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BAT SPECIES RICHNESS AND ACTIVITY OVER AN ELEVATION GRADIENT IN MEDITERRANEAN SHRUBLANDS OF CRETE

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ABSTRACT - The effect of elevation on bat species richness and activity was investigated in shrublands of central Crete (Greece) using broad-band acoustic surveys. Recordings of echolocation calls were made in 15 transects equally distributed in three distinct elevation zones (500, 1000 and 1500 m a.s.l.) during spring and autumn 2007-2008. Time-expanded calls were subsequently identified with the use of quadratic discriminant functions.

Out of 13 species recorded, *Hypsugo savii*, *Pipistrellus kuhlii* and *Tadarida teniotis* were the most common and abundant. Many *Rhinolophus hipposideros* were also recorded in all elevation zones. Thirteen species were recorded in the lower elevation zone, 7 species in the mid one and 8 species in the 1500 m a.s.l. sites. Species richness, the number of bat passes of the most abundant species, as well as the total number of bat passes were not significantly affected by elevation. In spring both species richness and bat activity were higher than in autumn, although the corresponding difference in temperature was not significant.

The high variability in both bat activity and the number of species found per transect in each elevation zone probably depended on the presence of other habitat types in the close vicinity, while roost availability and location might also have played an important role.

We suggest that the ability of bats to perform regular movements along the elevational gradient has to be taken in account when assessing elevational patterns in bat diversity and activity. The geology of the study area is also of considerable importance through its effect on foraging and roosting opportunities for bats.

Key words: bats, shrublands, elevation, activity, species richness

RIASSUNTO - ***Ricchezza specifica e attività dei chirotteri lungo un gradiente altitudinale nella macchia mediterranea di Creta***. L'effetto della quota su ricchezza in specie e attività dei chirotteri è stato investigato in siti di macchia mediterranea mediante rilevatori ultrasonori nella regione centrale dell'isola di Creta (Grecia). In primavera ed autunno 2007 e 2008, abbiamo registrato i segnali di ecolocalizzazione lungo 15 transetti egualmente distribuiti in tre fasce altitudinali (500, 1000 e 1500 m s.l.m.). I segnali registrati in "time expansion" sono stati successivamente identificati mediante funzioni discriminanti quadratiche. Delle 13 specie registrate, *Hypsugo savii*, *Pipistrellus kuhlii* e *Tadarida teniotis* sono risultate le più comuni e abbondanti. Nella fascia altitudinale più bassa abbiamo registrato 13 specie, 7 in quella intermedia e 8 nei siti a 1500 m s.l.m. La ricchezza specifica, il numero di passaggi delle specie più frequenti, così come il numero totale di passaggi non sono risultati significativamente influenzati dalla quota. In primavera, sia la ricchezza specifica sia l'attività sono risultate maggiori che in autunno, sebbene le corrispondenti differenze di temperatura non fossero significative.

L'elevata variabilità nell'attività dei chirotteri e nel numero di specie tra siti entro ciascuna fascia altitudinale si spiega probabilmente con la presenza di altri tipi di habitat nelle immediate circostanze dei siti investigati; anche la presenza e la localizzazione di rifugi può avere una influenza su tale variazione. Suggeriamo che la capacità dei chirotteri di spostarsi regolarmente lungo il gradiente altitudinale debba essere considerata negli studi che analizzano l'influenza della quota sulla diversità e abbondanza della chirotterofauna. Anche la natura geologica dell'area di studio, influendo sulla disponibilità di siti di alimentazione e rifugio, può svolgere un ruolo determinante.

Parole chiave: chirotteri, macchia mediterranea, altitudine, attività, ricchezza specifica

INTRODUCTION

Mountain landscapes are considered to be ideal for investigating the patterns of biodiversity and underlying mechanisms determining them, providing a predictable gradient of several factors (e.g. rainfall, temperature and productivity) in a relatively small area and thus minimizing the effect of evolutionary and other historical processes (Brown, 2001; Lomolino, 2001; McCain, 2007). The initial conception of monotonic decline in species richness with elevation (Brown and Gibson, 1983; Brown and Lomolino, 1998) has been questioned since it is now well known that species richness can also be higher at mid-elevation, or even increase with altitude (Rahbek, 1995; Brown, 2001; McCain, 2005). Additionally, patterns of altitudinal diversity may vary between different taxa and with respect to latitude (McCain, 2005).

