Use of foraging habitats by bats in a Mediterranean area determined by acoustic surveys: conservation implications

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We determined habitat use by foraging bats by broad-band acoustic surveys in 10 habitat types from a Mediterranean area (southern Italy). We applied discriminant functions to identify time-expanded echolocation calls from free-flying bats.

Moon phase and cloud cover had no effect on bat activity. Only *Hypsugo savii* was influenced by temperature, and activity of *Myotis daubentonii* and *Myotis capaccinii* was reduced at higher wind speeds. Both total numbers of bat passes and feeding buzzes were highest over rivers and lakes. *Pipistrellus kuhlii* and *H. savii* were most frequently recorded. *Pipistrellus kuhlii, Pipistrellus pipistrellus and Tadarida teniotis* proved generalists in using foraging habitats.

Water sites and conifer plantations were respectively the most and the least used habitats by *H. savii*. Rivers were especially important to *Myotis* bats, *Miniopterus schreibersii* and *Pipistrellus pygmaeus*. Unlike *P. kuhlii*, *P. pipistrellus* was frequent in beech woodlands; *P. pygmaeus* made a considerable use of chestnut woodlands and *Myotis* spp. were moderately active in both these woodland types.

A large number of endangered or vulnerable species featured in riparian habitats, broadleaved woodlands and olive groves. Riparian and woodland habitats constitute an important target for conservation. Typical land use forms such as woodlands used for chestnut production and traditionally managed olive groves should be encouraged in conservation plans. The negative impact of urbanisation on bats might be counteracted by fostering trees, gardens and small cultivated patches. Farmland practices should encourage landscape complexity and limit the use of pesticides.

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Transformation of foraging habitats may seriously affect insectivorous bat populations (Stebbings 1988, de Jong 1995, Vaughan et al. 1996, Law et al. 1999, Mitchell-Jones et al. 1999, Hutson et al. 2001). Habitat features and quality influence prey insect biomass, diversity and distribution (e.g. Fry and Lonsdale 1991). It is therefore essential to identify the habitat types and characteristics preferred by bat species to define appropriate conservation guidelines and to apply effective protection measures.

The habitat requirements of European bat species may differ according to latitude (Racey 1998). Although a considerable amount of information on bat

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habitat use is available for several geographical areas (e.g. Furlonger et al. 1987, Walsh and Harris 1996a, b, Vaughan et al. 1997a), little or nothing is known about habitat preferences by bats in the Mediterranean region, and specifically Italy.

Because of their peculiar climatic and ecological features (e.g. Blondel and Aronson 1999), Mediterranean countries differ remarkably from the other European areas where most data on habitat use have been gathered. Over the millennia, the Mediterranean landscape has been shaped into a unique mosaic of habitats by the profound influence of > 300 human generations (Blondel and Aronson 1999). Therefore, it may be

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inappropriate to apply conservation guidelines devised for other geographical areas in the management of Mediterranean biodiversity, especially to bats.

Although all chiropteran species have been protected by Italian law since 1939, and legal protection has been recently implemented following the EC "Habitats" Directive, no framework exists for the protection of foraging habitats. Stebbings (1988) emphasises the urgent need to obtain information on ecological requirements of Italian bats, and Hutson et al. (2001) highlight the importance of developing conservation plans for bats in the Mediterranean region.

Bat activity may be successfully surveyed using ultrasonic detectors (e.g. Kunz and Brock 1975, Rydell et al. 1994, Walsh et al. 1995, Walsh and Harris 1996a, b, Vaughan et al. 1997a). To determine species habitat use, objective and quantitative identification methods are recommended, otherwise surveys may lead to serious misinterpretation (Vaughan et al. 1997b, Jones et al. 2000). Italy is an area of high bat species diversity, the occurrence of over 30 bat species being in fact documented by historical records and recent studies (e.g. Lanza 1959, Mitchell-Jones et al. 1999, Russo and Jones 2000, Castella et al. 2000, Kiefer and Veith 2001, Spitzenberger et al. 2001). Such a high number of species makes the acoustic identification of bats in flight an especially challenging task. Therefore, it is important to rely on a discrimination method that makes it possible to quantify the degree of correct identification (Zingg 1990, Vaughan et al. 1997b, Parsons and Jones 2000, Russo and Jones 2002).

The aim in this project was to determine the exploitation of foraging habitats by bats in southern Italy -atypically Mediterranean area -as revealed by acoustic surveys. We aimed primarily to identify those habitats that merit priority conservation measures. This is the first study on bat habitat use ever conducted in the region.

Methods

Study sites

The study area lay between latitudes 41°20'N and 40°15'N, i.e. it was mostly confined to the Campania region (SW Italy); we chose only two sites slightly further north, in southern Lazio (Circeo National Park). The area we investigated occupies a central position in the Mediterranean, being located on the boundary of two of the quadrants (NW, NE) in which the Mediterranean Basin may be divided in biogeographical terms (Blondel and Aronson 1999). We investigated the following ten habitat types occurring in southern Italy as being representative: 1) Lakes. Five out of 6 replicates chosen were constituted by artificial basins. Mean elevation of sites 639 m a.s.l. (range

