Grebe	M	ad.	950	
<i>Podiceps nigricollis</i>	Black-necked Grebe	M	ad.	320	
<i>Tachybaptus ruficollis</i>	Little Grebe	M	ad.	180	
<i>Egretta garzetta</i>	Little Egret	M	ad.	450	
<i>Bubulcus ibis</i>	Cattle Egret	M	ad.	345	
<i>Nycticorax nycticorax</i>	Black-crowned Night Heron	M	ad.	630	
<i>Botaurus stellaris</i>	Eurasian Bittern	M	ad.	1150	
<i>Ixobrychus minutus</i>	Little Bittern	M	ad.	135	
<i>Anas platyrhynchos</i>	Mallard	M	ad.	1070	
<i>Anas crecca</i>	Eurasian Teal	M	ad.	315	
<i>Spatula querquedula</i>	Garganey	M	ad.	355	
Unidentified birds					
<i>Aves</i>	unidentified bird		ad.	180	
Mammals					

Contribution to diet				
Abundance (n)	Relative abundance (%)	Biomass (g)	Relative biomass (%)	Frequency of occurrence (%)
1	0.02 %	700	0.15 %	1 %
1	0.02 %	635	0.14 %	1 %
32	0.71 %	14780	3.27 %	
2	0.04 %	1900	0.42 %	2 %
5	0.11 %	1600	0.35 %	6 %
1	0.02 %	180	0.04 %	1 %
5	0.11 %	2250	0.50 %	6 %
4	0.09 %	1380	0.31 %	5 %
4	0.09 %	2520	0.56 %	5 %
1	0.02 %	1150	0.25 %	1 %
5	0.11 %	675	0.15 %	6 %
2	0.04 %	2140	0.47 %	2 %
2	0.04 %	630	0.14 %	1 %
1	0.02 %	355	0.08 %	1 %
6	0.13 %	1080	0.24 %	7 %
13	0.29 %	2525	0.56 %	

* Main phenological status on islands and adjacent urbanized coastline: B: summer breeder only; M: strictly migratory; R: resident; W: wintering

** Prey age class: ad.: adult; im.: imago; juv.: juvenile; cl.: age class; pul.: pullus

*** C. monedula and L. michahellis were classified separately from other *Corvidae* and *Laridae* due to their status as breeders in the study area.

Note: For species represented by multiple age classes, values for Abundance (n), Relative abundance (%), Biomass (g), and Relative biomass (%) correspond to the sum of all age classes.

Table 3. Comparison of dietary diversity indices by season and area

		Pomègues (urban vicinity, close to the city)	Other islands (uninhabited remote)		Breeding season	N o n breeding season					
		n=35	n=52	Kruskall-Wallis test			Kruskall-Wallis test				
		<i>M e d i a n</i> [IQR]	<i>Median</i> [IQR]	<i>Chi2</i>	<i>df</i>	<i>p-value</i>	<i>Median</i> [IQR]	<i>Median</i> [IQR]	<i>Chi2</i>	<i>df</i>	<i>p-value</i>
Species richness	<i>S</i>	35 [23 – 45]	10 [3 – 25]	25.384	1	< 0.001	26 [10 – 40]	6 [1 – 8]	19.442	1	< 0.001
Shannon index	<i>H'</i>	3.01 [2.83 – 3.35]	2.04 [1.04 – 2.85]	24.458	1	< 0.001	2 . 9 0 [2.17 – 3.14]	1 . 7 5 [0.00 – 2.04]	18.912	1	< 0.001
Pielou index	<i>J'</i>	0.89 [0.84 – 0.93]	0.94 [0.87 – 0.98]	5.7939	1	0.0161	0 . 9 0 [0.85 – 0.95]	0 . 9 8 [0.96 – 1.00]	11.521	1	< 0.001

and insectivorous passerine were significantly less abundant on the uninhabited/remote islands compared to Pomègues (-0.45 ± 0.12 ; -0.47 ± 0.11).

Seasonal shifts in diet composition were observed: Apodidae (2.69 ± 0.73), Phasianidae (3.38 ± 1.01) and Columbidae (1.30 ± 0.52) were consumed more during the breeding season than in the non-breeding season, while Turdidae (-0.73 ± 0.22) and Sturnidae (-1.13 ± 0.25) were significantly more abundant in the

non-breeding season.