The effect of elevation on bat species richness, range size and activity has been studied mainly in tropical, subtropical (Patterson *et al.*, 1996, 1998; Sanchez-Cordero, 2001) and temperate (Grindal *et al.*, 1999; McCain, 2005) regions of the new world. Only a few studies have examined the elevational pattern of bat diversity in the Palearctic region (Walsh and Harris, 1996a; Cerveny, 1998; Holzhaider and Zahn, 2001; Russo, 2002; Barataud, 2004; Kaňuch *et al.*, 2006), while no such study has regarded the Mediterranean. Although standardized sampling and quantitative data are needed for a robust evaluation of the effect of elevation on these species parameters (Lomolino, 2001; Willing *et al.*, 2003; Rahbek, 2005), most studies failed to fully meet these criteria (McCain, 2005), mainly due to difficulties posed by bats' nature (Willig *et al.*, 2003). Moreover, in most relevant studies, the examination of several habitat types in different elevation zones (but see Grindal *et al.*, 1999) may have obscured the effect of elevation *per se* and hindered the understanding of the mechanisms shaping the patterns of diversity (Patterson *et al.*, 1996; Brown, 2001).

Shrublands are typical Mediterranean habitats, thought to have resulted from various long-term human activities (Blondel and Aronson, 1999). This habitat type is dominated by evergreen sclerophyllous plants, with some of them (e.g. *Arbutus*, *Ceratonia*, *Quercus*) being occasionally taller than 2 m, while others (*Calicotome*, *Berberis*, *Genista*, *Sarcopoterium*) rarely exceeding 70 cm. On Crete (Greece), shrublands are the commonest semi-natural habitat type. They occur both in semi-arid regions like the lowlands of eastern Crete (mean annual precipitation ≈ 500 mm) and on the slopes of Mount Lefka Ori in the west, where annual precipitation reaches its maximum on the island (> 2500 mm). The use of Mediterranean shrublands by foraging bats has been poorly studied, (but see Carmel and Safriel, 1998; Russo and Jones, 2003) presumably due to the restricted geographic range, low productivity and lack of freshwater of this habitat type. Although wetlands and broadleaved forests have been considered more interesting by bat researchers, usually exhibiting the highest bat activity and diversity (Walsh and Harris, 1996a, 1996b; Vaughan *et al*., 1997a; Russo and Jones, 2003), shrublands are potentially important in the Mediterranean because in insular ecosystems they are widespread with respect to forests, while wetlands are generally scarce or absent.

In this study we investigated the effect of elevation on the distribution and activity of bats in the Mediterranean shrublands of Crete, the only habitat type found in all elevation zones of the island, from the sea level up to mountain tops (2456 m a.s.l.). More specifically, we analysed the altitudinal and seasonal variation in i) the species richness of the bat community ii) the overall bat activity and iii) the activity of the most abundant species.

STUDY AREA

Our study took place on Mount Psiloritis (2456 m a.s.l.) and the adjacent Talaia Ori Mountains (1083 m a.s.l.), central Crete (Fig. 1). The main part of this area is included in the NATURA 2000 network (SCI code: GR4330005). The extensive erosion and karstification of the carbonate rocks of the area (mainly Platy marbles, Tripali marbles and Tripolitsa rocks) has led to the formation of several hundred caves and potholes (Fassoulas *et al*., 2007). Furthermore, the intense tectonic history of Crete has resulted into the development of a bold relief with many steep cliffs and gorges (Fassoulas *et al*., 2007), which also provide suitable roosting sites for bats.

The lowlands of central Crete (and the whole island) comprise a mosaic of several habitat types (e.g. wetlands, forested areas, cultivations, human settlements, shrublands and rocky habitats). Habitat variability decreases with increasing elevation, due to the lack of soil, karstification and climatic conditions. Above 1000 m a.s.l. only shrublands, rocky habitats and a few small forests can be found, while above the tree line (ca. 1600 m a.s.l.) the “Alpine desert” is characterized by the presence of very few cushion-like shrubs (Rackham and Moody, 1996).