86-1040 m). 2) Rivers. Sampling focused on main rivers. Streams, although quite common in southern Italy, mostly dry up in summer and were not considered. Mean elevation of river transects 84 m a.s.l. (range 18-160 m). 3) Beech Fagus sylvatica L. woodlands. These are the typical high-altitude woodlands in the study area. Mean elevation 1259 m a.s.l. (range 1180–1340 m). Mature trees were dominant at all sites. 4) Sweet chestnut Castanea sativa Miller woodlands managed for chestnut production. They constitute a traditional form of chestnut woodland management in the study area, and are often characterised by mature trees. Undergrowth is normally either poor or absent as it is removed to facilitate chestnut cropping. Mean elevation 692 m a.s.l. (range 563-840 m). 5) Mediterranean macchia (cf. Blondel and Aronson 1999): evergreen shrublands characterised by the occurrence of sclerophyllous species such as Myrtus communis L., Pistacia lentiscus L., Arbutus unedo L., Quercus coccifera L., Laurus nobilis L. Mean elevation was 369 m a.s.l. (range 5–600 m). 6) Arable land. Farmland in the study area was generally characterised by a relatively complex mosaic of fields separated by tree lines, hedges, canals, etc. Mean elevation 96 m a.s.l. (range 40-200 m). 7) Rural towns. Generally structured in an older centre surrounded by modern settlements. Towns mostly had street lighting and comprised gardens and small fields. Mean elevation 477 m a.s.l. (range 150-700 m). 8) Olive Olea europea L. groves. Mean elevation 336 m a.s.l. (range 160-576 m). 9) Mediterranean and sub-Mediterranean woodlands. Low and mediumaltitude broadleaved woodlands, dominated by *Quercus* ilex L. (Mediterranean woodlands sensu stricto); mixed deciduous forests of Alnus cordata (Loisel.) Desf., Ostrya carpinifolia Scop., C. sativa; deciduous oak forests dominated by either Quercus cerris L. or Quercus pubescens Willd. Mean elevation 337 m a.s.l. (range 34–895 m). Mature woodland occurred at all sites. 10) Conifer (*Pinus* spp.) plantations. Four out of six sites were located along the coast at sea level, while the elevation of the remaining two was 350 and 510 m a.s.l.

Sampling design and sound recording

We selected sixty sites, corresponding to 6 replicates of each habitat type. They were large enough to enable a 2-km transect to be walked in a completely homogeneous habitat. We conducted sampling in 1998 and 1999, from May to October. Each year, we visited 30 sites in a random order to avoid any seasonal influence on sampling. We visited transects in advance in daylight, measuring their length carefully and when necessary marking with reflective tape trees and other conspicuous objects along the path to make navigation at night easier. When recording, we minimised the use of lights to avoid any interference with bat activity. Following methods of Vaughan et al. (1997a), we took care to walk at a constant speed, and covered the transects in 45 min each starting 30 min after sunset. On rare occasions, when transects had to cross habitat interruptions (e.g. clearances in woodland), we suspended recording for not more than 5 min. We chose sites as far apart as possible, and in most cases an inter-site distance of at least 4 km could be maintained. Before starting and at the end of each transect, we measured air temperature (C°) to the nearest 0.1°C with a digital thermometer and estimated wind speed according to the Beaufort scale. For each transect, we calculated a mean value of these variables and used it in data analyses. We also estimated percent cloud cover at the start of each transect. We obtained the percentage of the moon face illuminated on each night from Whitaker (1998, 1999).

We kept an S-25 bat detector (Ultra Sound Advice, London) switched to frequency division, and its HF output was connected to a PUSP (Portable Ultrasound Processor, Ultra Sound Advice, London). Whenever a bat pass – i.e. a series of clicks heard in frequency division as a bat flew within range (Fenton 1970) - was detected, we triggered manually the PUSP, sampling a 2 s sequence of calls at a rate of 448 kHz and time-expanding it $(10 \times)$. The corresponding sample of 20 s was automatically downloaded and recorded on one channel of Sony Metal XR cassettes by means of a Sony Professional Walkman WM D6C. We also recorded the S-25 frequency division output on the other tape channel. The S-25 microphone has a sensitivity of $-57dB \pm 3dB$ (ref. 1V μbar^{-1}) from 20-120 kHz. Because it is not possible to time-expand continuously (e.g. Jones et al. 2000), while downloading we could not expand any further incoming signal; we counted additional bat passes from frequency division recordings. We made no attempt to identify species or even genera from frequency-divided calls because the high species diversity of the study area would inevitably result in high misclassification.

Sound analysis and species identification

We analysed the recordings with the software BatSound release 1.0 (Pettersson Elektronik, Uppsala). We used a sampling frequency of 44.1 kHz, with 16 bits/sample, and a 512 pt. FFT with a Hamming window for analysis. We obtained a 112 Hz frequency resolution for spectrograms and power spectra. One echolocation call from each bat pass was analysed. We applied a quantitative method (Russo and Jones 2002) to identify 21 out of the 23 bat species that were reported to occur in the study area at the time of our investigation (Lanza 1959, Mitchell-Jones et al. 1999, Russo and Jones 2000, Russo unpubl.). *Myotis bechsteinii* (Kuhl) – very rare throughout Italy (Vergari et al. 1998) – was not in-

cluded. Moreover, we did not take into account the presence of *Nyctalus lasiopterus* (Schreber), also rare in Italy (Vergari et al. 1997), because only one observation – obtained with a heterodyne detector (Fornasari pers. comm.) – exists for the area (Zava et al. 1996). After Jones and Barratt (1999), in this study we term *Pipistrellus pipistrellus* (Schreber) the pipistrelles of the 45 kHz phonic type (Jones and Parijs 1993), and *Pipistrellus pygmaeus* (Leach) those of the 55 kHz phonic type.

