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ECHOLOCATION CALLS AND MORPHOLOGY IN THE MEHELYI’S (*RHINOLOPHUS MEHELYI*) AND MEDITERRANEAN (*R. EURYALE*) HORSESHOE BATS: IMPLICATIONS FOR RESOURCE PARTITIONING

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ABSTRACT - *Rhinolophus euryale* and *R. mehelyi* are morphologically very similar species and their distributions overlap extensively in the Mediterranean basin. We modelled their foraging behaviour using echolocation calls and wing morphology and, assuming niche segregation occurs between the two species, we explored how it is shaped by these factors. Resting frequency of echolocation calls was recorded and weight, forearm length, wing loading, aspect ratio and wing tip shape index were measured. *R. mehelyi* showed a significantly higher resting frequency than *R. euryale*, but differences are deemed insufficient for dietary niche segregation. Weight and forearm length were significantly larger in *R. mehelyi*. The higher values of aspect ratio and wing loading and a lower value of wing tip shape index in *R. melehyi* restrict its flight manoeuvrability and agility. Therefore, the flight ability of *R. mehelyi* may decrease as habitat complexity increases. Thus, the principal mechanism for resource partitioning seems to be based on differing habitat use arising from differences in wing morphology.

Key words: Rhinolophids, species discrimination, echolocation, wing morphology, niche segregation

RIASSUNTO: - ***Ecolocalizzazione e morfologia nei rinolofi di Mehely* (Rhinolophus mehelyi) *e euriale* (R. euryale): *implicazioni nella segregazione delle risorse trofiche***. *Rhinolophus euryale* e *R. mehelyi* sono specie morfologicamente molto simili, la cui distribuzione risulta largamente coincidente in area mediterranea. Il comportamento di foraggiamento delle due specie è stato analizzato in funzione delle caratteristiche dei segnali di ecolocalizzazione e della morfologia alare, ed è stata valutata l’incidenza di questi fattori nell’ipotesi di una segregazione delle nicchie. È stata rilevata la frequenza a riposo dei segnali ultrasonori, così come il peso, la lunghezza dell’avambraccio, il carico alare, e due indici di forma dell'ala (*aspect ratio* e *wing tip shape index*). *R. mehelyi* presenta una frequenza di riposo maggiore rispetto a *R. euryale*, ma la differenza non sembra sufficiente per spiegare la separazione delle nicchie trofiche. Il peso e la lunghezza dell'avambraccio risultano significativamente più elevati in *R. mehelyi*. I valori piú elevati relativamente ad *aspect ratio* e *wing loading* e il minor valore del *wing tip shape index* in *R. melehyi* indicano una minore manovrabilità in volo e una minore agilità. La capacità di *R. mehelyi* di sfruttare efficacemente un ambiente complesso decresce con il livello di complessità dell'habitat stesso. È possibile quindi ipotizzare un meccanismo di separazione nell’uso delle risorse basato su un differente uso dell’habitat, spiegabile in termini di differenze nella morfologia alare.

Parole chiave: Rinolofidi, identificazione specifica, ecolocalizzazione, morfologia alare, segregazione di nicchia.

INTRODUCTION

Given the substantial energy demands of flight, bats must optimise energy-expenditure by adapting to ecological factors such as the habitat type or food resources that they exploit. This optimisation is reflected in different morphoecological patterns that are based on body mass and wing morphology, which condition both flight speed and performance (e.g. Norberg and Rayner, 1987). Short and broad wings facilitate manoeuvrability in restricted spaces and are typical of forest species. In contrast, animals with large and narrow wings typically fly in open areas or above the forest canopy. Large volant animals need comparatively more wing surface area than small ones since with increasing volume, body mass is cubed whereas the wing surface area that supports this mass is only squared. Additionally, assuming similar wing shapes, heavier animals need to fly faster in order to remain airborne (de Juana, 1992). Since wing morphology in bats influences flight style and performance, its characterisation can facilitate inferences on habitat use.

Bats use echolocation to move in three-dimensional space and to get information from their environment and hunting targets. The accuracy of the information they receive depends on the ultrasound system of each species. Higher frequency echolocation calls provide better resolution of target detail, so bats with higher frequency calls are better suited to the detection of smaller targets (Schnitzler, 1968; Fenton, 1999: Jones, 1999). Additionally, higher frequency calls have higher echo attenuation due to atmospheric absorption and thus, they have a shorter range detection (Hartley, 1989).

