Aspects of ecomorphology in the five European horseshoe bats (Chiroptera: Rhinolophidae) in the area of sympatry

der Fakultät für Biologie
der EBERHARD KARLS UNIVERSITÄT TÜBINGEN

zur Erlangung des Grades eines Doktors
der Naturwissenschaften

von

Christian Dietz

aus Tübingen

vorgelegte
Dissertation

2007

Tag der mündlichen Prüfung: 14.11.2007
Dekan: Prof. Dr. H. Mallot
1. Berichterstatter: Prof. Dr. H.-U. Schnitzler
2. Berichterstatter: PD Dr. B.M. Siemers

Table of contents

General introduction

The study of mechanisms enabling species to coexist in sympatry is one of the most challenging topics in ecology. Competition avoidance and resource partitioning are of special interest in species exploiting similar resources. Groups of such species depending on similar resources are guilds, defined as a community of animals showing a considerable overlap in their ecology mainly due to a similar way of exploiting the same class of environmental resources, e.g. the members may use similar feeding or prey capture strategies (Root 1967). According to the competition exclusion principle, similar species evolve different ecological niches to reduce or avoid competition (Hardin 1960; Schoener 1974; Wiens 1977). Separation can be achieved by several mechanisms such as character displacement (Brown and Wilson 1956); selection of different habitats, prey types, foraging times and foraging styles (e.g., Aldridge 1986; Jones et al. 1993); morphological variation (Bogdanowicz et al. 1999; Findley et al. 1972; Van Valen 1965); and differences in sensory ecology (Kingston et al. 2000; Siemers and Swift 2006).

As animal communities are rarely structured by the limitation of a single resource but mostly by a combination of many resources with a changing importance in different stages of an individual’s life, an all-encompassing study on community-level coexistence would be a very demanding task. In addition, resource availability (e.g., prey abundance) may change a lot within the course of a year or may differ between years and thus might be unlimited at a certain time. To unravel all possible causes and mechanisms of coexistence unfortunately is much beyond the possibilities of a relatively short-termed research project like a PhD-project.

Within my project I focused on the flight-ecomorphology as one possible mechanism structuring a guild of sympatric bat species. The five species under study belong to the family Rhinolophidae and can be united in a single guild of ‘aerial insectivore narrow space flutter-detecting foragers’ (Schnitzler and Kalko 1998, 2001; Schnitzler et al. 2003) on the basis of the unique combination of echolocation call design, wing morphology, foraging style and prey consumed.

These 5 European horseshoe bat species (*Rhinolophus hipposideros, R. mehelyi, R. blasii, R. euryale* and *R. ferrumequinum*) are closely-related members of a single genus (Guillén et al. 2003) and have extensive overlap in their distribution in southeastern Europe (Mitchell-Jones et al. 1999), where they occur in sympatry on the Balkan Peninsula and the eastern Mediterranean. All of them produce long duration constant-frequency echolocation calls with a maximum energy concentrated in the 2nd harmonic (Griffin and Simmons 1974; Heller and von Helversen 1989; Jones and Rayner 1989; Möhres 1953; Russo et al. 2001; Siemers et al. 2005). Horseshoe bats use frequency and amplitude shifts modulated onto the echoes of their constant-frequency calls by the wing beats of insects as a means of detecting prey (Schnitzler 1983). All European horseshoe bats are similar in several morphological respects, including short and broad wings with a large wing area giving low wing loading, aspect ratio and tip shape index (Findley et al. 1972; Norberg 1987; Norberg and Rayner 1987). However, the European species differ in size and body mass: The average body mass and forearm length of the lesser horseshoe bat (*R. hipposideros*) are 6-7 g and 37-42 mm respectively, those of the greater horseshoe bat (*R. ferrumequinum*) 20-26 g and 54-61 mm, and those of the 3 medium-sized species (*R. mehelyi*, *R. blasii* and *R. euryale*) are quite similar (9-14 g and 42-54 mm, respectively - Schober and Grimmberger 1998; Dietz et al. 2007b). All 5 species catch prey by “flycatching” from a perch or during patrolling flights close to a cluttered background, and at least some species may also take prey from the ground (Bontadina et al. 2002; Jones and Rayner 1989; Russo et al. 2002, Siemers & Ivanova 2004). With the exception of the lesser horseshoe bat (*R. hipposideros*), these 5 horseshoe bat species prey predominately on nocturnal moths (Beck et al. 1989, 1997; Goiti et al. 2004; Valenciuc 1971). The lesser horseshoe bat (*R. hipposideros*) is distributed over most of southern and central Europe and has the northernmost limit of distribution of all rhinolophids in Europe, reaching Ireland, the