Following Vaughan et al. (1997b), we used Discriminant Function Analysis (DFA) to devise two separate quadratic functions with cross-validation to identify bats in flight - one for bats emitting FM calls, the other for those producing FM/QCF calls. They were developed from recordings of echolocation calls of 774 Italian bats (mainly from the south) of known identity. The model for bats emitting FM calls relied on start frequency, end frequency, frequency of maximum energy, and duration of the calls (Russo and Jones 2002). It covered nine species, providing the following percent classification rates: Barbastella barbastellus (Schreber), 90%; Myotis blythii (Tomes), 53%; Myotis capaccinii (Bonaparte), 88%; Myotis daubentonii (Kuhl), 87%; Myotis emarginatus (E. Geoffroy), 67%; Myotis myotis (Borkhausen), 67%; Myotis nattereri (Kuhl), 75%; Plecotus auritus (L.), 77%; Plecotus austriacus (Fischer), 73%. Unlike the function described by Russo and Jones (2002), the one used here did not include Myotis mystacinus (Kuhl), as this species was not recorded in the study area at the time of our study. Because M. mystacinus is present (although uncommon) in nearby regions, it might also occur in the study area. Had M. mystacinus been recorded, it would have probably been classified as M. daubentonii, M. blythii or other Myotis species (Russo and Jones 2002). When we added M. mystacinus calls recorded in Abruzzo (central Italy) to our model, these were frequently misclassified (classification rate was 38%; Russo and Jones 2002).

Eight FM/OCF species were identified with a function (Russo and Jones 2002) that relied on end frequency, centre frequency, duration, and inter-pulse interval, providing the following percent classification rates: Pipistrellus kuhlii (Kuhl), 98%; P. pipistrellus, 98%; P. pygmaeus, 89%; Hypsugo savii (Bonaparte), 97%; Eptesicus serotinus (Schreber), 80%; Nyctalus noctula (Schreber), 93%; Nyctalus leisleri (Kuhl), 77%; and Miniopterus schreibersii (Kuhl), 98%. Rhinolophus ferrumequinum (Schreber), Rhinolophus hipposideros (Bechstein), Rhinolophus euryale Blasius and Tadarida teniotis (Rafinesque) were easily identified from the frequency of maximum energy of their echolocation calls. We could not identify a number of Myotis passes to species level, and so classified them as "unidentified Myotis". This happened: a) when call structure was clearly that of *Myotis* bats but signals were too faint to take accurate measurements. In particular, start frequency – an important variable for DFA identification

- was most often affected by poor recording quality. b) When the DFA response attributed calls to M. *blythii*. For this species, the DFA model adopted provided the lowest correct classification (ca 1 in 2 calls was misclassified), a result we judged not sufficiently reliable to conduct confident analysis of habitat use to species level. Because the species appears to be relatively common in southern Italy, we preferred to keep it in the discriminant model because its removal would cause a higher and uncontrollable misclassification rate, as well as an overestimate of the identification performance for the other *Myotis* bats.

When we recorded *Pipistrellus* spp. social calls, they were employed for identification since their structure is diagnostic (Barlow and Jones 1997, Russo and Jones 1999, 2000).

Data analysis

We measured bat activity as the number of bat passes recorded, and pooled time-expanded bat passes with those recorded only in frequency division for total activity analysis. We applied analyses of variance and covariance (ANOVA, ANCOVA) to analyse both overall activity and that of species frequently recorded.

As in other studies (e.g. Furlonger et al. 1987, Walsh et al. 1995, Vaughan et al. 1997a), we commonly recorded feeding buzzes (i.e. call sequences produced by bats that attempt prey capture; Griffin et al. 1960), and also tested their overall number – a measure of foraging attempt – for effects of habitat and covariates.

Preliminary data exploration (scatter plots, correlation analysis) showed that cloud cover and moon phase had no effect over bat activity: hence, we did not use these variables in further analyses. In most cases the samples conformed to ANOVA and ANCOVA assumptions (Huitema 1980) after appropriate transformation (square-root, log_e, square-root log_e). In these cases we tested data for differences between habitat types, and entered variables that appeared to influence activity as covariates in an ANCOVA. In using AN-COVA the covariate has to be measured on a continuous scale (Huitema 1980). Beaufort scale is not continuous (each value corresponding to a defined wind speed range), so to use wind speed as a covariate, we converted the Beaufort values estimated in the field to the corresponding range means in km h^{-1} . For wind speed and ambient temperature, in the analyses we used a mean value of measures obtained at the start and at the end of each transect. Because elevation was actually a feature for some of the habitat types considered and not independent from the analysis "treatment", it could not be used as a covariate (Huitema 1980). We tested the data for interactions between "habitat type" and covariates, but removed them from models because in no case did they reach significance (Aitkin et al. 1989). Likewise, covariates were removed from models where their effect was not significant, and when no covariate was left in the model, we applied a one-way ANOVA. Here we present only the analysis final results. When we detected a significant habitat effect, we performed multiple post-hoc comparisons on means adjusted by ANCOVA with the Bryant-Paulson Tukey test (Day and Quinn 1989); a Newman-Keuls test followed the ANOVA. We applied the Ryan-Joiner test to verify data conformity to normal distribution, and used the Levene test to verify homogeneity of variance.

