

DIET OF REED WARBLERS *ACROCEPHALUS SCIRPACEUS*
AT TWO STOPOVER SITES IN MOROCCO DURING AUTUMN MIGRATION

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RÉSUMÉ

Le régime alimentaire de la Rousserolle effarvate (*Acrocephalus scirpaceus*) pendant la migration automnale (septembre-octobre 2000) a été étudié par analyse de régurgitats dans deux zones humides marocaines, Kerbacha en région Méditerranéenne et Sidi Bou Ghaba en région Atlantique. Dix-sept catégories de proies ont été identifiées dans 88 régurgitats totalisant 789 items, avec une prédominance de guêpes (Hyménoptères) et de coléoptères à Kerbacha, et de fourmis (aillées et non aillées) et coléoptères à Sidi Bou Ghaba. La distribution taxinomique des proies et leur diversité diffèrent significativement entre les deux sites. Les oiseaux consomment un plus petit nombre de proies de plus grande taille et de plus faible mobilité à Sidi Bou Ghaba, comparativement à Kerbacha où un grand nombre de petites proies volantes caractérisent la majorité des régurgitats. Ces différences sont vraisemblablement dues à des variations dans la disponibilité locale des proies qui peuvent expliquer en partie les stratégies migratoires différentes utilisées aux deux sites. Ainsi, le court séjour et le taux d'engraissement élevé à Kerbacha peuvent être associés à un taux d'alimentation supérieur grâce à l'abondance de quelques taxons fortement consommés. A Sidi Bou Ghaba, où la durée de stationnement est plus longue et le taux d'engraissement moindre, les rousserolles ont un régime alimentaire plus diversifié et un taux d'alimentation faible suggérant que les proies sont généralement peu abondantes à l'exception des fourmis volantes, une ressource alimentaire ponctuellement surabondante mais peu prévisible dont les rousserolles font bon usage.

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SUMMARY

Diet of the Reed Warbler (*Acrocephalus scirpaceus*) was estimated by means of forced regurgitations of captured individuals during autumn migration at Kerbacha and Sidi Bou Ghaba, two wetland sites located respectively on the Mediterranean and Atlantic coasts in Morocco. Overall, 88 emetic samples were collected and 17 prey taxa were identified from 789 food items with a predominance of wasps (Hymenoptera) and beetles (Coleoptera) at Kerbacha, and ants including alate forms (Hymenoptera) at Sidi Bou Ghaba. Prey diversity and taxonomic distribution differed significantly between the two sites. Birds at Sidi Bou Ghaba had a lower food intake but fed on larger and less mobile prey than at Kerbacha where most diet samples comprised a large number of small flying prey. These between-site differences are assumed to reflect local food availability and may partly explain the different migratory strategies observed. The short stay and high fattening rate of Reed Warblers at Kerbacha can be associated with the high food intake of a few, abundant prey. The longer stopover duration and lower fattening rate at Sidi Bou Ghaba can be associated with higher diet diversity and lower feeding rate suggesting that prey abundance is globally low except for ephemeral patchily distributed food source such as swarms of flying ants, which are extensively exploited by Reed Warblers whenever available.

INTRODUCTION

Food exploitation is a major factor influencing migratory strategies of avian species (Bairlein, 1996a; Bairlein & Gwinner, 1994; Bairlein & Simons, 1995; Biebach, 1990; Hedenström & Alerstam, 1992). To fulfil the energetic requirements of migration, birds often interrupt their flight at stopover sites to restore their fat reserves (Bairlein, 1985; Biebach *et al.*, 1986; Berthold, 1975, 2001; Blem, 1980; Bairlein, 2002). Frequency and duration of stopovers are highly variable among species and presumably influenced by food availability. Yet, few studies have documented the diet during migration (Bibby & Green, 1981; Titov, 2000). In Morocco, studies on bird diet are restricted to sedentary raptor species (Brosset, 1956; Barreau *et al.*, 1984; Saint Girons, 1973; Saint Girons *et al.*, 1974; Vein & Thévenot, 1978; Aulagnier *et al.*, 1999).