Netherlands and Poland (Mitchell-Jones et al. 1999). The species prefers to roost in buildings, but colonies in the south are also found in caves (Dietz et al. 2007b). The species preys mainly on small Diptera, Lepidoptera and other small insects, predominately in or close to forests (Beck et al. 1989; Bontadina et al. 2002; Jones and Rayner 1989). The greater horseshoe bat (*R. ferrumequinum*) is found in southern and central Europe as far north as southern England and Wales, the Netherlands and Poland (Mitchell-Jones et al. 1999). Breeding colonies in the north are mainly in buildings, in the south predominately in underground roosts (Dietz et al. 2007b). These bats forage in a wide variety of habitats from open meadows to parks and woodlands, where they prey mainly on coprophagous beetles and moths (Beck et al. 1997; Bontadina et al. 1995, 1997; Jones and Rayner 1989; Jones et al. 1995). The ecologies of the 3 medium-sized species are less well known. Their distribution in Europe is confined to the area around the Mediterranean. The Mediterranean horseshoe bat (*R. euryale*) has the widest distribution, extending north to central France, Italy, Slovakia and Romania; Mehely's horseshoe bat (*R. mehelyi*) is found in southern and central Iberia, southern France, Sardinia, Sicily, Greece and in the Balkans north to Romania; Blasius' horseshoe bat (*R. blasii*) is restricted to southeastern Europe from the Adriatic coast over the Balkans to Greece and Romania (Mitchell-Jones et al. 1999). All 3 species roost mainly in caves and other underground galleries (Dietz et al. 2007b) and prey predominately on moths (Goiti et al. 2004; Valenciuc 1971; Whitaker and Black 1976). *R. euryale* forages mainly in forests, while *R. mehelyi* prefers to forage in less densely vegetated habitats of a savannah-type (Russo et al. 2002, 2005). Habitat preferences of *R. blasii* remain unknown (Siemers and Ivanova 2004; Dietz et al. 2007b).

One of the most important mechanisms of character displacement is morphological variation (Bogdanowicz et al. 1999; Findley et al. 1972; Van Valen 1965). Especially in bats the morphology of the wings can be regarded as being highly adaptive. Beside its sensory ability to detect and recognize prey (Siemers and Schnitzler 2004), an insectivorous bat's ability to use its environment depends largely on its ability to maneuver through habitats (Norberg and Rayner 1987) and on its maneuverability when foraging for prey (Fenton 1990; Findley et al. 1972; Vaughan 1959). Changes in morphology result in differences in flight performance (Adams 1996; Aldridge 1986; Findley and Black 1983; Norberg 1981) which directly affect habitat use (Aldridge and Rautenbach 1987; Brigham et al. 1997; Jacobs 1996, 1999; Norberg 1994; Stockwell 2001). Differences in wing morphological features such as wing loading can be significant predictors of habitat use (Kalcounis and Brigham 1995), a fact used in ecomorphological approaches to the study of community structure (Brigham et al. 1997; Findley and Black 1983).

