ABSTRACT - The northern Dinaric karst in Slovenia (area 6880 km²) has 5470 caves of variable size (length 2–20570 m, depth up to 650 m) scattered along the entire elevation gradient of the region (74–1785 m above sea level). Sixteen bat species, of 26 known to occur in the area, were recorded in 156 caves (118 hibernacula) between 1990 and 2003. *Miniopterus schreibersii* was the most abundant species observed in these caves (74.0% of the total number of hibernating individuals), followed by three species of *Rhinolophus* (24.9%), but the remaining 12 species formed only a small proportion of those observed (1.1%). *Rhinolophus ferrumequinum* and *R. hipposideros* were the only widespread species, hibernating in 66 and 106 caves, respectively. The majority of hibernating bats (89.9%) occurred in ten caves whereas 71 hibernacula (60.2%) were occupied by ≤ 10 bats each. Hibernacula were 10–13092 m long (median = 160 m), 1–250 m deep (median = 21 m) and located 98–1200 m above sea level (median = 466 m). Wintering bats were not randomly dispersed among caves in the region and tended to occur in longer and deeper caves located at low elevations. Of the ten most important hibernacula in the study area, nine can be accessed by human visitors. One of the largest potential hibernacula had been progressively commercially exploited from the beginning of the 19th century and has thereby lost at least three cave-dwelling bat species, including *Rhinolophus blasii*, which is now locally extinct in the Dinaric karst of Slovenia.

Key words: Bats, *Rhinolophus*, *Miniopterus schreibersii*, hibernation, conservation, Slovenia

RIASSUNTO - Caratterizzazione dei siti di svernamento della chiotterofauna nel Carso Dinarico settentrionale, Slovenia. Nella porzione settentrionale del Carso Dinarico in Slovenia (superficie di 6880 km²) sono presenti 5470 grotte, con differenti dimensioni e caratteristiche (lunghezze comprese tra 2 e 20570 m, profondità sino a 650 m), distribuite lungo l'intero gradiente altitudinale proprio della regione (da 74 a 1785 m s.l.m.). Un totale di 16 specie di Chirotteri, rispetto alle 26 note per l'area, è stato studiato tra il 1990 e il 2003, in 156 diverse grotte (118 delle quali utilizzate per l'ibernazione). La specie più abbondante è risultata essere *Miniopterus schreibersii* (74% degli individui ibernanti censiti), seguita da tre specie del genere *Rhinolophus* (24.9%), mentre le restanti 12 specie costituiscono solo un'esigua porzione (1,1%) degli individui censiti. *Rhinolophus ferrumequinum* e *R. hipposideros* sono risultate essere le specie più diffuse, in quanto ritrovate in ibernazione in 66 e 106 grotte, rispettivamente. La maggioranza degli individui ibernanti è stata rilevata in 10 grotte, mentre in 71 siti di svernamento (60,2%) sono state censite aggregazioni di non più di 10 individui. Complessivamente, i siti di svernamento
studiani hanno uno sviluppo compreso tra 10 e 13092 m (mediana: 160 m) e profondità comprese tra 1 e 250 m (mediana: 21 m), e sono situati a quote comprese tra 98 e 1200 m s.l.m. (mediana: 466 m). I risultati indicano che i Chirotteri ibernanti non si disperdono casualmente nelle grotte del sistema carsico studiato, e che invece tendono a preferire grotte molto sviluppate e profonde poste alle quote più basse. Tra i 10 siti di ibernazione più importanti nell'area, 9 sono sfruttati turisticamente. Uno dei maggiori potenziali siti di svernamento è stato progressivamente sfruttato a partire dal XIX secolo, e attualmente è stata registrata la scomparsa di almeno tre specie troglofile, tra cui R. blasii, che attualmente è considerata localmente estinta nell'area del Carso Dinarico sloveno.