The models also suggested temporal variations. The relative abundance of Apodidae was significantly higher than in 1995 in four years of the second half of the monitoring period (2010; 2013; 2014; 2015). Phasianidae relative abundance showed significant declines relative to 1995 in the last decade of follow-up (2013; 2014; 2016; 2017; 2018; 2021; 2022; 2023; 2024). Compared to 1995, Turdidae relative abundance was signifi-

cantly lower in 2003, 2005, 2009, 2010 , **DISCUSSION**
2013, and 2015.

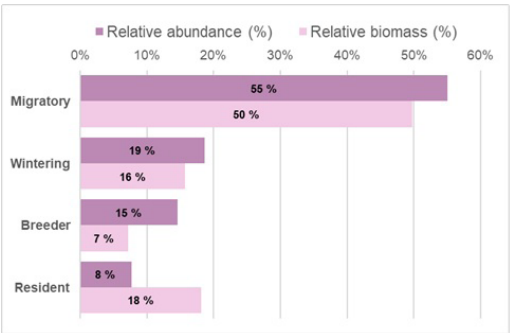


Figure 4. Relative abundance and biomass of bird prey, by phenological status (n=4,411 bird prey)

Predation on migratory birds

Our 30-year study, based on 4,483 prey remains, revealed a highly varied diet of Peregrine in the Marseille islands, comprising 180 species, almost exclusively birds and predominantly composed of species weighing less than 200 g. The most consumed species were either strictly migratory (passing through the islands, possibly in stopover): Common Quail, European Turtle Dove; species present during the winter: Song Thrush, Common Blackbird, Common Starling, and European Robin; summer breeder: Common and Pallid Swifts; or resident: Feral Pigeon and Eurasian Collared Dove. The importance of migratory birds in the diet of the Peregrine in the Marseille islands, particularly in the breeding period is consistent with the fact that these islands are located close to a major avian migratory pathway in the western part of the gulf of Lion (Bon *et al.*, 2022).

In terms of biomass, Columbidae were the most important prey taxa in the Peregrine diet (25% of total biomass) and accounted for 11% of total prey abundance. The higher abundance of Columbidae in the Peregrine diet on uninhabited or remote islands (Riou archipelago) and during the breeding season — which coincides with the spring migratory period — observed in our study may be largely driven by the abundance of the European Turtle Dove, the most consumed Colum-

idae species. These small-scale spatial differences around Marseille likely reflect the higher presence of this migratory bird in non-anthropized stopover areas, such as those surrounding the Riou archipelago, as also suggested by migratory trajectory data (Spina *et al.*, 2022). Overall, Columbidae abundance was slightly higher in our study compared to the only other available study conducted in a comparable setting near our study area, Porquerolles island (Port-Cros National Park, ca. 80 km southeast) in 2004, based on 119 prey items and 35 species (Lafont *et al.*, 2004). Feral Pigeon and Eurasian Collared Dove were the second and third most consumed Columbidae species in our findings, reflecting the greater availability of urban Columbidae associated with the proximity of a very large metropolitan area (Marseille) in our study, which was not the case for the study conducted within the Port-Cros National Park. Studies conducted on other coastal Mediterranean islands show similar Columbidae abundance in the Peregrine diet (Falcone & Seminara, 1981; Thiollay, 1981) or higher (Araújo *et al.*, 1977; Pieper & Ristow, 2002; Leonardi & Mannino, 2007) but the Eurasian Collared Dove was absent from these studies conducted several decades ago or sporadically. Consistently with a recent study in Sicily (Bondi *et al.*, 2023), our results highlight the increasing importance of the synanthropic Eurasian Collared Dove in the Peregrine diet near urban areas. This species has expanded across Western Europe and in France in recent decades (Éraud *et al.*,

2007) and its population has considerably increased in the urbanized area of Marseille within the last 50 years (Nève & Barthélemy, 2015) while European Turtle Dove populations have been declining at a European level (Estrada *et al.*, 2024). As regional population trends from 2001–2024 show a 54% decline for the European Turtle Dove and a 64% increase for the Eurasian Collared Dove (Charbonneau, 2025), a progressive shift in predation on the European Turtle Dove to the Eurasian Collared Dove may have occurred. This may explain the lack of temporal trend in overall Columbidae abundance in the Peregrine diet in our study, with opposing demographic trends likely offsetting each other. The low abundance of Common Wood Pigeon *Columba palumbus* in the Peregrine diet, despite its extensive use of the Mediterranean coastline migration corridor (Spina *et al.*, 2022) is consistent with other studies (Araújo *et al.*, 1977; Falcone & Seminara, 1981; Thiollay, 1981; Pieper & Ristow, 2002; Leonardi & Mannino, 2007) and may indicate a choice of this raptor for smaller Columbidae prey.