The aim of my PhD project was to predict habitat use and foraging mode of the five European horseshoe bat species from ecomorphological measurements of the wing. The predictions derived from the measurements should be tested by empirical field data obtained by telemetry. By this I intended to unravel some of the mechanisms enabling the coexistence of the five species in sympatry and possible aspects of competition avoidance. The studies were mainly carried out in Northern Bulgaria in the valley of the river Osăm close to where it flows into the Danube where all five species were believed to have occurred prior to the beginning of the project. During the project it was found that the former occurrence of *Rhinolophus blasii* has become extinct. To compensate for the lack of the fifth species additional studies were carried out in the southern part of Bulgaria (Strandža mountains, Rhodope mountains), the North of Greece (Rhodope mountains) and Western Turkey, where all five horseshoe bat species still occur in sympatry.

Structure of this thesis

The thesis consists of seven chapters related to the morphology and ecomorphology of the five European horseshoe bats. The first two parts are basic descriptive chapters establishing and outlining identification (chapter 1) and age classification characters and signs of reproduction (chapter 2). Next, methodological aspects of the applied marking method (ringing) are evaluated (chapter 3), followed by results obtained by this method in terms of regional movements and migration (chapter 4). These first four chapters provide the methodological grounds upon which the morphological results are presented, that constitute the core of the thesis (chapters 5-7). First the results of studies on growth of horseshoe bats and the influence of climate are presented (chapter 5), followed by a detailed analysis of external measurements of several wing bone elements (chapter 6) allowing some predictions about a possible niche segregation and habitat use between the five sympatric species. In the last part (chapter 7), predictions based on extensive data from wing photogrammetry and wing area measurements are compared with ecological data obtained mainly by telemetry in the field. Possible mechanisms structuring the guild of the European horseshoe bats are discussed.

Publication of the results

All parts of this thesis with the exception of chapter 1 are written to be published in scientific journals. The identification key (chapter 1) has already been published as part of an electronic publication accessible in the internet (Dietz and Helversen 2004) and in a book on the bats of Europe and North-western Africa (Dietz et al. 2007b). Chapter 2 has not been published yet, but will be submitted soon. Chapter 3 is already accepted (Dietz et al. in press) and chapters 4-6 (Dietz et al. 2006a; Dietz et al. 2006b; Dietz et al. 2007a) have been published in peer-reviewed scientific journals. Chapter 7 is not published yet but will be submitted to a scientific journal soon.

Author information and contributions from others

I (C. Dietz) planned the projects, established the methods, collected the data and undertook the field work, did the data analyses and statistical analyses and wrote the thesis and the manuscripts included in the thesis. The contributions of others are acknowledged and are specified in the following: Prof. Dr. H.-U. Schnitzler will be coauthor in the publication on the wing morphology (chapter 7) as he was the supervisor of the dissertation and provided valuable comments on the underlying principles possibly structuring guilds. Dr. B.M. Siemers is / will be co-author in most publications (chapters 3-7); he supplied the technical equipment, was supervisor of this thesis and provided valuable comments on each of the chapters. Isabel Dietz is / will be co-author in the majority of the publications (chapters 2-7); she participated in all aspects of field work and data collection and provided help in all respects. Dr. T. Ivanova is / will be co-author in two of the publications (chapter 3 and chapter 7) as she was involved in parts of the field work and provided valuable help in establishing the project in Bulgaria. Prof. Dr. O. von Helversen and Dietmar Nill are co-authors in the two publications containing the identification key (chapter 1) as they contributed to other parts of these publications.

References

ADAMS, R.A. 1996. Size-specific resource use in juvenile little brown bats, *Myotis lucifugus* (Chiroptera: Vespertilionidae): Is there an ontogenetic shift? Canadian Journal of Zoology 74: 1204-1210.

ALDRIDGE, H. 1986. Manoeuvrability and ecological segregation in the little brown (*Myotis lucifugus*) and Yuma (*M. yumanensis*) bats (Chiroptera: Vespertilionidae). Canadian Journal of Zoology 64: 1878-1882.

ALDRIDGE, H.D.J.N. AND I.L. RAUTENBACH. 1987. Morphology, echolocation and resource partitioning in insectivorous bats. Journal of Animal Ecology 56: 763-778.