Parole chiave: Chirotteri, Rhinolophus, Miniopterus schreibersii, ibernazione, conservazione, Slovenia

INTRODUCTION

Bats in temperate zones are entirely insectivorous and must therefore cope with seasonally fluctuating food supplies by hibernation, migration, or both (Raesly and Gates, 1986). Bats hibernate only in places providing suitable microclimatic conditions and safety from predation and disturbance (Kryštufek, 2004). Both of these requirements are met in caves, where the world’s largest aggregations of bats are found (Hutson et al., 2001). Caves, however, are scarce in many parts of the world and their availability influences the distribution and abundance of bats (Humphrey, 1975). A shortage of roosts results in large aggregations in hibernacula; for example, there are around 20000–30000 bats in artificial underground passages of Nietoperek in western Poland, where natural roosting sites are scarce (Urbanczyk, 1989; Hutson et al., 2001). Very little is known about the dispersal of bats among hibernacula in regions where caves are plentiful. Previous studies mainly focused on large aggregations of hibernating bats (e.g. Djulić, 1961) but rarely considered bat dispersion among available caves in a landscape. Bats do not disperse in a uniform or random way among potential roosts because certain habitat variables associated with caves influence their selection and exploitation by bats (Raesly and Gates, 1986). The focus of this study was on cave utilisation by hibernating bats in the northern Dinaric karst in Slovenia. Karst is defined as terrain with distinctive landforms arising from the combination of high rock solubility (Mesozoic limestone in the case of Slovenia) and underground channel porosity, resulting from aqueous dissolution (Ford, 2004). Underground passages of various sizes, ranging from narrow cracks to large and spacious caverns, are common features of karst landscapes and provide bats with a broad range of potential roosts. This paper addresses two questions in particular. First, which species from the local bat assemblage utilise caves in the Dinaric karst of Slovenia and what is the pattern of cave occupancy? Secondly, are hibernacula predictable by some simple macroecological parameters of caves?

STUDY AREA

The Dinaric karst encompasses mountains and plateaus in the southwestern corner of
Bat hibernacula in Dinaric karst

Slovenia, extending along the Adriatic coast as far as the Kosovo basin in the southeast. The northern margin of the study area, which was arbitrarily defined by the Krka and Idrijca Rivers, roughly coincides with the northern border of the ‘cave-dwelling area’ as defined for bats by Horáček (1984). Western and southern limits of the study area were set at the borders of Italy and Croatia, respectively, but the coastal mudstone zone, without caves, was excluded. Our survey covered an area of 6880 km². This is a largely wooded (57.6% forest cover) and sparsely populated region (53 inhabitants per km²) with a mean elevation of approximately 560 m (Gams, 1974; Perko and Orožen Adamič, 1999). Thus far, 5470 caves (average 0.8 caves per km²) of variable size (length 2-20570 m, depth up to 650 m) and scattered along the entire elevation gradient of the region (74-1785 m above sea level) have been identified.

METHODS

This study is based on data collected from 1990 to 2003, but mainly during the last two years due to the field surveys within the framework of the Natura 2000 project. Although the main goal was to detect as many roosts as possible, sites were visited based on their accessibility and previous information on the presence of bats. Caves were thoroughly searched for roosting bats during daylight hours in all months of the year but most intensively during the hibernation period (mid-October–March/April). The number of visits per cave ranged between one and 37, and larger hibernacula were inspected more frequently. In the case of multiple observations from the same site, only the largest number of bats recorded was considered in subsequent analyses. Although this practice ignored occasional bat movements among sites during hibernation (Hutson et al., 2001; Berková and Zukal, 2006), it adequately represented the numbers of torpid bats. Repeated surveys of large aggregations showed bat numbers to be of comparable magnitude within the same season and between years. Miniopterus s. s. was an exception to this trend, because the number of individuals in a roost fluctuated widely even over short periods; consequently, its abundance might have been overestimated. For further details see Kryštufek et al. (2003) and Kryštufek and Režek Donev (2005).

Information on caves was provided by the Institute for Karst Research and included geographic coordinates and three macro-habitat variables: elevation (at entrance), length of passages and depth (elevation difference between the cave entrance and its highest/lowest point). This evidence was available for 5282 caves out of 5470 (96.6%).