The Common Quail was the second most important contributor to the Peregrine diet, with higher abundance during the breeding season and on uninhabited, remote islands. Since this species is a discreet terrestrial bird and nocturnal migrant crossing the Mediterranean at low altitude (Kane, 1993), this pattern may reflect the species' preference for less anthropized areas during migration. This significant predation on the Common Quail by Peregrines in Marseille has also been

reported on the nearby-Porquerolles island (Lafont *et al.*, 2004), but it is relatively minor in studies from Sardinia, Sicily, Crete, Tunisia, and the Balearic Islands (Araújo *et al.*, 1977; Thiollay, 1981; Schenk *et al.*, 1982; Pieper & Ristow, 2002; Leonardi & Mannino, 2007; Ouni *et al.*, 2014). Nevertheless, our study shows a recent decrease in Phasianidae consumption, likely reflecting the severe decline of the Common Quail populations, estimated at nearly 90% in the PACA region between 2001 and 2024 (Charbonneau, 2025). Given the high contribution of the Common Quail to the Peregrine diet in Marseille, this trend is of particular concern.

Turdidae and Sturnidae, medium-sized prey, represented 17% of total abundance and 13% of total biomass. They were mainly partially migratory species, with populations passing through Marseille during migration as well as wintering locally (Song Thrush, Common Blackbird, Common Starling). This explains their higher abundance in the Peregrine diet during the non-breeding season in our study, reflecting the falcon's adaptation to seasonal prey availability. Consistently, the Porquerolles study reported a low contribution of these taxa during the breeding season (Lafont *et al.*, 2004). Our results also suggest a decline in Turdidae abundance over the years in the Peregrine diet, likely reflecting the moderate decrease in regional populations of the Common Blackbird, and the Song Thrush (Charbonneau, 2025).

The higher biomass and prey diversity, together with the greater dominance

of certain species in the diet during the breeding season, may reflect increased hunting activity of Peregrines when energetic demands for reproduction and chick rearing are greatest, and opportunistic feeding on a wide range of spring migratory birds, as well as targeting particularly abundant or preferred species such as Common Quail, European Turtle Dove, and Common Swift. In the coastal study area, Peregrines hunt over the sea and benefit from the vulnerability of weakened continental migratory birds crossing the water. The hunting success rate of the Peregrine varies according to prey species (Thiollay, 1981). Prey selection appears to be related to species- or individual-specific vulnerability factors, such as mass, plumage patterns, flight traits, unusual appearance or behavior, molt or accidental feather loss, and sickness or injury (White *et al.*, 2024). Temporal trends in the abundance of certain species in the Peregrine diet, highlighted in our study, are broadly consistent with trends observed in the populations of these prey species (for example Common Quail or *Turdus spp.*). Thus, like for other apex predators, monitoring Peregrine diet could also be used to quantify relative population trends of its preys.

Spatial and seasonal hunting strategies

Although they represented less than 10% of the biomass consumed, small-sized prey taxa such as insectivorous passerines and Apodidae (<50g) were highly

abundant in the Peregrine diet, with relative abundances of 19% and 14%, respectively. The abundance of Apodidae (mainly Common Swift and, to a lesser extent, Pallid Swift) in the Peregrine's diet was higher in Pomègues (urban vicinity) than in other islands, and much higher overall in our study compared to previous reports in the Mediterranean basin (Araújo *et al.*, 1977; Thiollay, 1981; Schenk *et al.*, 1982; Pieper & Ristow, 2002; Leonardi & Mannino, 2007; Ouni *et al.*, 2014), likely due to the high local abundance of swifts near urban habitats favorable for nesting. Their abundance was higher during the Peregrine's breeding season, reflecting the fact that they winter in Africa (Chantler *et al.*, 2020; Kirwan *et al.*, 2025). The abundance of insectivorous passerines in the Peregrine diet was comparable to previous studies in Porquerolles island, Tunisia, Crete, and the Balearic islands, but higher than in Sardinia and Sicily (Araújo *et al.*, 1977; Thiollay, 1981; Schenk *et al.*, 1982; Pieper & Ristow, 2002; Leonardi & Mannino, 2007; Ouni *et al.*, 2014). This group comprised 53 poorly represented species, 51 of which were migratory. Their abundance, as well as overall species richness and Shannon diversity index, were higher on Pomègues. This suggests that, compared to Riou, Peregrines on Pomègues opportunistically predate a wider range of insectivorous passerines, possibly including individuals passing further north during migratory movements. Each insectivorous passerine species, however, contributed only marginally to the overall diet, and lower