BECK, A., S. GLOOR, M. ZAHNER, F. BONTADINA, T. HOTZ, M. LUTZ AND E. MÜHLETHALER. 1997. Zur Ernährungsbiologie der Großen Hufeisennase in einem Alpental der Schweiz. Tagungsband: „Zur Situation der Hufeisennasen in Europa“ Nebra, den 26.-28. Mai 1995, Arbeitskreis Fledermäuse Sachsen-Anhalt e.V. 1997: 15-18. IFA-Verlag, Berlin, Germany.

BECK, A., H.-P.B. STUTZ AND V. ZISWILER. 1989. Das Beutespektrum der Kleinen Hufeisennase *Rhinolophus hipposideros.* Revue suisse de zoologie 96: 643-650.

BOGDANOWICZ, W., M.B. FENTON AND K. DALESZCZYK. 1999. The relationship between echolocation calls, morphology and diet in insectivorous bats. Journal of Zoology (London) 247: 381-393.

BONTADINA, F., A. BECK, S. GLOOR, T. HOTZ, M. LUTZ AND E. MÜHLETHALER. 1995. Jagt die Grosse Hufeisennase *Rhinolophus ferrumequinum* im Wald? Grundlagen zum Schutz von Jagdgebieten der letzten grösseren Kolonie in der Schweiz. Der Ornithologische Beobachter 92: 325-327.

BONTADINA, F., T. HOTZ, S. GLOOR, A. BECK, M. LUTZ AND E. MÜHLETHALER. 1997. Schutz von Jagdgebieten der Großen Hufeisennase. Umsetzung der Ergebnisse einer Telemetrie-Studie in einem Alpental der Schweiz. Tagungsband: „Zur Situation der Hufeisennasen in Europa“ Nebra, den 26.-28. Mai 1995, Arbeitskreis Fledermäuse Sachsen-Anhalt e.V. 1997: 33-40. IFA-Verlag, Berlin, Germany.

BONTADINA, F., H. SCHOFIELD AND B. NAEF-DAENZER. 2002. Radio-tracking reveals that lesser horseshoe bats (*Rhinolophus hipposideros*) forage in woodland. Journal of Zoology (London) 258: 281-290.

BRIGHAM, R.M., R.L. FRANCIS AND S. HAMDORF. 1997. Microhabitat use by two species of *Nyctophilus* bats: a test of ecomorphology theory. Australian Journal of Zoology 45: 553-560.

BROWN, W.L. AND E.O. WILSON. 1956. Character displacement. Systematic Zoology 5: 49-64.

DIETZ, C. AND O. VON HELVERSEN. 2004. Identification key to the bats of Europe. 72 pp. Electronical publication, version 1.0, available at www.uni-tuebingen.de/tierphys/Kontakt/mitarbeiter_seiten/dietz.htm.

DIETZ, C., I. DIETZ AND B. M. SIEMERS. 2006a. Wing measurement variations in the five European horseshoe bat species (Chiroptera: Rhinolophidae). Journal of Mammalogy 87: 1241-1251.

DIETZ, C., I. DIETZ, T. IVANOVA AND B.M. SIEMERS. 2006b. Effects of forearm bands on horseshoe bats (Chiroptera: Rhinolophidae). Acta Chiropterologica 8: 523-535.

DIETZ, C., I. DIETZ AND B. M. SIEMERS. 2007a. Growth of horseshoe bats (Chiroptera: Rhinolophidae) in temperate continental conditions and the influence of climate. Mammalian Biology 72: 129-144.

DIETZ, C., O. VON HELVERSEN AND D. NILL. 2007b. Handbuch der Fledermäuse Europas und Nordwestafrikas, 399 pp.; Kosmos, Stuttgart, Germany.

DIETZ, C., I. DIETZ, T. IVANOVA AND B.M. SIEMERS. In press. Movements of horseshoe bats (*Rhinolophus*, Chiroptera: Rhinolophidae) in northern Bulgaria. Myotis; Bonn.