METHODS

1. Sound recording

We investigated bat activity in three elevation zones: 400-600 m a.s.l., 900-1100 m a.s.l. and 1400-1600 m a.s.l. (henceforth 500,

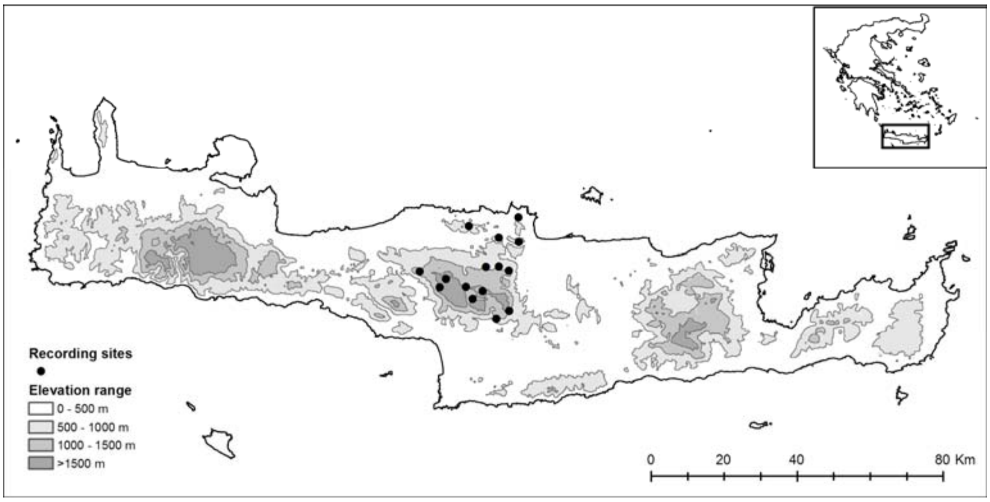

Figure 1 - Map of the study area. Recording sites are marked with filled circles.

1000 and 1500 m zones). In each elevation zone we selected five sites with low shrubs (less than 1 m tall), mainly *Sarcopoterium spinosum*, *Genista acanthoclada*, *Quercus coccifera, Berberis cretica*. The selected shrublands were large enough to allow recordings on 2 km long transects. The minimum distance between sites was 5 km, except for two sites in the 1500 m zone which were ca. 2 km apart.

Each site was sampled once in spring and once in autumn. Recordings took place in late spring 2007 (30 April to 16 June, 11 sites) and 2008 (12 May to 5 June, 4 sites) and autumn 2007 (10 October to 26 November, 15 sites). For each year and season, sites from different elevation zones were sampled in a random order.

We measured both air temperature and percent relative humidity with a digital data logger at the beginning and the end of each sampling and used the mean values of these variables for the analyses. Wind speed never exceeded 30 km/hr and was not included in the analyses.

At each site we walked at a constant speed of 2.7 km per hour, starting 30 min after sunset (Vaughan *et al*., 1997a; Russo and Jones, 2003). Recordings were made with a D-980 ultrasound detector (Pettersson Elektronik AB, Uppsala, Sweden) connected to a Voice Bank DDR 5100 stereo MP3 recorder (Diasonic Technology Co., LTD., MP3 encode: 256 Kbps, recording ModeQ: 32 Kbps, Frequency response 300 Hz ~ 4.0 KHz (-6dB), signal to noise ratio: 60dB). When a bat pass was heard in the frequency division channel, we triggered time expansion and recorded the output to the MP3 recorder. Because time expansion cannot work continuously, we also recorded the output of the frequency division channel to obtain the total number of bat passes and feeding buzzes in each recording.

2. Species identification

The MP3 files were later converted with the software CDex (v. 1.51), using a Lame MP3 Encoder (version 1.30, engine 3.92 MMX). The resultant stereo wave files (Bit Rate: 1411Kbps, 16 bits/sample) were analyzed with the software BatSound, release 1.2 (Pettersson Elektronik, Uppsala). For both spectrograms and power spectra, we selected a 512 pt. FFT with a Hamming window, resulting in an 1120 Hz frequency resolution in real time. One echolocation call per bat pass was analysed.

Calls of *Tadarida teniotis* and *Rhinolophus* spp. were easily identified to species level from time expansion or frequency division, since their frequency of maximum energy is species-characteristic (*T. teniotis*: 13.03±1.68 kHz, *R. blasii*: 96.39±0.57 kHz, *R. hipposideros*: 114.64±1.84 kHz and *R. ferrumequinum*: 81.77±0.65 kHz; P. Georgiakakis, unpublished data).