values of Pielou indices on Pomègues indicate that prey consumption was more uneven, possibly reflecting a focus on a few abundant species, particularly the Common Swift. No seasonal differences were observed in insectivorous passerine abundance, which may suggest that Peregrines in Marseille islands also benefit from the availability of synanthropic species present during the non-breeding season, including partial migratory or resident such as the European Robin and the Eurasian Blackcap *Sylvia atricapilla*.

But small-scale spatial variations in the diet of Peregrine pairs nesting in different areas of our study likely reflect localized prey availability due to habitat characteristics and migration routes, and suggest that individual pairs on Riou archipelago maintain relatively small, well-defined hunting territories centered around their nesting sites. It could also reflect individual or pair preferences for particular prey species, as some falcons target very selectively specific species or classes of prey, likely enhancing their skill in capturing them (White *et al.*, 2024). For instance, while during the whole study the small Feral Pigeon population of the Frioul archipelago was constant (about a dozen pair in and around Port-Frioul), the proportion of Feral Pigeon in the breeding season diet of the Peregrine on Pomègues varied greatly (data not shown). These variations reflect shifts in the hunting strategy of the Pomègues Peregrine pair during certain multi-year spans, the possibility being that in some periods at least one of the birds left the

Frioul to the mainland and captured Feral Pigeons in the urban area where they are numerous.

Predation on synanthropic birds

It is thus likely that Peregrines breeding in Pomègues hunt also on the urbanized mainland. First, Peregrines are regularly observed in Marseille, particularly in the Joliette port area: 54 observations have been recorded during the 9-year period 2016-2024 in the collaborative database *faune-paca* of the local association of the LPO (Birdlife France), including three birds flying towards the Frioul archipelago, one of which was carrying a prey (Faune-PACA, 2025). The Pomègues Peregrine breeding site is 4.7 km from the closest mainland point, and *ca.* 7 km from the Joliette port but Peregrines are able to hunt in a radius of over 15 km (Ratcliffe, 2010; Drewitt *et al.*, 2026). Secondly a number of prey species of the Pomègues Peregrine pair are rare on the Frioul archipelago but are very common on the urbanized mainland, notably the Eurasian Collared Dove, the Eurasian Magpie *Pica pica*, and the Ring-necked Parakeet *Psittacula krameri* (respectively 64, 10 and 7 individuals prey individuals but only 7, 9 and 0 observations recorded on the Frioul archipelago during the study period - Faune-PACA, 2025). The latter species appeared among the prey only in 2022. First observed in Marseille in 1996, this introduced parrot has quickly established a breeding population in the city, with an estimated total population of 1,900 indi-

viduals in 2016 (Le Louarn, 2017). It must be expected to play an increasing role in the diet of Marseille's Peregrines, as already documented in England (Mak *et al.*, 2023; Drewitt *et al.*, 2025).

Higher prey biodiversity in the diet of the Pomègues Peregrine pair can be partly explained by the impact of human activities in and near the Frioul archipelago. Thus the 2 Red-legged Partridges *Alectoris rufa* and the Common Pheasant *Phasianus colchicus* found among the prey were most probably illegally released on the islands (prior to the creation of the Calanques National Park), and the 4 Budgerigars *Melopsittacus undulatus* and the Pionus Parrot *Pionus sp.* could only be captive escapes.

Predation on Mediterranean seabirds

Predation on Laridae and on other seabirds was low in our study (2.6% and 0.4% of prey abundance, respectively), although the islands of Marseille are a breeding site for over 13,000 pairs of Yellow-legged Gull (Soulaimana-Mattoir, 2025), *ca.* 550 pairs of Scopoli's Shearwater *Calonectris diomedea*, *ca.* 40 pairs of Yelkouan Shearwater *Puffinus yelkouan*, several dozen pairs of European Storm Petrel *Hydrobates pelagicus*, and *ca.* 65 pairs of Mediterranean Shag (Parc national des Calanques & Conservatoire du Littoral, 2020; Parc national des Calanques *et al.*, 2020).