FENTON, M.B. 1990. The foraging behaviour and ecology of animal-eating bats. Canadian Journal of Zoology 68: 411-422.

FINDLEY, J.S. AND H. BLACK. 1983. Morphological and dietary structuring of a Zambian insectivorous bat community. Ecology 64: 625-630.

FINDLEY, J.S., E.H. STUDIER AND D.E. WILSON. 1972. Morphological properties of bat wings. Journal of Mammalogy 53: 429-444.

GOITI, U., J.R. AIHARTZA AND I. GARIN. 2004. Diet and prey selection in the Mediterranean horseshoe bat *Rhinolophus euryale* (Chiroptera, Rhinolophidae) during the pre-breeding season. Mammalia 68: 397-402.

GRIFFIN, D.R. AND J.A. SIMMONS. 1974. Echolocation of insects by horseshoe bats. Nature 250: 731-732.

GUILLÉN, A., C.M. FRANCIS AND R.E. RICKLEFS. 2003. Phylogeny and biogeography of the horseshoe bats. Pp. XII-XXIV in Horseshoe bats of the world (Chiroptera: Rhinolophidae) (G. Csorba, P. Ujhelyi and N. Thomas, eds.). Alana Books Shropshire, United Kingdom.

HARDIN, G. 1960. The competitive exclusion principle. Science 131: 1292-1297.

HELLER, K.-G. AND O. VON HELVERSEN. 1989. Resource partitioning of sonar frequency bands in rhinolophid bats. Oecologia 80: 178-186.

JACOBS, D.S. 1996. Morphological divergence in an insular bat, *Lasiurus cinereus semotus*. Functional Ecology 10: 622-630.

JACOBS, D.S. 1999. Intraspecific variation in wingspan and echolocation call flexibility might explain the use of different habitats by the insectivorous bat, *Miniopterus schreibersii*. Acta Chiropterologica 1: 93-103.

JONES, G., P.L. DUVERGÉ AND R.D. RANSOME. 1995. Conservation biology of an endangered species: field studies of greater horseshoe bats. Symposia of the Zoological Society of London 67: 309-324.

JONES, G., M. MORTON, P.M. HUGHES AND R.M. BUDDEN. 1993. Echolocation, flight morphology and foraging strategies of some West African hipposiderid bats. Journal of Zoology (London) 230: 385-400.

JONES, G. AND J.M.V. RAYNER. 1989. Foraging behavior and echolocation of wild horseshoe bats *Rhinolophus ferrumequinum* and *R. hipposideros.* Behavioral Ecology and Sociobiology 25: 183-191.

KALCOUNIS, M.C. AND R.M. BRIGHAM. 1995. Intraspecific variation in wing loading affects habitat use by little brown bats (*Myotis lucifugus*). Canadian Journal of Zoology 73: 89-95.

KINGSTON, T., G. JONES, A. ZUBAID AND T.H. KUNZ. 2000. Resource partitioning in rhinolophoid bats revisited. Oecologia 124: 332-342.

MITCHELL-JONES, A.J., G. AMORI, W. BOGDANOWICZ, B. KRYSTUFEK, P.J.H. REIJNDERS, F. SPITZENBERGER, M. STUBBE, J.B.M. THISSEN, V. VOHRALIK AND J. ZIMA. 1999. The atlas of European mammals. 484 pp. Poyser Natural History, London, United Kingdom.

MÖHRES, F.P. 1953. Über die Ultraschallorientierung der Hufeisennasen. Zeitschrift für Vergleichende Physiologie 34: 547-588.

NORBERG, U.M. 1981. Flight, morphology and the ecological niche in some birds and bats. Symposia of the Zoological Society of London 48: 173-197.

NORBERG, U.M. 1987. Wing form and flight mode in bats. Pp. 43-56 in Recent advances in the study of bats (M.B. Fenton, P. Racey and J.M.V. Rayner, eds.). Cambridge University Press, Cambridge, United Kingdom.