For the identification of the calls from the genera *Myotis*, *Hypsugo*, *Pipistrellus* and *Miniopterus* we developed quadratic Discriminant Function Analyses (DFA) with cross-validation relying upon a database of calls of known identity (see Vaughan *et al.* 1997b; Russo and Jones, 2002; Preatoni *et al.*, 2005; Papadatou *et al.*, 2008). The latter was set up from recordings taken on Crete. Two independent functions were devised; one for *Myotis* spp. (FM calls) and one for *Hypsugo savii*, *Pipistrellus* spp. and *Miniopterus schreibersii* (FM/QCF calls). The first model included start frequency, lower frequency, end frequency, frequency of maximum energy, middle frequency, duration and inter-pulse interval. In this way, we obtained the correct classification for 96.4% *Myotis blythii*: (N = 56), 88.9% *M. capaccinii* (N = 27) and 93.9% *M. emarginatus* (N = 49).

The second model was based on start frequency, end frequency, middle frequency and duration and provided the following classification rates: *H. savii*: 86.7% (N = 52), *Pipistrellus kuhlii*: 88.4% (N = 43), *Pipistrellus hanaki*: 89.4% (N = 42), *Miniopterus schreibersii*: 100% (N = 69).

Myotis mystacinus s. l., *Nyctalus leisleri*, *Pipistrellus nathusii, Eptesicus serotinus*, *Plecotus kolombatovici* and *Plecotus macrobullaris* were not included in the Discriminant Analyses due to the small available sample of reference calls. These species are rare on Crete (Skiba, 2007; Benda *et al.*, 2009) and the same holds true for this study (Tab. 1). *N. leisleri* and *P. nathusii* have never been reported for the study area and probably do not breed on the island (Benda *et al.*, 2009). The two species of the genus *Plecotus* have been treated as a species group.

Whenever possible, several unexpanded and/or faint passes were assigned to the *P. kuhlii* / *H. savii* and *M. schreibersii* / *P. hanaki* species pairs, based on their spectral characteristics in the frequency division channel. Their identification to species level was not attempted, due to the large overlap of the ultrasound call characteristics recorded on Crete (P. Georgiakakis, unpublished data).

3. Data analysis

For each recording, the numbers of bat passes and feeding buzzes attributed to a certain species were filed and considered as a relative index of that species' feeding activity. The sum of passes recorded in frequency division was considered as an index of bats' overall activity. We checked for differences between both elevation zones and seasons in air temperature, species richness, overall commuting activity (No of bat passes), as well as in the commuting activity of the most abundant species. The effect of temperature on total bat activity (in spring and autumn) was tested by Spearman's test. Exploratory data analysis (scatterplots, correlation analysis) showed that temperature and relative humidity did not follow the assumptions of ANCOVA (Quinn and Keough, 2002) and thus they could not be used as covariates in the analysis of species richness, commuting and foraging activity. Consequently, to test for differences between elevation zones, we performed a one-way ANOVA. Data were tested for normality by Kolmogorov-Smirnov's test. The assumption of homogeneity of variance was tested by Levene's test. When the assumptions of normality and homogeneity of variance were not met, even after appropriate transformation, a

Kruskal-Wallis test was used. Seasonal variation in total bat activity, feeding buzzes and bat passes for the more abundant species for both each elevation zone independently and pooled data were tested by paired samples t-tests. When data failed to meet the assumptions of normality and homogeneity of variance even after transformation, Wilcoxon's signed-rank test was used. All tests were performed with SPSS 15.

RESULTS

Overall, we recorded 639 bat passes from 13-15 species; 469 in spring and 170 in autumn. We identified to species level 432 passes (67.6%); 142 passes were assigned to *Rhinolophus* spp. and *T. teniotis* after visual inspection of their spectrograms, while 290 passes were classified with the use of quadratic discriminant functions. Additionally, 43 passes were classified as *E. serotinus / N. leisleri* and 4 passes were classified as *Plecotus sp.* (Tab. 1). Very faint or unexpanded calls (141 passes) were classified as *P. kuhlii / H. savii* or *M. schreibersii / P. hanaki*. Finally, 19 passes recorded only in frequency division could not be assigned to any species or species pair. *H. savii*, *T. teniotis* and *P. kuhlii* were the most abundant species in both seasons (Tab. 1).

In total, we recorded 45 feeding buzzes, 37 in spring (18, 14 and 5 in, respectively, the 500 m, 1000 m and 1500 m

Table 1 - Number of passes per species recorded. Percentages are given in parentheses.