Data were analyzed using univariate and multivariate statistical tests. Because the data deviated from normality (Shapiro-Wilks normality test P > 0.05), they were transformed to a base-10 logarithmic scale prior to analysis. To assess whether hibernacula were selected at random from all caves that were known and characterized in the region, the three cave variables were subjected to principal components analysis (PCA; James and McCulloch, 1990). Statistical tests were run in Statistica 5.5 (StatSoft Inc., 1999).

RESULTS

Of the 26 bat species known to occur in the study area (Kryštufek and Režek Donev, 2005), we found no evidence of cave use in the study area by ten species: Myotis nattereri, M. bechsteinii, M. brandtii, Nyctalus leisleri, Vespertilio murinus, Pipistrellus pygmaeus, P. nathusii, P. kuhlii, Hypsugo savii and Plecotus macrobullaris. Exploitation of caves by the remaining
16 species is summarised in Tab. 1. Large species of *Myotis* (*M. myotis* and *M. blythii*) and two species of long-eared bats (*Plecotus auritus* and *P. austriacus*) were pooled by genus because field identifications were not reliable in all reports. In spite of this, all four species were confirmed for the study area and were also found hibernating in caves.

Bats were recorded in 156 caves and their presence in another 18 caves was documented prior to, but not during, the study period. The majority of the 156 caves were used as hibernacula (118 sites) and only 12 caves housed maternity roosts. Records from the remaining sites were of transitional bats or could not be ascribed to one of the two categories due to incomplete evidence. All 16 species found in caves were recorded during hibernation. More caves were utilised as hibernacula than as maternity colonies and the total number of bats observed in hibernation was approximately twice the number observed in nurseries (Tab. 1).

**Table 1** - Cave utilisation by bats in the Dinaric karst of Slovenia. Species are arranged by the total number of hibernating individuals observed across all caves, in descending order. Frequencies of relative abundance are given in parentheses.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of caves</th>
<th>Number of individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Hibernacula</td>
<td>Nurseries</td>
</tr>
<tr>
<td><em>Miniopterus schreibersii</em></td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td><em>Rhinolophus hipposideros</em></td>
<td>106</td>
<td></td>
</tr>
<tr>
<td><em>Rhinolophus ferrumequinum</em></td>
<td>66</td>
<td>5</td>
</tr>
<tr>
<td><em>Rhinolophus euryale</em></td>
<td>9</td>
<td>3</td>
</tr>
<tr>
<td><em>Nyctalus noctula</em></td>
<td>4</td>
<td></td>
</tr>
<tr>
<td><em>Myotis cappaccinii</em></td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td><em>Barbastella barbastellus</em></td>
<td>16</td>
<td></td>
</tr>
<tr>
<td><em>Myotis myotis/blythii</em></td>
<td>14</td>
<td>4</td>
</tr>
<tr>
<td><em>Eptesicus serotinus</em></td>
<td>3</td>
<td></td>
</tr>
<tr>
<td><em>Plecotus auritus/austriacus</em></td>
<td>4</td>
<td>4 (&lt;0.1)</td>
</tr>
<tr>
<td><em>Myotis daubentonii</em></td>
<td>4</td>
<td></td>
</tr>
<tr>
<td><em>Myotis emarginatus</em></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td><em>Myotis mystacinus</em></td>
<td>1</td>
<td>1 (&lt;0.1)</td>
</tr>
<tr>
<td><em>Pipistrellus pipistrellus</em></td>
<td>1</td>
<td>1 (&lt;0.1)</td>
</tr>
</tbody>
</table>
The majority of bats recorded in hibernacula were *M. schreibersii* (74.0%), followed by three species of *Rhinolophus* (*R. ferrumequinum, R. hipposideros* and *R. euryale*; 24.9%). The remaining 12 species composed only a small fraction of bats observed hibernating (1.1%) and were excluded from the subsequent analysis. The majority of hibernacula contained only one of the four most common species (54.3%), followed by sites that housed two (38.1%) and three (7.6%) species. Two species of *Rhinolophus* were the most widespread, occurring in 66 (*R. ferrumequinum*) and 106 (*R. hipposideros*) caves, respectively. Thus, nearly every hibernacula had at least one of these two species of *Rhinolophus* (117 caves) and in 95 caves (80.5%) they were the only bats recorded.