Morphology and echolocation calls are inter-related elements of the adaptive complex that determines foraging strategies in bats (Aldridge and Rautenbach, 1987; Kingston *et al.*, 2000). For example, bats with narrow and pointed wings are fast and open-air flyers and therefore, tend to have low frequency echolocation calls to discriminate prey-items from long distances. On the other hand, bats with broad and rounded wings exhibit slow and manoeuvrable flight, and tend to have high frequency echolocation calls to forage in cluttered environments. Consequently, species with similar echolocation calls and wing morphology can be assumed to have similar foraging behaviour, raising issues of competition if such species occur in sympatry (Saunders and Barclay, 1992). Assuming that resources are limiting, the stable coexistence of two species within the same community should be associated with a mechanism of resource partitioning (Competitive Exclusion Principle or Gause's principle).

Horseshoe bats (genus *Rhinolophus*) emit high and long constant CF echolocation calls, which are followed and often preceded by brief FM components (Fenton, 1999). In all species investigated so far the wingtips are very rounded and short, and flight is slow and manoeuvrable with some hovering capability (Norberg and Rayner, 1987). High constant-frequency echolocation and manoeuvrable flight allow horseshoe bats to forage in cluttered environments. Among horseshoe bats, *Rhinolophus mehelyi* and *R. euryale* are two similar Mediterranean species that diverged from the same ancestor only 3 My ago (Guillén *et al.*, 2003) and have distributions that overlap extensively (Mitchel-Jones *et al.*, 1999).

The mechanism facilitating resource partitioning in these two species is unknown. Although features of the echolocation calls of *R. mehelyi* and *R. euryale* are known from different geographical areas (e.g. Schnitzler, 1968; Heller and Helversen, 1989; Ahlén, 1990; Guillén, 1996; Russo *et al.*, 2001), little is known about co-roosting individuals. Similarly, studies on the wing morphology of these species are scarce in the literature. Norberg and Rayner (1987) reviewed the wing morphology of a number of bats including *R. mehelyi* and *R. euryale*, but their measurements are incomplete for both species (see Tab. 1 in Norberg and Rayner 1987) and their sources are not entirely reliable (U. Norberg, *pers. comm.*).

The aims of this study are to provide a novel and complete data set on the wing morphology and echolocation call structure of *R. mehelyi* and *R. euryale* from the same roost; and to infer a foraging behaviour model for these species. Finally, we predict a niche-partitioning scenario based on the differences between the two species.

METHODS

1. Study colony

The study was carried out in June 2003 at the Sierra Norte Nature Park (Seville,

Table 1 - Morphological measurements of *R. euryale* and *R. mehelyi*. Mean and standard deviation are shown for both species, together with the Mann-Whitney's U test comparing morphological measurements. Significance is indicated by asterisks (NS = not significant; ** = P<0.001; *** = P<0.0001).

	R. euryale (N=19)	*R. mehelyi* (N=20)	U value	P
Mass (g)	12.0 ± 0.1	15.0 ± 0.2	4.833	***
Forearm length (mm)	48.1 ± 0.89	50.7 ± 1.20	4.869	***
Wingspan (m)	0.30 ± 0.008	0.32 ± 0.007	5.315	***
Wing area (m^2)	0.015 ± 0.001	0.016 ± 0.001	4.382	***
Aspect ratio	6.18 ± 0.31	6.68 ± 0.27	4.274	***
Wing loading (N/m^2)	7.94 ± 1.15	9.25 ± 1.12	3.677	**
Wing tip shape index	2.78 ± 1.57	2.54 ± 0.51	0.730	NS

Spain), where *R. mehelyi* and *R. euryale* bred in the same cave (37 56’ 1,05’’ N, 5 55’ 47,77’’ W). 21 *R. mehelyi* (11 females and 10 males) and 20 *R. euryale* (6 females and 14 males) were captured with a harp-trap (2 x 2 m; Tuttle, 1974) while entering the roost. We discriminated *R. mehelyi* from *R. euryale* by nose leaf morphology - the shape of the lancet in *R. euryale* being essentially triangular, whereas the lancet in *R. mehelyi* is notably concave laterally and very narrow distally. The connecting process is also narrower and more pointed in *R. euryale* than in *R. mehelyi* (Miller, 1912; Cabrera, 1914; de Paz and Benzal, 1990).