The Reed Warbler *Acrocephalus scirpaceus* is a West Palaearctic breeding species that winters in tropical Africa (Moreau, 1972; Cramp, 1992; Urban *et al.*, 1997; Cramp, 1992). In Morocco, the distributional range of the Reed Warbler is limited to reed and bulrush marshes, which constitutes its preferred habitat as in Europe (Géroudet, 1980; Bairlein, 1983). The species is particularly common during spring and autumn migrations, with rare observations of wintering individuals (Rguibi Idrissi, 2002; Thévenot *et al.*, 2003) and breeding reports limited to a few Moroccan wetlands (Brosset, 1961; Pineau & Giraud-Audine, 1979; Franchimont *et al.*, 1990; Barreau & Bergier, 2001; Rguibi Idrissi *et al.*, 2002). Although the diet of the Reed Warbler has been the subject of several studies in Europe (e.g. Davies & Green, 1976; Bussman, 1979; Bibby & Green, 1983; Bibby & Thomas, 1985; Evans, 1989), it has never been described in Morocco.

This study reports on the diet of the Reed Warbler at two stopover sites where the species exhibits a different relative abundance, length of stay, and fattening rate (Rguibi Idrissi *et al.*, 2003). We attempt to describe the diet in terms of prey composition and characteristics to further interpret these data in relation to the migration strategy used at each site.

MATERIAL AND METHODS

STUDY SITES

The biological reserve of Sidi Bou Ghaba (SBG) on the Atlantic coast ($34^{\circ}03'N-06^{\circ}07'W$) is a Ramsar site located 30 km north of Rabat, south of the wad Sebou (Fig. 1). Bird mist-netting was carried out in the southernmost part of the reserve, next to a natural lake (merja) of brackish water rich in hydrophilic vegetation bordered by tall emergent plants including sedge (*Juncus maritimus* and *Juncus acutus*), bulrush (*Typha angustifolia*), and common reed (*Phragmites australis*) (Atbib, 1979; Harrache, 1994). The riparian site of Kerbacha (KER) is located on the Mediterranean coast ($35^{\circ}05'N-02^{\circ}22'E$), at the western limit of the hills of Oued Mansour, 8 km from Saidia along the right side of the wad Moulaya. The riparian woody vegetation is dominated by *Tamarix canariensis* shrubs, intermingled with Chenopodiaceae, Juncaceae, Crussulaceae, and *Phragmites australis* (Dakki *et al.*, 2002).



Figure 1. — Location of the two study sites in Morocco.

BIRD SAMPLING

Mist-netting was carried out between 4 September and 16 October 2000 at Sidi Bou Ghaba, and on 5-6 October at Kerbacha. Captured birds were ringed (Helgoland rings, Wilhelmshaven, Germany), measured, and some individuals were administered a 1% solution of antimony potassium tartrate (BDH Laboratory Supplies, UK), according to the method of Poulin & Lefebvre (1995). The solution was made one month before sampling to reduce the toxicity of the chemical. Because the presence of dew on vegetation reduces foraging activities, only the birds captured over two hours after sunrise were forced to regurgitate. Treated birds were given 0.08 ml of solution per 10 g body mass through a 1.5 mm diameter flexible plastic tube attached to a 1 ml syringe. The tube was inserted through the bird's throat as far as possible, presumably into the gizzard. The chemical was then slowly administered, and the bird placed in a small dark box lined with absorbent paper. Birds were released 20-30 minutes later, and regurgitated items were preserved in 70% ethanol. No mortality was observed and only 4 of the 92 birds treated did not regurgitate. Fragmented arthropods in diet samples were identified in the laboratory under a 10 × 40 stereoscope to the taxonomic order and assigned to 2.5 mm size classes. We distinguished ants, flying ants and wasps within the Hymenoptera, and classified arthropod developmental stages as eggs, pupae, and larvae without taxonomic differentiation.