NORBERG, U.M. 1994. Wing design, flight performance, and habitat use in bats. Pp. 205-239 in Ecological morphology (P.C. Wainwright and S.M. Reilly, eds.). University of Chicago Press, Chicago, Illinois.

NORBERG, U.M. AND J.M.V. RAYNER. 1987. Ecological morphology and flight in bats: wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society of London B. Biological Sciences 316: 335-427.

ROOT, R.B. 1967. The niche exploitation pattern of the blue-grey gnat-catcher. Ecological Monographs 37: 317–50.

RUSSO, D., D. ALMENAR, J. AIHARTZA, U. GOITI, E. SALSAMENDI AND I. GARIN. 2005. Habitat selection in sympatric *Rhinolophus mehelyi* and *R. euryale* (Mammalia: Chiroptera). Journal of Zoology (London) 266: 327-332.

RUSSO, D., G. JONES AND A. MIGLIOZZI. 2002. Habitat selection by the Mediterranean horseshoe bat, *Rhinolophus euryale* (Chiroptera: Rhinolophidae) in a rural area of southern Italy and implications for conservation. Biological Conservation 107: 71-81.

RUSSO, D., G. JONES AND M. MUCEDDA. 2001. Influence of age, sex and body size on echolocation calls of Mediterranean and Mehely's horseshoe bats, *Rhinolophus euryale* and *R. mehelyi* (Chiroptera: Rhinolophidae). Mammalia 65: 429-436.

SCHNITZLER, H.-U. 1983. Fluttering target detection in horseshoe bats. Journal of the Acoustical Society of America 74: 31.

SCHNITZLER, H.-U. AND E.K.V. KALKO. 1998. How echolocating bats search and find food. Pp. 183-196 in Bat biology and conservation (T.H. Kunz and P.A. Racey, eds.). Smithsonian Institution Press, Washington, D.C.

SCHNITZLER, H.-U. AND E.K.V. KALKO. 2001. Echolocation by insect-eating bats. Bioscience 51: 557-569.

SCHNITZLER, H.-U., C.F. MOSS AND A. DENZINGER. 2003. From spatial orientation to food acquisition in echolocating bats. Trends in Ecology and Evolution 18: 386-394.

SCHOBER, W. AND E. GRIMMBERGER. 1998. Die Fledermäuse Europas. Kosmos-Naturführer, Stuttgart, Germany.

SCHOENER, T.W. 1974. Resource partitioning in ecological communities. Science 185: 27-39.

SIEMERS, B.M., K. BEEDHOLM, C. DIETZ, I. DIETZ AND T. IVANOVA. 2005. Is species identity, sex, age or individual quality conveyed by echolocation call frequency in European horseshoe bats? Acta Chiropterologica 7: 259-274.

SIEMERS, B.M. AND T. IVANOVA. 2004. Ground gleaning in horseshoe bats: comparative evidence from *Rhinolophus blasii*, *R. euryale* and *R. mehelyi*. Behavioral Ecology and Sociobiology 56: 464-471.

SIEMERS, B.M. AND H.-U. SCHNITZLER. 2004. Echolocation signals reflect niche differentiation in five sympatric congeneric bat species. Nature 429: 657-661.

SIEMERS, B.M. AND S.M. SWIFT. 2006. Differences in sensory ecology contribute to resource partitioning in the bats *Myotis bechsteinii* and *Myotis nattereri* (Chiroptera: Vespertilionidae). Behavioral Ecology and Sociobiology 59: 373 - 380.

STOCKWELL, E.F. 2001. Morphology and flight manoeuvrability in New World leaf-nosed bats. Journal of Zoology (London) 254: 505-514.

VALENCIUC, N. 1971. Donées concernant la nourriture et la manière de se la procurer chez quelques espèces de la faune de Roumanie. Studii si Comunicari 1971: 353-357.

VAN VALEN, L. 1965. Morphological variation and width of ecological niche. American Naturalist 99: 377-390.