Hibernacula were 10-13092 m long (median = 160 m), 1-250 m deep (median = 21 m) and located 98-1200 m above sea level (median = 466 m). Multiple regression of the number of hibernating bats against these three parameters revealed significant relationships (F = 12.33, P <0.0001) but the coefficient of determination was low (R^2 = 0.24). Large caves tended to have larger roosts of hibernating bats than small caves but the proportion of residual variability was high. Although not evident from the regression results, the majority of hibernacula were at low elevations (upper quartile range = 565 m) and only four sites with roosts totalling 32 bats were found at elevations higher than 700 m (Tab. 2). There were also differences in cave use among species. The only two large aggregations of *M. schreibersii* were in long (> 5 km) and deep caves (> 140 m). Of the two large colonies of *R. euryale* (275 and 267 bats), one was in a long (1870 m) and fairly deep cave (47 m), the other in a short (62 m) and shallow cave (5 m). Of the two most widespread rhinolophids, *R. hipposideros* appeared to be less selective regarding cave length (4.4% of individuals in short caves [<50 m]) than *R. ferrumequinum* (0.2% of bats in short caves).

In a principal components analysis (PCA) on the three cave variables, cave length and depth had high positive loadings for the first principal component (PC1) and altitude had a high positive loading for the second principal component (PC2). Projection of 5282 caves onto the first two principal components (90.2% of variance explained) showed that hibernacula attained high scores for PC1 and low scores for PC2 (Fig. 1). One-way ANOVA revealed significant differences between occupied and unoccupied caves for both PC scores (F > 130, P <0.001). Preferred hibernacula thus tended to be in longer and deeper caves at lower elevations. It is noteworthy that the two largest hibernacula (1570 and 9885 bats, respectively) were outside the 95% confidence ellipse of parameters for available caves. Based on the above conditions, the number of potential hibernacula in the area was tentatively estimated to be 5025 caves (95.1% of the total number of caves with complete data; N = 5282). This proportion declines rapidly with an increase in the number of bats occupying the site. Thus, 21.7% of
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caves might have a potential to roost (0.06%) appear to be suitable >100 bats each, but only three caves hibernacula for colonies >1000 bats.

Table 2 - Distribution of caves utilised for hibernation and number of hibernating bats according to 100 m elevation belts in the Dinaric karst of Slovenia. Frequencies (in %) are in parentheses.

<table>
<thead>
<tr>
<th>Elevation (m a.s.l.)</th>
<th>Number of caves</th>
<th>Number of hibernating bats</th>
</tr>
</thead>
<tbody>
<tr>
<td>≤ 100</td>
<td>2 (1.7)</td>
<td>3 (&gt;0.1)</td>
</tr>
<tr>
<td>101–200</td>
<td>11 (9.3)</td>
<td>802 (5.4)</td>
</tr>
<tr>
<td>201–300</td>
<td>15 (12.7)</td>
<td>408 (2.7)</td>
</tr>
<tr>
<td>301–400</td>
<td>11 (9.3)</td>
<td>113 (0.8)</td>
</tr>
<tr>
<td>401–500</td>
<td>33 (28.0)</td>
<td>12280 (82.4)</td>
</tr>
<tr>
<td>501–600</td>
<td>29 (24.6)</td>
<td>733 (4.9)</td>
</tr>
<tr>
<td>601–700</td>
<td>13 (11.0)</td>
<td>529 (3.6)</td>
</tr>
<tr>
<td>&gt; 700</td>
<td>4 (3.4)</td>
<td>32 (0.2)</td>
</tr>
<tr>
<td>Total</td>
<td>118</td>
<td>14900</td>
</tr>
</tbody>
</table>

Figure 1 - Projection of caves onto the first two principal components derived from a principal components analysis of three log10-transformed cave variables. The percentage of variance explained by a component is in parentheses. Character vectors (right upper insert) show relative contribution of the cave variable to PCs. The 95% confidence ellipses encircle the available cave pool (dashed line) and 118 recorded hibernacula (bold line). Symbols are placed for hibernacula with 100-440 bats (diamonds) and >1000 bats (triangles), respectively.
DISCUSSION

The number of bats per hibernaculum exhibited a characteristic pattern of rarity (Brown, 1995). The majority of caves contained only a small number of hibernating individuals and only few had large roosts. The largest hibernaculum contained 67.0% of all bats counted in the region and this high proportion was due to an aggregation of M. schreibersii in the cave. In any case, 89.9% of all bats were in ten caves while 71 hibernacula (60.2%) had ≤10 bats each.