Species	Spring		Autumn		Both seasons	
Rhinolophus blasii	3	(0.64)	5	(2.94)	8	(1.25)
Rhinolophus ferrumequinum	13	(2.77)	1	(0.59)	14	(2.19)
Rhinolophus hipposideros	10	(2.13)	11	(6.47)	21	(3.29)
Myotis blythii	6	(1.28)	0	(0.00)	6	(0.94)
Myotis capaccinii	5	(1.07)	1	(0.59)	6	(0.94)
Myotis emarginatus	3	(0.64)	0	(0.00)	3	(0.47)
Pipistrellus kuhlii	82	(17.48)	8	(4.71)	90	(14.08)
Hypsugo savii	107	(22.81)	69	(40.59)	176	(27.54)
P. kuhlii/H. savii	105	(22.39)	33	(19.41)	138	(21.60)
Pipistrellus hanaki	0	(0.00)	2	(1.18)	2	(0.31)
Miniopterus schreibersii	1	(0.21)	6	(3.53)	7	(1.10)
M. schreibersii/P. hanaki	3	(0.64)	0	(0.00)	3	(0.47)
E. serotinus/N. leisleri	43	(9.17)	0	(0.00)	43	(6.73)
Plecotus spp.	0	(0.00)	4	(2.35)	4	(0.63)
Tadarida teniotis	69	(14.71)	30	(17.65)	99	(15.49)
Unidentified	19	(4.05)	0	(0.00)	19	(2.97)
Total	469	(100.00)	170	(100.00)	639	(100.00)

zones) and 8 in autumn (7 in the 500 m zone and 1 in the 1000 m zone). A strong and significant positive correlation was found between the number of feeding buzzes and bat passes from all species, except for the rhinolophids, in spring (Spearman's $r = 0.885$, d.f. = 14, $P < 0.001$), autumn ($r = 0.704$, d.f. = 14, $P < 0.01$) and when data from both seasons were pooled ($r = 0.856$, d.f. = 28, $P < 0.001$). Therefore, the number of bat passes can be considered as a reliable estimator of feeding activity (Russo and Jones, 2003).

The highest mean temperature recorded was 22 °C and the lowest 9 °C (both in autumn). In spring, the highest mean temperature recorded was 21 °C and the lowest 14 °C. One-way ANOVA showed no significant difference in air temperature between elevation zones ($F_{2, 12} = 1.261$, N.S, in spring and $F_{2,12} = 2.198$, N.S., in autumn). Air temperature did not vary significantly between seasons in each elevation zone (Paired samples t-test: $t_{(4)} = 1.095$, N.S., in the 500 m zone, $t_{(4)} = 1.130$, N.S., in the 1000 m zone and $t_{(4)} = 0.881$, N.S., in the 1500 m zone) and when data from all elevations were pooled ($t_{(14)} = 0.868$, N.S.).

Total bat activity was not significantly affected by elevation ($F_{2,12} = 0{,}735$, N.S., in spring and $F_{2, 12} = 0{,}310$, N.S., in autumn), although some differences between elevation zones were observed (Fig. 2). Pearson's test showed that there was no correlation between air temperature and the total number of bat passes ($r = 0{,}423$, d.f. = 14, N.S., in spring and $r = 0{,}349$, d.f. = 14, N.S., in autumn). Total bat activity was significantly higher in spring than in autumn ($t_{(14)} = 4.451$, $P < 0.05$, $r = 0.765$), particularly in the 500 m elevation zone ($t_{(4)} = 5.162$, $P < 0.05$, $r = 0.932$). No statistically significant difference between seasons was found in the 1000 m

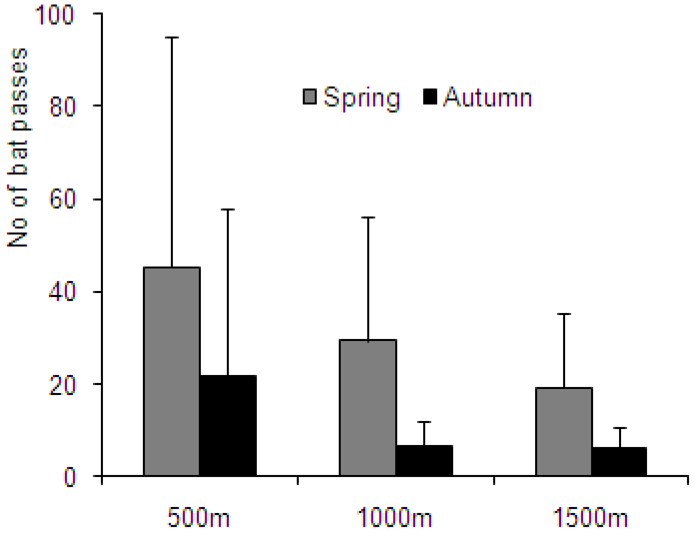

Figure 2 - Mean number of bat passes (all species) in each elevation zone in spring and autumn. Error bars denote standard deviations.