DATA ANALYSIS

Various parameters were used to characterize the diet of the Reed Warbler at the study sites (Henry, 1977; Cardenas *et al.*, 1984): (1) prey frequency (proportion of items from each prey taxa); (2) percent occurrence (proportion of samples comprising each prey taxa); and (3) diet diversity, calculated with the Shannon-Wiener index ($H' = -\sum p_i \log p_i$, where p_i corresponds to the number of prey belonging to the category i divided by the total number of prey taken).

Diet characteristics were compared between sites by means of classical statistical tests (Likelihood ratio G-tests, ANOVAs, t-tests). In case of statistical significance, we used standardized residuals of likelihood χ^2 tests to identify the group of data responsible for these differences (Everitt, 1992). Regurgitates were collected over a longer period at Sidi Bou Ghaba to compensate for the lower feeding rates of Reed Warblers. To verify that diet differences between sites were not attributable to temporal variation in either prey availability or feeding behaviour, diet parameters from Sidi Bou Ghaba were compared among the three periods corresponding to 1-16 September, 17-30 September and 1-16 October. Eight all diet samples which were not dated were excluded from these analyses. Statistical tests were carried out using True-Epistat (Version 5.1, Epistat Services) and Statistica (version 6 for Windows, Statsoft) softwares.

RESULTS

Some 392 and 397 prey were identified in the 65 and 23 emetic samples collected at Sidi Bou Ghaba and Kerbacha, respectively. The number of prey items per sample differed significantly between the two sites with an average of 6.0 (SD = 4.7) at Sidi Bou Ghaba and 16.5 (SD = 12.3) at Kerbacha (t-test for unequal

variances: $t = 4.02$, $df = 25$, $P < 0.001$). The mean number of items per sample at Sidi Bou Ghaba did not vary over the sampling period (ANOVA, $F = 0.91$, $df = 2,5$; $P = 0.4$), suggesting that between-site differences in food intake hold throughout the migration period.

TABLE I

Reed Warbler diet during autumn migration at Kerbacha and Sidi Bou Ghaba with number of items taken, prey frequency and flying capabilities (NF: non-flying arthropod, SF: slow-flying insect, FF: fast-flying insect). Between-site differences in prey intake are estimated from standardized residuals of likelihood χ^2 tests

Prey category	Kerbacha		Sidi Bou Ghaba		P-values	Prey mobility
	N	%	N	%		
Coleoptera	131	33	85	21.7	> 0.001	SF
Araneae	7	1.8	14	3.6	NS	NF
Diptera	5	1.3	10	2.6	NS	FF
Hymenoptera (wasps)	135	34	58	14.8	> 0.001	FF
Hymenoptera (ants)	21	5.3	87	22.2	> 0.001	NF
Hymenoptera (alate ants)	14	3.5	100	25.5	> 0.001	SF
Homoptera	32	8.1	4	1.0	> 0.001	FF
Heteroptera	33	8.3	2	0.5	> 0.001	SF
Odonata	7	1.8	1	0.3	> 0.05	FF
Lepidoptera (caterpillar)	3	0.8	5	1.3	NS	NF
Lepidoptera (moths)	3	0.8	1	0.3	NS	FF
Larvae	0	-	5	1.3	> 0.05	NF
Dermaptera	1	0.3	1	0.3	NS	NF
Insect eggs	0	-	2	0.5	NS	NF
Pseudoscorpionida	0	-	5	1.3	> 0.05	NF
Neuroptera	0	-	1	0.3	NS	FF
Isopoda	0	-	6	1.5	> 0.05	NF
Fruit	5	1.3	5	1.3	NS	-
Total	397		392			
Diet diversity		0.76		0.85		
Prey evenness		0.69		0.68		