2. Data collection and analysis

Wing morphology was characterised by wingspan, wing area, wing loading, aspect ratio and wing tip shape index. Wing loading is the weight of the bat divided by the area of its flight membrane and is correlated with flight speed. As wing loading increases, so too does the speed required to fly. Aspect ratio is the square of the wingspan divided by the wing area and is related to energy efficiency. A higher aspect ratio usually corresponds to lower energy loss in flight (Altringham, 1996; de Juana, 1992). Wing tip shape index is determined by the relative size of arm- and hand-wings and is related to manoeuvrability. High index values correspond to rounded or nearly square wingtips and indicate high manoeuvrability (Norberg and Rayner, 1987). These parameters were determined from wing tracings of live bats (Fig. 1). We adopted Norberg and Rayner´s (1987) method where flight surface included the combined area of both wings, the entire tail membrane, and the body area between the wings excluding the head. In order to calculate the wing area one tracing of the left wing was made for each bat, which was scanned at 600 dpi and incorporated into a GIS (Arcview 3.2, ESRI, USA; ESRI, 1996). A ruler was included in each trace as a scale reference. Body mass and left forearm lenght were measured to the nearest 0.25 g and 0.05 mm respectively.

We adopted the method of Guillén (1996) and Russo *et al.* (2001) to record echolocation calls, with each bat hand-held about 20 cm from a microphone and several calls recorded. Since the bat was held motionless, calls were not affected by Doppler shift compensation and thus, their frequency corresponded to resting frequency (RF). Recordings were made with a Pettersson Elektronik D-980 ultrasound detector, connected to a DAT (Sony TCD-D7), which sampled at a rate of 448 kHz and time-expanded the sequence of calls to 3 seconds. The resulting sequence was then analysed (SoundEdit Pro, Macromedia Inc.; Macromedia, 1991) using a sampling frequency of 44.1 kHz and a 1024 pt FFT. A sample of ten echolocation calls from each bat was chosen at random, and we measured the RF from the power spectrum of a 15 ms portion in the CF component of each call. Subsequently, a mean RF value for the ten calls of each individual was calculated and considered for analysis (Russo *et al.*, 2001). In addition, for the ten calls for each individual we measured call duration and frequency range of the FM component both preceding and subsequent to the CF component.

We compared values of wing morphology and echolocation in both species by Mann-Whitney U tests, with significance level established at $p<0.05$ (Zar, 1999).

RESULTS

Body mass, forearm length, wingspan and wing area were significantly higher in *R. mehelyi* than in *R. euryale* (Tab. 1). Wing loading and aspect ratio also reached significantly higher values in