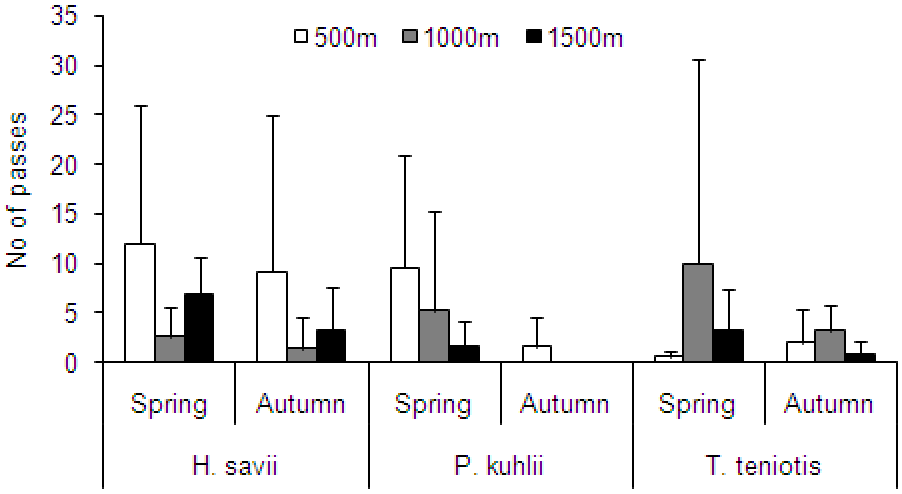

Figure 3 - Mean number of passes of *H. savii*, *P. kuhlii* and *T. teniotis* per elevation zone in spring and autumn. Error bars denote standard deviations.

and 1500 m zones ($t_{(4)}$ = 1.926, N.S. and $t_{(4)}$ = 2.183, N.S., respectively). *H. savii* was recorded in 13 out of 15 sites. Again, no significant difference was observed between elevation zones, in each season ($F_{2,\ 12}$ = 1.693, N.S., in spring and Kruskal-Wallis test: $H_{(2)}$ = 1.205, N.S., in autumn; Fig. 3). No significant difference was found between spring and autumn for each elevation zone separately (z = 1.095, N.S. in the 500 m zone, z = 0.557, N.S. in the 1000 m zone and z = 1.511, N.S. in the 1500 m zones) and when data from all elevations were pooled (z = 1.822, N.S.). Feeding buzzes of *H. savii* were recorded in the 500 m (N = 6) and 1500 m (N = 2) zones in spring and in the 500 m (N = 3) and 1000 m (N = 1) zones in autumn.

P. kuhlii was recorded in seven sites. In spring it was present in all elevation zones, whilst in autumn it was recorded only at 500 m (Fig. 3). No significant difference in the activity of *P. kuhlii,* between the three elevation zones, were observed in spring or autumn ($H_{(2)}$ = 1,182, N.S. in spring and $H_{(2)}$ = 4.286, N.S. in autumn). This species was more active in spring, when activity was tested irrespective of elevation (z = 2.366, $P < 0.05$, r = 0.611). No statistically significant difference between seasons was found in the 500 m, 1000 m and 1500 m zones (z = 1.604, N.S., z = 1.342, N.S., and z = 1.342, N.S., respectively). In spring, 10 feeding buzzes of *P. kuhlii* were recorded at 500 m and 1000 m, while in autumn only 1 buzz was recorded at 500 m.

T. teniotis was recorded in all elevation zones, in both seasons (13 sites). The number of passes did not vary significantly among the three elevation zones ($F_{2,\ 12}$ = 0.698, N.S., in spring and $F_{2,\ 12}$ = 1.43, N.S., in autumn; Fig. 3). No seasonal variation in the activity of this species was found, for each elevation

Table 2 - Species occurrence in the different elevation zones (1 = 500 m, 2 = 1000 m, 3 =1500 m), in spring, autumn and both seasons. Only the minimum possible number of species is considered in the last three rows.