Diet composition also differed between the two sites (Likelihood test on prey taxa represented by at least 10 items: $G = 219.5$, $df = 8$, $P < 0.001$; Table I), but did not vary at Sidi Bou Ghaba throughout the three sampling periods ($G = 15.2$, $df = 10$, $P = 0.12$). Wasps and beetles were the most common prey at Kerbacha (Fig. 2), while ants (including alate forms) and beetles were the most common prey

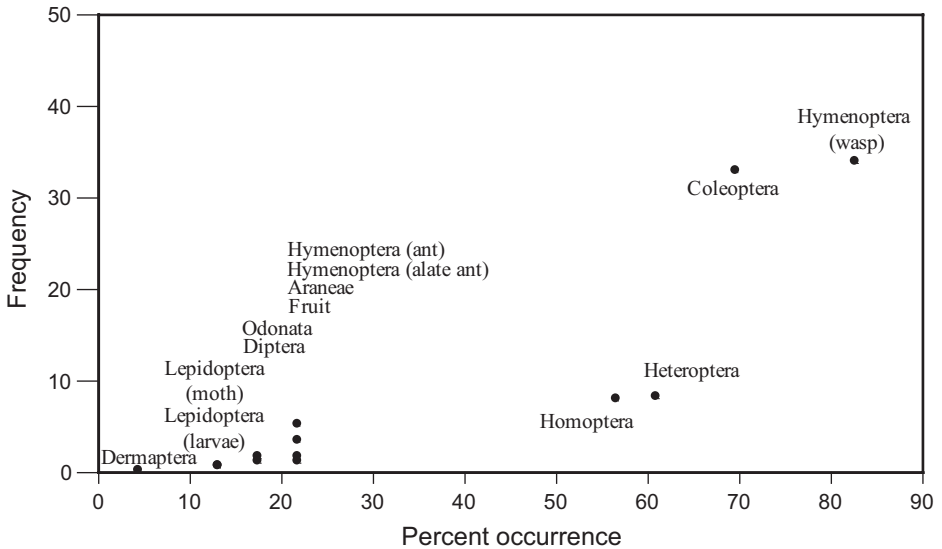


Figure 2. — Frequency of prey taxa relative to their percent occurrence at Kerbacha.

at Sidi Bou Ghaba (Fig. 3). Percent occurrence of beetles was similar at both sites, but their frequency was lower at Sidi Bou Ghaba. Diet diversity was significantly higher at Sidi Bou Ghaba than at Kerbacha (Table I). This difference was mainly attributable to the higher prey richness at Sidi Bou Ghaba, since prey evenness was similar between the two sites (Table I). Fruits were taken in small amounts by a few individuals at both Kerbacha and Sidi Bou Ghaba (Table I).

Size of most prey ranged between 2.5 and 7.5 mm (Fig. 4) but prey size distribution differed significantly between the two sites ($G = 84.6$, $df = 4$, $P < 0.001$). Birds at Sidi Bou Ghaba fed on significantly larger prey than at Kerbacha, and this trend was constant among the three sampling periods ($G = 13.8$, $df = 8$, $P < 0.09$). This trend also holds within the most common prey groups (beetles: $G = 34.6$, $df = 4$, $P < 0.001$; wasps: $G = 12.6$, $df = 4$, $P = 0.01$; flying ants: $G = 71.7$, $df = 3$, $P < 0.001$), indicating that prey size differences were not related to a taxonomic bias.

Each prey taxon was subjectively assigned to a mobility class among non-flying arthropods, slow-flying insects, and fast-flying insects. Prey distribution based on flying capabilities also differed significantly between the two sites ($G: 105.0$, $df = 2$, $P < 0.001$). Reed Warblers included a higher proportion of non-flying insects at Sidi Bou Ghaba, and a higher proportion of fast-flying insects at Kerbacha, while slow-flying insects were taken in a relatively high proportion at both sites (Fig. 5).