The species richness of the foraging bat community was analysed in two ways: we tested with an ANOVA the effect of habitat on the mean number of species detected in each habitat (mean S), and compared between habitats the total number of species recorded in each habitat type (total S).

Means are presented \pm SD. We performed all analyses, except Levene, Newman-Keuls and Bryant-Paulson Tukey tests with MINITAB release 9.2.

Results

Bat activity

Overall, we recorded 3744 bat passes, and identified to species 3106 of them (83.0% of total; Table 1). We

Table 1. Numbers of bat passes recorded along 60 2-km transects (6/habitat type), each walked for 45 min. Calls recorded in frequency division were not identified. "*Myotis* sp." includes all *Myotis* passes that were not identified to species level.

Species	Number of	% of		
	bat passes	totai		
Rhinolophus ferrumequinum	12	0.32		
Rhinolophus hipposideros	13	0.35		
Rhinolophus euryale	1	0.03		
Myotis capaccinii	92	2.46		
Myotis daubentonii	146	3.90		
Myotis emarginatus	12	0.32		
Myotis myotis	6	0.16		
Myotis nattereri	4	0.11		
Myotis sp.	128	3.42		
Nyctalus leisleri	40	1.07		
Nyctalus noctula	8	0.21		
Eptesicus serotinus	9	0.24		
Pipistrellus kuhlii	1570	41.93		
Pipistrellus pipistrellus	412	11.00		
Pipistrellus pygmaeus	132	3.53		
Hypsugo savii	457	12.20		
Plecotus auritus	1	0.03		
Plecotus austriacus	0	0.00		
Barbastella barbastellus	5	0.13		
Miniopterus schreibersii	71	1.89		
Tadarida teniotis	115	3.07		
Unidentified (time expansion)	27	0.72		
Frequency division	483	12.91		
Total (time expansion)	3261	87.10		
Total	3744	100.00		

made no identification attempt for 483 passes recorded only in frequency division and 27 very faint time-expanded sequences. Finally, we attributed 128 passes (32.8% of which classified as M. blythii) to the "unidentified Myotis" category. We also recorded 569 feeding buzzes (i.e. on average 15.2% of bat passes included a feeding buzz). A strong positive correlation $(r = 0.85, DF = 58, p < 0.001, r^2 = 0.72)$ between numbers of feeding buzzes and bat passes (i.e. between foraging attempts and activity rates) recorded at each site confirmed that the number of bat passes was a reliable estimator of foraging activity. The species most frequently recorded were (in decreasing order): P. kuhlii, H. savii, P. pipistrellus, M. daubentonii, P. pygmaeus, T. teniotis, M. capaccinii and M. schreibersii (Table 1). The numbers of passes recorded from all other species (Table 1, Table 2) were too low to be used for analysis. Plecotus austriacus was not recorded (Table 1).

Overall bat activity (Fig. 1a) differed significantly between habitat types ($F_{9,50} = 3.91$, p < 0.001, log transformed data). We observed high levels of activity on rivers and lake shores. Likewise, the number of feeding buzzes recorded in such habitats was the highest ($F_{9,50} = 8.61$, p < 0.001, log transformed data; Fig. 1b). We recorded relatively large numbers of bat passes and of foraging attempts at some rural town, arable land and olive groves sites, but this trend was not confirmed statistically on account of the large sample variability (Fig. 1a, b).

Pipistrellus kuhlii occurred in all habitats (Fig. 2a), often with high activity levels. Although we detected some significant differences between habitats ($F_{9,50} = 3.91$, p < 0.005, square root transformed data; Fig. 2a), the species was quite generalist in exploiting foraging habitats. Feeding buzzes of *P. kuhlii* (n = 186) were recorded at 83.3% of sites.

Hypsugo savii activity increased significantly with temperature (ANCOVA: habitat $F_{9,49} = 6.29$, p < 0.001; temperature $F_{1,49} = 17.25$, p < 0.001, log transformed data). Once activity was adjusted for temperature, it was significantly higher on lake and river shores (Fig. 2b). Conifer plantations were the least used habitat. We recorded only 34 *H. savii* feeding buzzes, mainly (76.5%) on lake shores.



Fig. 1. Mean log transformed counts of total bat passes (a) and of total feeding buzzes (b) recorded in the 10 habitat types. La = lakes, Ri = rivers, Bw = beech woodlands, Cw = chestnut woodlands, Mm = Mediterranean macchia, Al = arable land, Rt = rural towns, Og = olive groves, Mw = Mediterranean and sub-Mediterranean woodlands, Cp = conifer plantations. Habitats in which no significant difference in bat activity was detected are labelled with the same letter. Standard deviations are shown.

Like *P. kuhlii*, *P. pipistrellus* also showed limited, although significant, differences in activity ($F_{9,50} = 4.40$, p < 0.001, log transformed data; Fig. 3a), which was relatively higher for lakes and beech woodlands. We recorded feeding buzzes (n = 80) at 45 sites in all habitats. Unlike *P. kuhlii*, *P. pipistrellus* made quite a large use of beech woodlands: in all, in this habitat we recorded 95 passes from the latter species vs. 42 from the former (Figs 2a, 3a).

Pipistrellus pygmaeus proved more selective ($F_{9,50} = 4.73$, p < 0.001; square roots of log transformed data). Activity was significantly higher over rivers and in chestnut woodlands (Fig. 3b). We recorded no passes in rural towns and olive groves. We recorded only 17 *P. pygmaeus* feeding buzzes.