Species	Spring			Autumn			Both seasons		
	1	2	3	1	2	3	1	2	3
R. blasii	x		x	x			x		x
R. ferrumequinum	x	x		x			x	x	
R. hipposideros	x	x	x		x	x	x	x	x
M. blythii	x						x		
M. capaccinii	x			x			x		
M. emarginatus	x		x				x		x
P. kuhlii	x	x	x	x			x	x	x
H. savii	x	x	x	x	x	x	x	x	x
P. hanaki				x			x		
M. schreibersii	x			x			x		
E. serotinus/N. leisleri	x	x	x				x	x	x
Plecotus spp.				x	x		x	x	
T. teniotis	x	x	x	x	x	x	x	x	x
No of species	11	6	8	9	4	3	13	7	8
Mean (± SD)	4.4 (2.7)	3.0 (0.4)	3.0 (0.8)	3.0 (2.8)	2.0 (0.5)	1.0 (0.4)	5.6 (3.8)	3.6 (0.5)	3.4 (0.9)
Min-max	2-9	3-4	2-4	1-8	1-2	1-2	1-9	1-4	1-4

zone separately ($t_{(4)}$ = 0.558, N.S in the 500 m zone, $t_{(4)}$ = 0.045, N.S. in the 1000 m zone and $t_{(4)}$ = 1.230, N.S. in the 1500 m zone) and when data from all elevations were pooled ($t_{(14)}$ = 0.221, N.S.). Feeding buzzes of *T. teniotis* were recorded only in spring, in all elevation zones. A considerable variability in the total bat activity, as well as in the activity of the most abundant species, per transect in each elevation zone was found, as shown by the high standard deviations (Fig. 2 and 3).

The most abundant rhinolophid was *R. hipposideros* (21 passes); it was recorded in all elevation zones in spring and in the 1000 m and 1500 zones in autumn. Calls of the species pair *E. serotinus* / *N. leisleri* were recorded only in spring, in all elevation zones (two, three and one sites for, respectively, the 500 m, 1000 m and 1500 m zones).

In the 500 m elevation zone we recorded a minimum of 13 species (Tab. 2): 11 fully identified, one *Plecotus* sp.

(one pass) and *E. serotinus* / *N. leisleri* (12 passes in two sites). In the 1000 m zone we recorded at least seven species: five species confidently identified, plus *E. serotinus* / *N. leisleri* (30 passes in three sites) and 1-2 species of the genus *Plecotus* (three passes in one site). Finally, in the 1500 m zone we recorded 8-9 species (Tab. 2): six species confidently identified, *E. serotinus* / *N. leisleri* (one pass) and *Miniopterus schreibersii* / *Pipistrellus hanaki* (two passes in two sites). No significant difference in species richness between elevation zones was found, due to the high variability in the number of species recorded per transect in the lower zone (Tab. 2). At least 11 species were recorded in spring, while in autumn we recorded 10 or 11 species. Species richness was significantly higher in spring in both the 1000 m (Wilcoxon signed-rank test, $z = 2.070$, $P < 0.05$, $r = 0.926$) and 1500 m (Wilcoxon signed-rank test, $z = 2.041$, $P < 0.05$, $r = 0.913$) zones, as so as when data from all elevation zones were pooled (Wilcoxon signed-rank test, $z = 3.236$, $P < 0.005$, $r = 0.835$; Tab. 2).

DISCUSSION

In our study area elevation did not play a main role in shaping the composition and activity of the bat community. Although, on average, more passes and species were recorded in the lower elevation zone, the high sample variability among sites did not allow to stress a sound altitudinal pattern. The proportion of bat passes that we identified to the species level (67.6%) was lower than in other similar studies (e.g., 83% in Russo and Jones, 2003), but even if all passes classified as *P. kuhlii* / *H. savii* had been ascribed to one of these species, the overall results would have not changed.