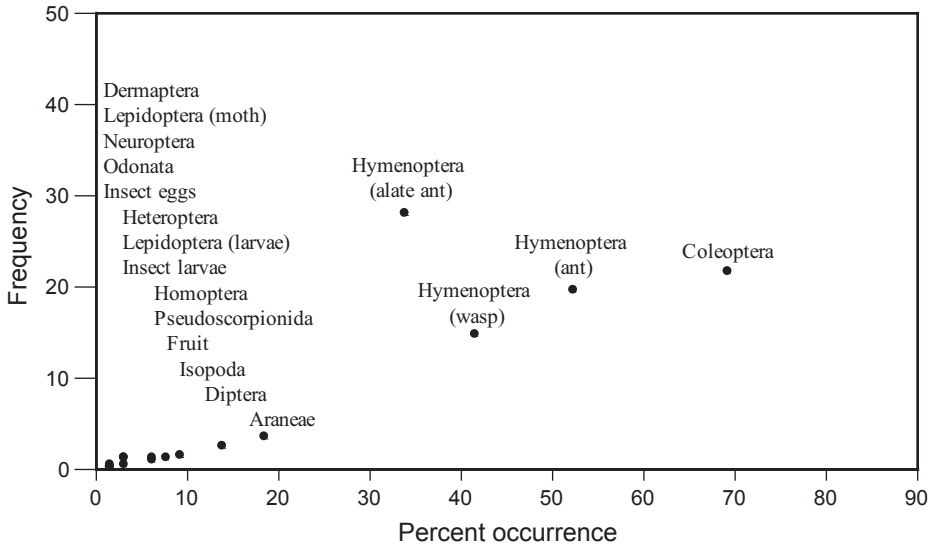


Figure 3. — Frequency of prey taxa relative to their percent occurrence at Sidi Bou Ghaba.

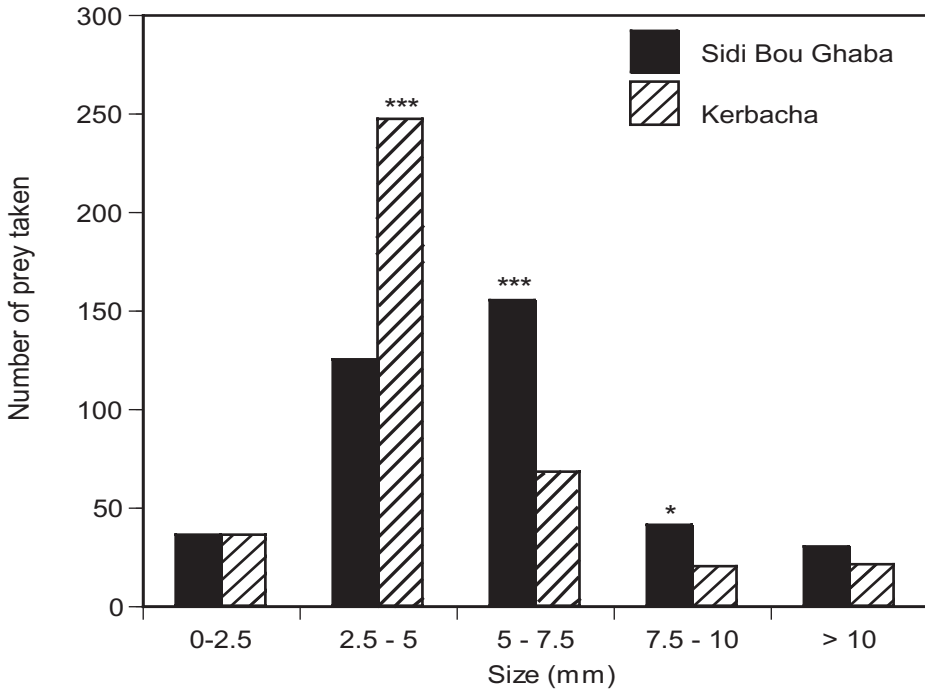


Figure 4. — Prey size distribution at Kerbacha and Sidi Bou Ghaba.