Table 2. Number of passes of bat species infrequently recorded in each habitat. Abbreviations as in Figs 1-5.

Species	La	Ri	Bw	Cw	Mm	Al	Rt	Og	Mw	Ср
Rhinolophus ferrumequinum	0	5	0	1	1	0	0	3	2	0
Rhinolophus hipposideros	0	2	2	1	3	0	0	0	5	0
Rhinolophus euryale	0	0	0	0	0	0	0	0	1	0
Myotis emarginatus	3	2	2	2	0	0	0	1	0	2
Myotis myotis	0	3	0	0	0	1	0	2	0	0
Myotis nattereri	0	0	2	2	0	0	0	0	0	0
Nyctalus leisleri	3	3	1	28	1	0	2	1	1	0
Nyctalus noctula	6	0	0	2	0	0	0	0	0	0
Eptesicus serotinus	2	0	1	0	1	2	2	1	0	0
Plecotus auritus	0	0	1	0	0	0	0	0	0	0
Barbastella barbastellus	0	0	1	2	0	0	0	1	1	0



Fig. 2. (a) Mean square root transformed counts of *Pipistrellus kuhlii* passes and (b) mean log transformed counts of *Hypsugo savii* passes (adjusted for effect of temperature) recorded in the 10 habitat types. La = lakes, Ri = rivers, Bw = beech woodlands, Cw = chestnut woodlands, Mm = Mediterranean macchia, Al = arable land, Rt = rural towns, Og = olive groves, Mw = Mediterranean and sub-Mediterranean woodlands, Cp = conifer plantations. Habitats in which no significant difference in bat activity was detected are labelled with the same letter. Standard deviations are shown.

(P. pipistrellus passes+1) (a) 3 Log 2 ٥ La Ri Bw Cw Mm AI Rt Og Μw Ср Habitat (Loge (P. pygmaeus passes + 1)) (b) 3 Square root 2 1 0 Ср La Ri B٧ C٧ Mm A Rt Og Habitat

Fig. 3. (a) Mean log transformed counts of *Pipistrellus pip-istrellus* passes and (b) mean square root log transformed counts of *Pipistrellus pygmaeus* passes recorded in the 10 habitat types. La = lakes, Ri = rivers, Bw = beech woodlands, Cw = chestnut woodlands, Mm = Mediterranean macchia, Al = arable land, Rt = rural towns, Og = olive groves, Mw = Mediterranean and sub-Mediterranean woodlands, Cp = conifer plantations. Habitats in which no significant difference in bat activity was detected are labelled with the same letter. Standard deviations are shown.

Miniopterus schreibersii also was most active over rivers ($F_{9,50} = 2.78$, p < 0.05, square roots of log transformed data); we never recorded it in Mediterranean macchia and arable land (Fig. 4a).

Tadarida teniotis activity varied considerably within habitats. We recorded a low activity in all habitats except lakes (mean number of passes 9.7 ± 18.7 , range 0-47) and Mediterranean and sub-Mediterranean woodlands $(4.5 \pm 6.6, \text{ range } 0-16)$. We did not record any passes in beech woodlands, arable land and rural towns. Activity did not differ significantly between habitats ($F_{9,50} = 1.57$, NS; square roots of log transformed data). In all cases T. teniotis clearly flew high up, i.e. away from clutter, and in woodlands foraged well over the canopy. The activity of Myotis spp. (Myotis passes identified to species + "undetermined Myotis") differed significantly between habitats $(F_{9.50} = 14.7, p < 0.001;$ square root transformed data; Fig. 4b). It was highest along lake and river shores (we recorded 92% of Myotis passes at water sites), and also relatively high in chestnut and beech woodlands. We recorded no Myotis passes in Mediterranean macchia and rural towns.

Despite data transformation, the number of passes of *M. daubentonii* and *M. capaccinii* failed to meet the

analysis of variance assumptions. However, it was obvious that rivers and lakes were most used by both species, only a few passes having been recorded in other habitats (some of the woodland types analysed; Fig. 5a). Samples obtained from rivers and lakes met the analysis of variance requirements, and so we could compare activity between these habitats for both species. Preliminary data exploration suggested some influence of wind speed, which we then entered as a covariate. Once adjusted for the significant effect of wind speed by ANCOVA (M. capaccinii $F_{1,9} = 17.14$, p < 0.005; M. daubentonii $F_{1.9} = 14.77, p < 0.005), M.$ capaccinii activity showed no difference between lakes and rivers ($F_{1,9} = 0.29$, NS), unlike *M. daubentonii* $(F_{1,9} = 17.04, p < 0.005)$ which preferred rivers (analysis of square-root transformed counts).

Because *M. capaccinii* activity did not differ between rivers and lakes, we could lump together data from all water sites for correlation analysis and confirmed the occurrence of a strong negative correlation (r = -0.86, DF = 10, p < 0.001, r² = 0.74) between activity and wind speed (Fig. 5b). We detected feeding buzzes of both species only over lakes (*M. daubentonii* n = 8, *M. capaccinii* n = 24) and rivers (*M. daubentonii* n = 14, *M. capaccinii* n = 7).