A monotonic decline in bat species richness with increasing elevation (Pandurska, 1996; Patterson *et al.*, 1996, 1998; Sanchez-Cordero V., 2001; Willig *et al.*, 2003; McCain, 2005; Kaňuch and Krištín, 2006), or a hump-shaped pattern (Sanchez-Cordero V., 2001; Barataud, 2004; McCain, 2005), have been reported for several mountain areas worldwide. However, the ability of bats to travel over long distances and perform seasonal movements has been largely neglected in these studies. Regular movements of bats along the elevation gradient, e.g. swarming behaviour (Parsons *et al.*, 2003) and shift of roosting sites (Altringham, 1996) can increase species richness in high elevations on a seasonal basis. Although *P. hanaki*, *E. serotinus*, *P. kolombatovici*, *P. macrobullaris*, *M. schreibersii* and species of the genus *Myotis* were absent or rare in the higher elevation zones in this study, they have been reported to roost in caves above 1000 m.a.s.l., during the swarming and hibernation period (Benda *et al.*, 2009). Thus it is not likely that the 1500 m zone supports considerably fewer species than lowlands.

In a similar study conducted on lakes and forest clearings in Canada, Grindal *et al.* (1999), attributed the decrease in bat foraging activity and capture rates with elevation to the lowering of air temperature with altitude, which may result in food scarcity (Taylor, 1963). In our study area air temperature did not significantly differ between elevation zones and thus it could not considerably affect the elevational distribution and activity pattern of bats.

The high variability in the number and the activity of species found per transect in each elevation zone may depend on the availability of food and roosting sites. The extent of habitat heterogeneity is thought to affect species richness and activity (Patterson *et al*., 1996; Lomolino, 2001; Willig *et al*., 2003) and this seems to be the case in our study, since the Cretan landscape (especially the lowlands) comprises a mosaic of many different habitat types (Rackham and Moody, 1996). The predominance of *H. savii*, *P. kuhlii* and *T. teniotis* and the presence (in some sites) of *Rhinolophus* spp. and *Myotis* spp., which all use rock crevices or caves as roosts (Schober and Grimmberger, 1997), agree with this hypothesis. Unfortunately, data from other Mediterranean areas for comparisons are lacking.

McCain (2005) stressed the importance of sampling the whole elevation gradient of the study area, an approach we could not follow, due to the lack of enough suitable sampling sites below 500 m a.s.l. and above 1500 m a.s.l. Thus, the observed lack of a clear elevational pattern could be attributed to this sampling deficiency, and our results represent a truncated portion of a either monotonic or bimodal pattern. Anyway, although annual precipitation on Mount Psiloritis increases with elevation, productivity follows an opposite trend due to the lack of soil, partly as a result of human degradation (Rackham and Moody, 1996) and the high water permeability of the limestone which prevails above 1000 m a.s.l. (Fassoulas *et al*., 2007). Therefore, habitat productivity and variability are higher in lowland landscapes, in contrast to McCain (2005), and it is not likely that bat species richness is higher in the sub-alpine and alpine zones compared to low-elevation ones.

Another possible explanation of our results is the effect of insularity; population size, niche breadth and individual behaviour may deeply differ between insular and mainland populations of the same species (Blondel and Aronson, 1999). Scarcity of suitable habitats may lead to deeply altered habitat use patterns in island-dwelling bats. For example, on Zakynthos (western Greece), high levels of activity have been recorded for the long fingered bat, *Myotis capaccinii*, in woodlands (Davy *et al*., 2007), although this species usually forages over water (Schober and Grimmberger, 1997). Furthermore, the long term deforestation and fire practices in the Mediterranean basin (Blondel and Aronson, 1999) and the more recent abandonment of cultivations and overgrazing on Crete (Papanastasis, 2004) have favoured the expansion of shrublands and may be partly responsible for the peculiar situation recorded.

The number of species recorded, overall bat activity and that of *P. kuhlii* were significantly higher in spring, although these trends could not be attributed to thermoregulatory constraints faced by the bats in autumn. Reduced activity in autumn might depend on the timing of these bats' circannual clock (Altringham, 1996 and references therein). Adult females have higher need for food during late spring, due to gestation and rearing of their young. Additionally, Cretan bats undergo some form of hibernation during winter, and/or reduce their foraging activity (P. Georgiakakis, unpublished data); this may lead to the depletion of their fat reserves at the end of winter and to increased energy demands in spring.

Data from more species are needed in order to elucidate the seasonal pattern of bat activity on Mediterranean insular ecosystems such as on Crete. Similarly, more research is needed to investigate if the activity of insects on the Mediterranean is sharply influenced by elevation and seasonality and which bat species feed, mate or hibernate in the alpine areas of the Cretan mountains.

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