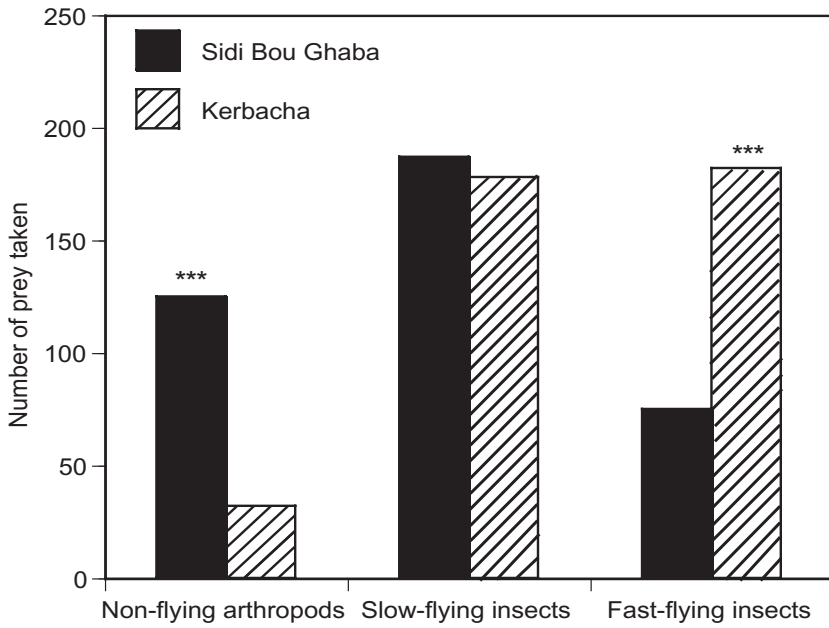


Figure 5.— Prey distribution according to their flying capabilities at Kerbacha and Sidi Bou Ghaba.

TABLE II

Frequency distribution of prey taxa between juveniles and adults at Kerbacha and Sidi Bou Ghaba. Between-age differences in diet are estimated from standardized residuals of likelihood χ^2 tests

Prey category	Kerbacha			Sidi Bou Ghaba		
	Juveniles	Adults	P-values	Juveniles	Adults	P-values
	N (%)	N(%)		N(%)	N(%)	
Coleoptera	67 (29)	58 (40)	> 0.05	33 (29)	37 (25)	NS
Hymenoptera (wasps)	98 (42)	34 (24)	> 0.001	12 (9)	23 (15)	NS
Hymenoptera (ants)	3 (1)	17 (12)	> 0.001	18 (14)	31 (21)	NS
Hymenoptera (alate ants)	12 (5)	2 (1)	NS	47 (36)	34 (23)	NS
Homoptera	14 (6)	14 (10)	NS			
Heteroptera	23 (10)	9 (6)	NS			
Araneae				6 (5)	5 (3)	NS
others	16	18		6	19	
Total	233 (100)	143 (100)		131 (100)	149 (100)	

Respectively 46 and 22 individuals forced to regurgitate at Sidi Bou Ghaba and Kerbacha could be identified as first year juveniles or adults. Frequency distribution of prey taxa (represented by a minimum of 10 items in the emetic samples) was similar between juveniles and adults at Sidi Bou Ghaba ($G = 8.6$, $df = 4$, $P = 0.07$), but not at Kerbacha ($G = 38.3$, $df = 5$, $P < 0.001$). At Kerbacha, juveniles fed more intensively on wasps, while adults fed more intensively on ants (Table II). Prey size distribution (SBG, $G = 5.8$, $df = 4$, $P = 0.22$; KER, $G = 8.6$, $df = 4$, $P = 0.07$), and the mean number of prey per sample (SBG, $t = -0.56$, $df = 44$, $P = 0.57$; KER, $t = -0.64$, $df = 19$, $P = 0.53$) were similar between juveniles and adults at both sites.