Fig. 4. (a) Mean square root log transformed counts of *Miniopterus schreibersii* passes and (b) mean square root log transformed counts of *Myotis* spp. passes recorded in the 10 habitat types. La = lakes, Ri = rivers, Bw = beech woodlands, Cw = chestnut woodlands, Mm = Mediterranean macchia, Al = arable land, Rt = rural towns, Og = olive groves, Mw = Mediterranean and sub-Mediterranean woodlands, Cp = conifer plantations. Habitats in which no significant difference in bat activity was detected are labelled with the same letter. Standard deviations are shown.

Species richness

The mean number of foraging species differed significantly between habitats ($F_{9,50} = 5.57$, p < 0.001; square root transformed data). On average, rivers had significantly more species than all habitats except lakes and chestnut woodland (Table 3). Lakes and chestnut woodland also had a high mean number of species, although this was not confirmed statistically. Mediterranean macchia, arable land and conifer plantations had the lowest mean number of species.

We recorded large total numbers of species (> 10) in chestnut woodlands, followed by rivers, beech woodlands, lakes, Mediterranean and sub-Mediterranean woodlands and olive groves (Table 3). A considerable percentage (> 40%) of the species found in these habitats are classified as endangered or vulnerable in Italy. The remaining habitats had a lower total number of species, mostly belonging to the "low risk" category.

Discussion

Effect of habitat on bat activity

The identification rate we achieved is identical to that

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Fig. 5. (a) Mean log transformed counts of *Myotis daubentonii* and *M. capaccinii* passes recorded in the 10 habitat types. La = lakes, Ri = rivers, Bw = beech woodlands, Cw = chestnut woodlands, Mm = Mediterranean macchia, Al = arable land, Rt = rural towns, Og = olive groves, Mw = Mediterranean and sub-Mediterranean woodlands, Cp = conifer plantations. Standard deviations are shown. (b) Relationship between square root transformed passes of *Myotis capaccinii* at 12 water sites (6 rivers, 6 lakes) and estimated wind speed (r = -0.86, p < 0.001). Two dots overlap (arrow).

(83%) obtained by Vaughan et al. (1997a), who used the same sampling method for their study on bats in England. The importance of riparian foraging habitats we observed confirms findings for other geographical areas (e.g. Rydell et al. 1994, Walsh et al. 1995, Vaughan et al. 1997a, Racey 1998, Grindall et al. 1999). Such habitats support a higher prey insect density than other habitat types (e.g. Barclay 1991). In this study, we recorded high levels of activity of Myotis bats, H. savii, P. pygmaeus and M. schreibersii over rivers and lakes, and generalist species such as P. kuhlii and P. pipistrellus were also abundant at water sites. Vaughan et al. (1997a) showed rivers and lakes to be the main foraging habitats for P. pygmaeus in England. At a British riparian site, however, Warren et al. (2000) found that P. pygmaeus was scarce, and P. pipistrellus frequent. As these authors pointed out, elevation (as well as other unknown environmental factors) might influence the relative distribution of the two pipistrelle species. The observed use of rivers by M. schreibersii may not be

Table 3. Bat species recorded in each habitat type, their status in Italy (after Bulgarini et al. 1998), total number of species/habitat (total S) and mean (mean S), SD and range of the number of species detected at each site. Habitat abbreviations as in Figs 1–5. LR = Low Risk; VU = Vulnerable; EN = Endangered. In the "NK test results" row, habitats whose mean S did not differ significantly (p > 0.05) according to the Newman-Keuls multiple comparison test are labelled with the same letter (analysis was performed on square-root transformed data).

Species	Status in Italy	Habitat									
		La	Ri	Bw	Cw	Mm	Al	Rt	Og	Mw	Ср
Rhinolophus ferrumequinum	VU		\checkmark		\checkmark	\checkmark			\checkmark	\checkmark	
Rhinolophus hipposideros	EN		\checkmark	\checkmark	\checkmark	\checkmark				\checkmark	
Rhinolophus euryale	VU									\checkmark	
Myotis capaccinii	EN	\checkmark	\checkmark		\checkmark						
Myotis daubentonii	VU	\checkmark	\checkmark	\checkmark							\checkmark
Myotis emarginatus	VU	\checkmark	\checkmark	\checkmark	\checkmark				\checkmark		\checkmark
Myotis myotis	VU		\checkmark				\checkmark		\checkmark		
Myotis nattereri	EN			\checkmark	\checkmark						
Nyctalus leisleri	VU	\checkmark	\checkmark	\checkmark	\checkmark	\checkmark		\checkmark	\checkmark	\checkmark	
Nyctalus noctula	VU	\checkmark			\checkmark						
Éptesicus serotinus	LR	\checkmark		\checkmark		\checkmark	\checkmark	\checkmark	\checkmark		
Pipistrellus kuhlii	LR	\checkmark									
Pipistrellus pipistrellus	LR	\checkmark									
Pipistrellus pygmaeus	_	\checkmark	\checkmark	\checkmark	\checkmark	\checkmark	\checkmark			\checkmark	\checkmark
Hypsugo savii	LR	\checkmark									
Plecotus auritus	LR			\checkmark							
Plecotus austriacus	LR										
Barbastella barbastellus	EN			\checkmark	\checkmark				\checkmark	\checkmark	
Miniopterus schreibersii	LR	\checkmark	\checkmark	\checkmark	\checkmark			\checkmark	\checkmark	\checkmark	\checkmark
Tadarida teniotis	LR	\checkmark	\checkmark		\checkmark	\checkmark			\checkmark	\checkmark	\checkmark
Total S		12	13	13	14	9	6	6	11	11	8
N EN+VU species (% of total S)		5 (41.7)	7 (53.8)	6 (46.2)	8 (57.1)	3 (33.3)	1 (16.7)	1 (16.7)	5 (45.4)	5 (45.4)	2 (25.0)
Mean S (SD)		65(15)	8 2 (2.5)	43(10)	57(27)	30(14)	33(12)	37(10)	38(12)	41(15)	30(18)
Range		5_9	5-12	3-6	3_9	1-5	2-5	3-5	2-5	2-6	1-5
NK test results		a, b	a	b, c	a, b, c	c	c	b, c	b, c	b, c	c

limited to foraging, as this species seems to follow rivers as navigation landmarks (Sierra-Cobo et al. 2000).