Yellow-legged Gulls contributed to 0.8% of the preys (12 adults and 25 pulli

at different stages of development). The situation can be quite different in other similar insular contexts, *i.e.*, on islands where Peregrine breed and which also shelter large colonies of both shearwaters and large gulls (genus *Larus*). On Lundy, a small island located in the Bristol Channel, England, Manx Shearwater *Puffinus puffinus* and European Herring Gull *Larus argentatus* represent respectively 47.3% and at least 13.8% among 520 Peregrine prey identified during the breeding period (Sutton & Loram, 2023). It should be noted that all gulls were full-grown birds, either immature or adult (Sutton *et al.*, 2017). The low predation on adult gulls in the Marseille islands is likely due to subspecies differences: *F. peregrinus brookei* (known as the Mediterranean Peregrine Falcon) is much lighter (up to 920 g for an adult female) than the nominal *F. peregrinus peregrinus* breeding in Lundy island (according to Wink, 2018) which may weigh up to 1,300 g for an adult female (Cramp & Simmons, 1980), whereas adult Mediterranean Yellow-legged Gull *L. michahellis michahellis* breeding on the French Mediterranean coast is heavier (average adult male and female combined 1160 g according to Launay, 1983) than adult Western European Herring Gull *L. argentatus argenteus* (971 g according to Sutton *et al.*, 2017). This may limit the ability for a Mediterranean Peregrine to overpower an adult Mediterranean Yellow-legged Gull.

Procellariidae represented only 0.3% of total prey abundance in the Peregrine diet, similar to findings from Sardinia

(Schenk *et al.*, 1982; Mocci Demartis & Murgia, 1986), whereas this taxon represented 13% and 39% of the diet in studies from Crete and Tunisia, respectively (Pieper & Ristow, 2002; Ouni *et al.*, 2002). The reason for this low level of predation remains unexplained and - although previous studies have raised concerns about potential negative effects of Peregrine predation on another Procellariidae endemic to the Mediterranean Sea, the Balearic Shearwater *Puffinus mauretanicus* (Garda, 2009; Wynn *et al.*, 2010) - our results suggest a minimal impact on colonial seabirds in the Marseille islands. Not so, the Eurasian Eagle Owl *Bubo bubo*, present on these islands, whose two pairs nesting in the Riou archipelago, prey on 35% and 5% of Yellow-legged Gull and shearwaters, respectively (N = 1,396 prey – Ferreira & Bayle, 2023). These findings are particularly noteworthy as they suggest that, unlike in other Mediterranean contexts, the Peregrine Falcon is not the principal avian predator of shearwaters in the Marseille islands.

CONCLUSION

Despite the robustness of the long-term dataset, certain limitations should be acknowledged. Apart from the already mentioned biases related to the material studied (Rosenberg & Cooper, 1990; Simmons *et al.*, 1991), sampling effort varied across sites and years, which may influence the comparability of some results. Nevertheless, the systematic identification and quantification approach applied

here provides a reliable overview of major dietary patterns. This study provides one of the most comprehensive descriptions of the Peregrine diet in a Mediterranean island context. The diet exhibits a broad trophic spectrum and is characterized by the exploitation of synanthropic and migratory species, reflecting the trophic flexibility of Peregrines in a highly biodiverse study area situated at the crossroads of a major metropolis, protected coastal and island habitats, and migratory corridors. These results provide valuable insights into the feeding ecology of Peregrines and may inform the management of islands and the conservation of local bird communities.

AUTHORS' CONTRIBUTION

YK identified all feathers in the prey remains. MF designed and performed the statistical analysis plan, conducted literature research, and drafted the manuscript. EG supervised the statistical analyses methodology and critically revised the manuscript. PB collected prey remains, identified bones and pellet contents, compiled all prey identification data, conducted literature research, and coordinated the work. All authors collectively interpreted the statistical analyses and read and approved the final version of the manuscript.

SUPPLEMENTARY MATERIALS

Electronic Supplementary Materials can be accessed via the article landing

page.

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