DISCUSSION

Diet of Reed Warblers differed between the two stopover sites studied during autumn migration in Morocco. These differences presumably reflect discrepancies in local food availability, which is not surprising considering the floristic and structural differences in the vegetation at the two sites. The great diversity of feeding substrates used by the Reed Warbler (ground, reed, air, bush), coupled with diet differences observed among sites sampled during breeding (Catchpole, 1974; Davies & Green, 1976; Henry, 1977, 1978; Grim & Honza, 1996) or migration (Bibby & Green, 1981), suggest that the Reed Warbler is a highly opportunistic species of which the diet is primarily influenced by temporal fluctuations in prey availability (Catchpole, 1974; Grim & Honza, 1996). This behaviour allows the Reed Warbler to exploit a large diversity of prey taxa, as well as to take advantage of short-term surplus of food resources such as swarms of flying ants.

Beetles, wasps and alate ants were the most commonly taken prey overall. The frequency/occurrence ratio suggests that beetles had a more aggregated spatial distribution at Kerbacha than at Sidi Bou Ghaba where they were taken as regularly but in smaller number. Flying ants showed a high frequency/occurrence ratio at Kerbacha, which is consistent with their spatio-temporal pattern of abundance. Intake of dipterans was low relative to what has been reported during breeding (Davies & Green, 1976; Grim & Honza, 1996), and at the onset of migration (Evans 1989). Davies & Green (1976) have noted that fledged juveniles feed less frequently on flying insects than adults in summer. However, this factor alone cannot explain the low intake of dipterans since half the Reed Warblers forced to regurgitate at Sidi Bou Ghaba were adults, and only ten dipterans were identified in the samples. This low intake is probably related to their lower availability at this time of year relative to other prey taxa. The high occurrence/frequency ratio in the diet suggests that dipterans are a favourite but rare prey at the study sites. Another characteristic of the Reed Warbler diet during migration is the occasional intake of fruit, which had previously been noted by Evans (1989). This partial frugivory is a common feature of insectivores during migration, which allow them to accumulate fat reserves more rapidly and efficiently when energetic demands are high (Bairlein, 1996b).

The Reed Warblers captured in autumn at Sidi Bou Ghaba and Kerbacha are mostly individuals interrupting their flight from their northern breeding grounds to wintering areas further south. Predictive models on migration strategy generally assume that there is a negative relationship between length of stay and fattening rate (Bairlein, 1985, 1990; Biebach *et al.*, 1986; Alerstam & Linderström, 1990; Yong & Moore, 1997). Mist-netting sessions of 50 to 70 consecutive days during autumn

migration have been carried out at Sidi Bou Ghaba in 1994, 1999, and 2000, and at Kerbacha in 1994 and 1996. These data have revealed a higher relative abundance of Reed Warblers at Kerbacha, a significantly longer stay at Sidi Bou Ghaba, and a net daily gain in body mass significantly higher at Kerbacha (Rguibi Idrissi *et al.*, 2003). The foraging strategy at Kerbacha can be summarized as follows: birds feed predominantly on small prey captured on the wing in large amount. These results support the hypothesis of Brandl *et al.*, (1994), according to which small predators can maximize their body mass gain by foraging on small prey because their manipulation requires low costs in time and energy. The foraging strategy used at Sidi Bou Ghaba is rather to exploit a greater diversity of prey which are predominantly of large size and captured on the vegetation. The higher prey richness at Sidi Bou Ghaba is revealing of a more intense pursuit of prey, which is confirmed by the lower food intake. Individuals foraging on ephemeral swarms of alate ants, a patchily distributed food resource rich in fat reserves (Redford & Dorea, 1984), can probably increase their fattening rate. Unfortunately, it is not possible to link the migratory and feeding strategies at the individual level.

Further studies should address the effect of annual variations in food availability on the migratory behaviour, which is potentially highly variable from one year to the next due to differences in climatic conditions, and their subsequent impact on the entomofauna. Concurrent data on food availability, fattening rate, and diet in various years and sites will be necessary to fully understand the migratory strategy of the Reed Warbler.

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