The highly opportunistic choice of foraging sites by P. kuhlii and P. pipistrellus, also observed in England in the latter species (Vaughan et al. 1997a), is probably made possible by their plasticity in echolocation (Schnitzler et al. 1987, Jones and Parijs 1993, Kalko and Schnitzler 1993). This feature may allow the bats to exploit a variety of differently structured foraging habitats (Norberg and Rayner 1987) and feed upon a larger prey spectrum (Swift et al. 1985, Beck 1995, Barlow 1997, Arlettaz et al. 2000). Both species frequently feed by street lamps (e.g. Haffner and Stutz 1985/6, Barak and Yom-Tov 1989, Rydell 1992, Blake et al. 1994, Russo and Jones 1999). In Italy, P. kuhlii is the most abundant bat species (Lanza 1959). Pipistrellus pipistrellus is widespread and abundant across its European range (Mitchell-Jones et al. 1999). The "success" of P. pipistrellus and P. kuhlii may be due to the observed lack of habitat preferences, plasticity in roost selection (Schober and Grimmberger 1997) and "r-selected features" (Begon et al. 1986) – i.e. relatively short life span, first parturition at one year of age and frequent birth of twins (Arlettaz et al. 2000). The observed difference in the use of beech woodlands (all sites occurring over 1000 m a.s.l.) between P. pipistrellus and P. kuhlii may be determined by an elevational effect. In fact, P. kuhlii is associated with lower altitudes (Schober and Grimmberger 1997, Vernier and Bogdanowicz 1999).

Although during this study we failed to record *T.* teniotis in beech woodlands, arable land and towns, in Campania and Abruzzo (central Italy) it has been observed foraging in high flight over villages, beech woodlands, cultivated fields – especially if bordered by illuminated roads – and even large cities (Russo and Mastrobuoni 1998). Ahlén (1990) reported that *T. teni*otis forages over illuminated villages. This species may tend to forage in built-up sites later at night, as occasionally observed in some of the towns we visited (Russo unpubl.), when the temperature is appreciably higher than elsewhere.

Influence of other environmental variables

The absence of influence of cloud cover and moon phase over bat activity we detected was found by other authors (Geggie and Fenton 1985, Negraeff and Brigham 1995, Vaughan et al. 1997a, Gaisler et al. 1998). Unlike bats in England (Vaughan et al. 1997a), those from southern Italy were not influenced by temperature, with the sole exception of *H. savii*. The mild ambient temperatures we recorded ($>10^{\circ}$ C at all study sites but one, mean 18.3°C) is likely to have had limited or null influence on insect availability (Williams 1940, 1961, Taylor 1963) and, consequently, on bat activity (Catto et al. 1995, Walsh et al. 1995, Vaughan et al. 1997a). In a bat activity survey in a Czech urban area (Gaisler et al. 1998) in which no field work was conducted at temperatures $< 10^{\circ}$ C, a thermal influence emerged only for the activity of *E. serotinus*. Because our surveys started half an hour after sunset and lasted less than one hour, it cannot be ruled out that temperature might affect activity later in the night. In Ireland, *N. leisleri* activity was correlated with temperature only after the first third of the night (Shiel and Fairley 1998).

The sensitivity to wind of M. capaccinii and M. daubentonii may be due to the fact that on windy days bats prefer sheltered foraging sites (Boonman 1996), where insect density is higher (Lewis and Stephenson 1966, Lewis 1967, 1969). Prey occurrence at windy sites may be too low to meet the high prey capture rate pursued by the bats (see e.g. Kalko and Braun 1991 for M. daubentonii). Wind also increases the number and size of ripples on water surface, and thus it may affect echolocation in M. capaccinii and M. daubentonii, which both generally hunt very close to the water surface (Jones and Rayner 1988, Kalko and Schnitzler 1989, Barataud 1996). Myotis daubentonii tends to avoid turbulent or cluttered water surfaces which produce ultrasonic noise and confusing echoes (Boonman et al. 1998, Rydell et al. 1999, Warren et al. 2000).

Number of foraging species

Data on infrequently recorded species were insufficient for confident analysis of habitat preference but were used to assess species richness. Rare species may not be detected in transect surveys (Kunz et al. 1996). Although the species we recorded infrequently were often those occurring in lower numbers in the study area such as B. barbastellus and M. nattereri – this was not always the case. In the study area, R. ferrumequinum and *R. hipposideros* are widespread, although generally with rather low densities (Russo unpubl.). We may have overlooked rhinolophids and Plecotus spp. because their echolocation calls are difficult to detect (Waters and Jones 1995, Vaughan et al. 1997a, Gaisler et al. 1998). However, in our study we could compare the species richness of the foraging bat community across habitats as the above limitations probably affected all transects equally.