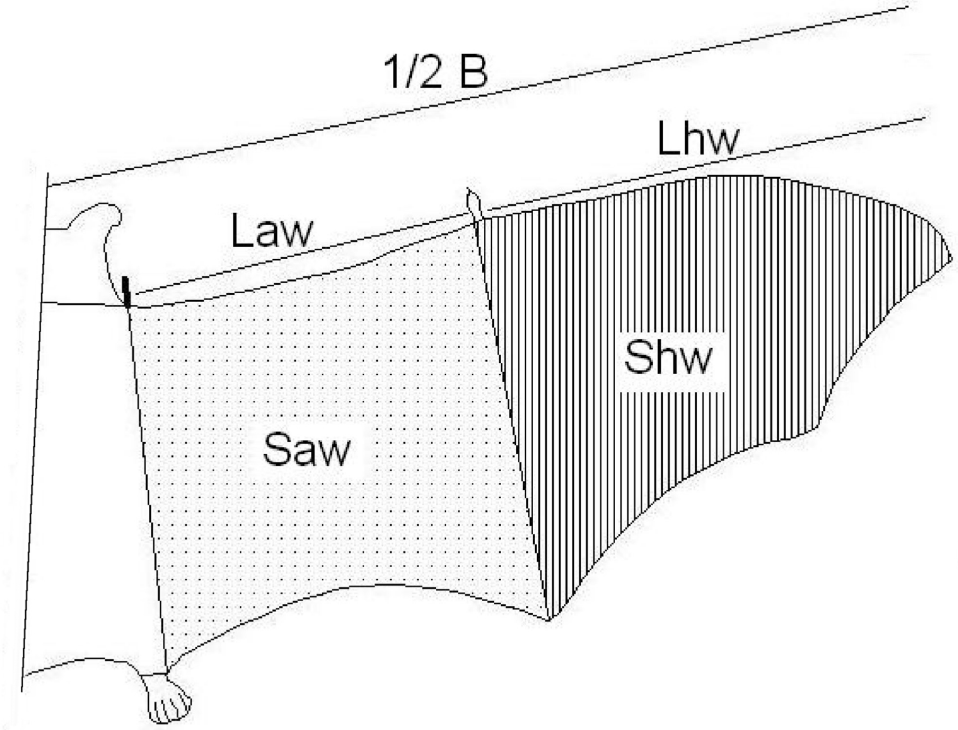

Figure 1 - Left wing tracing of a bat indicating the measured wing dimensions. B = wingspan; Law = arm-wing length; Lhw = hand-wing length; Saw = arm-wing area; Shw = hand-wing area. The wing area is the sum of arm-wing area, hand-wing area, the tail membrane area, and the area of the body between the wings, excluding the projected area of the head. These measurements are used to define wing loading, aspect ratio, and wingtip shape index as in Norberg and Rayner (1987).

R. mehelyi. On average, wing tip shape index was lower in *R. mehelyi*, although the difference was not significant (Tab. 1).

R. mehelyi emitted echolocation calls at a significantly higher frequency than *R. euryale* (Tab. 2). The amplitude of the first FM component of the echolocation call (FM_1) of *R. euryale* was significantly lower than that of *R. mehelyi*. The amplitude of the second FM component (FM_2) was on average lower in *R. euryale*, but in this case the difference was not significant. There was no significant difference in call durations (Tab. 2).

DISCUSSION

Forearm length and body mass measurements for *R. mehelyi* from our study colony fall into the ranges previously published for this species (e.g. Miller, 1912; Cabrera, 1914; Norberg and Rayner, 1987). However, our values for wing morphology contrast sharply with those of Norberg and Rayner (1987). Deviations in the measurement proce-

Table 2 - Echolocation call variables of *R. euryale* and *R. mehelyi*. Mean and standard deviation are shown for both species, together with the Mann-Whitney's U test values for variable comparisons. FM1 is the amplitude of the FM component preceding the CF and FM2 is the component following the CF. Statistical significance is indicated with asterisks (NS = not significant; * = p<0.05; ** = p<0.001).

	R. euryale (N=20)	*R. mehelyi* (N=21)	U value	P
Frequency (kHz)	104.4 ± 0.70	106.8 ± 0.99	5.16	**
FM_1 amplitude (kHz)	3.90 ± 2.32	6.98 ± 3.49	3.13	*
FM_2 amplitude (kHz)	19.42 ± 3.72	20.30 ± 3.17	0.65	NS
Call duration (ms)	19.56 ± 3.09	19.99 ± 2.87	0.37	NS

dure of the wing membrane may explain the differences in wing area and wing loading (U. Norberg, *pers. comm.*). To our knowledge, this is the first study where measurements of wingspan, aspect ratio and wing tip shape index are reported for *R. mehelyi*. Average echolocation call frequency of *R. mehelyi* also falls within published values (Heller and Helversen, 1989; Ahlén, 1990; Russo *et al.*, 2001).

Our results for body mass and forearm length in *R. euryale* are in complete agreement with other authors (e.g. Miller, 1912; Cabrera, 1914). Our data on the wing morphology of *R. euryale* correspond to those obtained by Norberg and Rayner (1987). Wing tip shape index is described in *R. euryale* for the first time. Average echolocation call frequency in *R. euryale* falls within the published range for the species (Schnitzler, 1968; Heller and Helversen, 1989; Ahlén, 1990; Russo *et al.*, 2001).