Surprisingly, a high proportion of bat species (38.5%) were not found in the studied caves. Some of these species have low monitoring potential (The Bat Conservation Trust, 2001) and thus are easily overlooked during surveys. However, this alone cannot explain the profound differences in species composition of hibernating bat assemblages between the northern Dinaric karst and central and eastern Europe (cf. Handtke, 1968, Zima et al., 1994; Iljin, 1989; Anděra et al., 1992; Smirnov et al., 1999). A hypothesis still to be verified could consist in a presumption that at least some of bats in the study area possibly find roosts in cracks, fissures and smaller caverns which are numerous in scarps, canyons and pit caves throughout the area (cf. Gaisler and Chytil, 2002). The potential use of such roosts by bats is unknown because of their inaccessibility.

Bats were not randomly dispersed among hibernacula but seemed to preferred longer and deeper caves situated at lower elevations. Elevation alone may not be an important ecological factor given that large caves are typically situated at low elevations because of the way they form (Gams, 1974). Given that thermal regimes through the winter are major determinants of hibernation use by bats, size is perhaps just a surrogate for a greater diversity of microecological conditions (Ransome, 1990). Although the structure of a cave may compensate for its size, in effectively extending the ambient range available to bats (Ransome, 1990), large caves should clearly have priority when planning monitoring activities and conservation strategies in a landscape as rich in caves as the northern Dinaric karst. From a conservation standpoint, bats showing preference for the largest caves is of particular importance because these same caves have the highest potential to attract the general public. Of the ten most important bat hibernacula in the study area, five are frequently accessed by human visitors and another four are sporadically visited. Tourism generates a wide range of impacts upon such caves (Hamilton-Smith, 2004) and the accompanying disturbances are known to pose a threat to hibernating bats (Gaisler and Chytil, 2002). Rhinolophids and M. schreibersii often roost in very visible locations, making them even more vulnerable to disturbance by human visitors (Hutson et al., 2001). Although assessing and monitoring change is a vital part of good conservation management in any tourist cave (Hamilton-Smith, 2004), such activities are currently not required of tourist cave concessionaires in Slovenia.

Our results suggest that there might be only three caves suitable for large bat aggregations in the northern Dinaric karst (>1000 hibernating bats). Two of
these caves are also the largest known hibernacula in the area, while the remaining site (Postojnska jama) is at present not exploited by cave-dwelling bats. *Rhinolophus hipposideros, R. blasii* and *M. schreibersii* were documented roosting in Postojnska jama during the 19th and early 20th centuries (Toschi and Lanza, 1959; Kryštufek and Režek Donev, 2005), but this cave has been progressively commercially exploited since the beginning of the 19th century and is currently one of the main tourist attractions of the region. *Rhinolophus blasii* vanished not only from Postojnska jama, but has also been extirpated from its marginal area in the northern Dinaric karst (Kryštufek and Đulić, 2001). This raises concerns regarding the future welfare of species that depend on caves, particularly because the northern ranges of two of the four common cave-dwelling species of the region extend into the Dinaric karst of Slovenia: *R. euryale* (Gaisler, 2001) and *M. schreibersii* (Boye, 2004). Species are frequently less abundant and consequently more vulnerable to extinction at the edge of their range (Gaston, 1994; Brown, 1995), and cave-dwelling bats are not likely to be an exception. As evident from our results, there are many caves in the Dinaric karst of Slovenia, but only a few were used by bats and fewer still hosted large aggregations during winter. Clearly, cave-dwelling bats are not a priori safe in a karst terrain simply because of the abundance of caves.

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REFERENCES


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