The high numbers of species observed on river and lake shores confirmed the importance of riparian habitats for bats. Many species featured in all broadleaved woodland types although in these habitats activity was considerable only for a few of them – especially *P. pipistrellus* (Fig. 3a), *P. pygmaeus* (Fig. 3b) and *Myotis* spp. (Fig. 4b). Radio-tracking revealed that *R. euryale* in southern Italy foraged primarily in broadleaved woodland and significantly in olive groves (Russo et al. 2002), and avoided urban sites, open areas and conifer plantations. The present study shows that conifer plantations have limited value for foraging: few species were recorded in this habitat, where even the widespread H. savii showed a low activity - it was recorded only in three out of six conifer sites. Bats may prefer broadleaved woodlands to conifer ones because the former support more prey insects (Waring 1988, 1989, Entwistle et al. 1996). Mediterranean macchia was the least important natural habitat in terms of species richness as well as bat activity: tall vegetation and water, both valuable to bats, are scarce in this habitat. Arable land and rural towns were used for foraging only by few "opportunistic" species, best adapted to anthropogenic habitats. The importance of olive groves was probably enhanced by the traditional management and structural diversity occurring at most sites.

Managing bat foraging habitats in Mediterranean areas

The protection and correct management of water habitats are undoubtedly key points in planning bat conservation in Mediterranean areas. Italian riverine habitats and fauna are threatened by many factors (e.g. Martino 1992, Prigioni 1997) such as pollution, channelisation, dredging, damming, alteration and destruction of riparian vegetation. Degradation of riparian habitats influences their insect communities (Jeffries and Mills 1990, Fry and Lonsdale 1991), and consequently foraging bats (Stebbings 1988, Vaughan et al. 1996). The effect of water eutrophication on foraging bats is still unclear (Racey 1998). Vaughan et al. (1996) found that the overall bat activity, as well as that of both pipistrelle cryptic species, was affected negatively by sewage effluents, which favoured M. daubentonii. Racey et al. (1998) showed that water nutrient enrichment favoured both pipistrelles and M. daubentonii. European populations of *M. daubentonii* may be growing as a result of eutrophication (Kokurewicz 1995). No information on the effect of water enrichment on more vulnerable bat species is available.

Riparian vegetation should be protected and encouraged because it shelters foraging sites from the wind, improving their quality (Zahn and Maier 1997). Bank vegetation favours the presence of prey insects that are directly associated with the availability of food plants and sheltered sites and mitigates the effect of wind on water turbulence (Peng et al. 1992, Warren et al. 2000). This study showed that *M. capaccinii* – greatly endangered in Europe (Guillén 1999) – and *M. daubentonii* are wind-sensitive and would probably benefit much from conservation of riparian vegetation.

The high temperatures and scarcity of water typical of a Mediterranean summer (Blondel and Aronson 1999) are likely to enhance the importance of water habitats as providing opportunities for drinking. Bats face the risk of dehydration, especially in summer (Racey 1998), and this is all the more crucial in the Mediterranean climate. In the beech woodlands and pastures of central Italy, even cattle troughs are important summer drinking sites for many bat species: as many as 11 species have been found to drink regularly at a single trough (Russo unpubl.). Favouring even small drinking sites (such as ponds, troughs) may increase the value of arid areas for bat foraging.

Broadleaved woodlands are also important targets for bat conservation in Mediterranean areas as elsewhere, because we found that they were used by a considerable number of threatened bat species (Table 3). The occurrence of old or dead trees provides treedwelling bat species with roosts (Mayle 1990); and dead wood and undergrowth may sustain prey insects, so that areas of largely or completely unmanaged woodland should be maintained where possible. Because habitat connectivity is important to bats (Walsh and Harris 1996a), habitat interruptions should be avoided in logging protocols. The size of logged patches should be minimised, and corridors between main blocks of woodland should be maintained. Where feasible, reforestation with broadleaved trees rather than conifers should be preferred (see also Russo et al. 2002). Castanea sativa woodlands managed for chestnut production - where old trees are often present - sustained a significant number of bat species, including several threatened ones. This traditional form of chestnut woodland management, which in some areas of Italy has economical significance, should be encouraged where possible.

We found that some towns and farmland sites had an intense bat activity. The rural towns we investigated were mostly illuminated, and generally scattered with small gardens, orchards and fields. The presence of vegetation may sustain insect prey populations, and lights attract insects and improve the prey capture success rates by bats (e.g. Furlonger et al. 1987, de Jong and Ahlén 1991). In southern Italy, urban parks and gardens are tending to disappear as towns develop and spread. The negative effects of urbanisation on bats (Kurta and Teramino 1992, Gaisler et al. 1998) might be mitigated by maintaining trees, gardens and small patches of cultivated land.

Throughout Europe, the degradation of farmland associated with intensive agricultural practices is threatening bats (Stebbings 1988), and although no detailed data are available, this is likely to be the case in Mediterranean regions too. Simplification of the agricultural landscape may have adverse effects on both prey availability and the occurrence of linear landscape elements used by bats as commuting landmarks (e.g. Limpens and Kapteyn 1991). Farmland practices should maximise landscape complexity, favour structural variation and connectivity, and limit the spread of pesticides, which has harmful effects on bat populations (Stebbings 1988, Hutson et al. 2001). Such considerations also apply to olive groves, which are used by a speciose chiropteran community. Non-intensive, or even organic farming is probably the most promising management option for bat conservation in many areas of the Mediterranean countryside.

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