R. mehelyi were significantly larger than *R. euryale*, with higher measures of body mass and forearm length, in agreement with abundant data provided elsewhere (e.g. Norberg and Rayner, 1987; Schober and Grimmberger, 1993; Guillén, 1996; Russo *et al.*, 2001; Palomo and Gisbert, 2002; Csorba *et al.*, 2003). Our measurements of wing area and wing loading are higher in *R. mehelyi* than in *R. euryale* as also reported by Norberg and Rayner (1987), although our difference in wing area was tenfold greater (see Tab. 1) presumably due to methodological differences as highlighted above. Echolocation call frequency is significantly higher in *R. mehelyi* than in *R. euryale*, although there is a small degree of overlap as documented elsewhere (e.g. Heller and Helversen, 1989; Ahlén, 1990; Guillén, 1996; Russo *et al.*, 2001). In our study, call frequency shows higher variability in *R. mehelyi* than in *R. euryale*. This characteristic has been previously reported both at a within-colony and at a geographical scale (Schnitzler, 1968; Heller and Helversen, 1989; Ahlén, 1990; Guillén, 1996; Russo *et al.*, 2001; Tab. 3).

1. Resource partitioning

Aspect ratio correlates well with flight manoeuvrability, with lower aspect

Table 3 - Geographical differences in Resting Frequency (kHz) reported by other authors in different localities.

R. mehelyi	*R. euryale*	Local	Source
-	104.0	Italy	Schnitzler, 1968
-	102.6	Southern France	Heller and Helversen, 1989
106.0	104.0	Asia Minor	Heller and Helversen, 1989
109.7	105.3	Greece	Heller and Helversen, 1989
106.0	103.0	Spain	Ahlén, 1990
106.5	103.8	Southern Iberian Peninsula	Guillén, 1996
107.7	104.3	Sardinia and Southern Italy	Russo *et al.*, 2001
106.8	104.4	Southern Spain	This study

ratios endowing greater manoeuvrability. In addition, wing loading correlates well with flight speed and assuming a similar wing shape, bats with higher wing loadings tend to fly faster (Norberg and Rayner, 1987; Altringham, 1996). Therefore, the higher aspect ratio and wing loading observed in *R. mehelyi* indicate reduced manoeuvrability and faster flight speed compared to *R. euryale*. Consequently, *R. euryale* seems to be better adapted to forage in cluttered habitat and *R. mehelyi* is precluded to fly in more open environments.

As the frequency of echolocation calls increases the size of prey-targets that a bat is able to detect decreases (Pye, 1993), potentially facilitating dietary resource partitioning. Previous studies show that the bulk of the diet of both species is comprised of very similar prey categories, mainly Lepidoptera, and to a lesser extent Coleoptera and Neuroptera (Koselj and Krystufek, 1999; Sharifi and Hemmati, 2001; Goiti *et al*., 2004). Although the higher echolocation call frequency of *R. mehelyi* would allow them to detect smaller targets within prey categories compared to *R. euryale*, the minimal wavelength differences between the two species are presumably too small to allow any substantial differences in target size detection (Schnitzler, 1968; Jones, 1995; Russo *et al*., 2001).

Several authors have emphasised the relationship between habitat use and wing morphology (e.g. Aldridge, 1986; Aldridge and Rautenbach, 1987; Crome and Richards, 1988; Heller and Helversen, 1989; Kingston *et al*., 2000). Concordantly, we postulate that the differences in wing morphology facilitate differing habitat use and is the main mechanism promoting resource partitioning in sympatric *R. mehelyi* and *R. euryale*. Although, in the case of these two species, we also expect that they share foraging habitats to some extent, since their wing morphology measurements overlap. This hypothesis is supported by a preliminary radio-tracking survey carried out on *R. mehelyi* and *R. euryale* from our study colony (Russo *et al.*, 2005). In contrast, partitioning of dietary resources is unlikely to operate between species.

In short, differences in habitat use rather than diet present a more likely mechanism for resource partitioning, with wing morphology the principal contributing factor in establishing disparate habitat use. Consequently, the coexistence of *R. mehelyi* and *R. euryale* in sympatry will endure if habitat diversity can be guaranteed, thereby allowing spatial resource partitioning. In contrast, as habitat diversity and availability decrease, competition between both species will increase.

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