VAUGHAN, T.A. 1959. Functional morphology of three bats: *Eumops, Myotis*, and *Macrotus.* University of Kansas, Museum of Natural History 12: 1-153.

WHITAKER, J.O. JR. AND H. BLACK. 1976. Food habits of cave bats from Zambia, Africa. Journal of Mammalogy 57: 199-204.

WIENS, J.A. 1977. On competition and variable environments. American Scientist 65: 590-597.

Chapter 1

Identification key to the horseshoe bats (Chiroptera: Rhinolophidae) of Europe

By C. Dietz

Parts of the ms. were published in:

Dietz, C. and O. von Helversen (2004): Identification key to the bats of Europe. 72 pp. Electronical publication, version 1.0, available at www.uni-tuebingen.de/tierphys/Kontakt/mitarbeiter_seiten/ dietz.htm.

and in:

Dietz, C., O. von Helversen and D. Nill (2007): Handbuch der Fledermäuse Europas und Nordwestafrikas, 399 pp.; Frankh-Kosmos, Stuttgart.

Identification key to the horseshoe bats (Chiroptera: Rhinolophidae) of Europe

By C. Dietz

Animal Physiology, Zoological Institute, Tübingen University, Tübingen, Germany.

INTRODUCTION

Since the 1990ies several studies have shown that bats can display unexpected high levels of genetic differentiation and a strong geographic structure. Several new cryptic bat species were discovered (Barratt et al. 1997; Castella et al. 2000; Helversen et al. 2001; Mayer and Helversen 2001; Kiefer and Veith 2002; Mucedda et al. 2002; Spitzenberger et al. 2003; Ibáñez et al. 2006; Mayer et al. 2007) and the screening with molecular techniques revealed strong hints for further new species. However, cryptic species were detected in European bats only in the family of the Vespertilionidae, while higher levels of genetic differentiation are absent in the other families (Molossidae, Miniopteridae, Rhinolophidae), especially in the horseshoe bats (Rhinolophidae; Rossiter et al. in prep.; Mayer pers. com.; Kiefer pers. com.).

Despite the fact that clear identification characters for the five European species of horseshoe bats are available since a long time (e.g. summarized in Helversen 1989; Schober and Grimmberger 1998) and neither genetically nor morphologically cryptic species are known at present (Rossiter et al. in prep.; Mayer pers. com.; Kiefer pers. com.), the identification of the three medium-sized species *Rhinolophus blasii*, *R. euryale* and *R. mehelyi* remained difficult. Due to identification difficulties in the field, the distribution of these three medium-sized species remained uncertain, especially on the Balkans (see Mitchell-Jones et al. 1999).

Aim of the identification key presented here is to help in a reliable species identification of all five European horseshoe bat species in the field. The ID-key was tested in the field on more than 7.200 horseshoe bats and the limits of species identification noted.

IDENTIFICATION KEY TO THE FAMILIES OF BATS IN EUROPE

1) Tail extending up to a half beyond the narrow tail membrane (Fig. 3). Lower part of the posterior margin of the ear with pronounced lobes (Fig. 2). No nasal process or nose leaf (Fig. 1). Only one species in Europe. – **MOLOSSIDAE**.

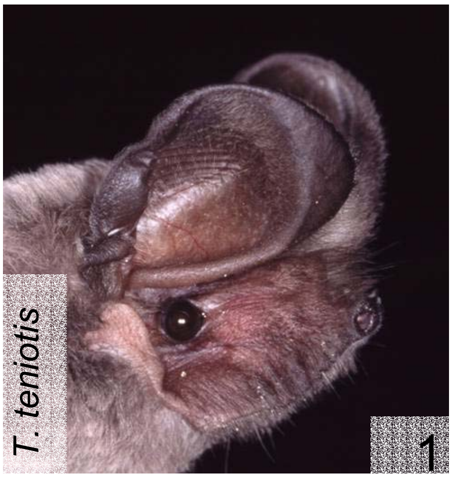
► Tail included completely in the broad tail membrane or except for the last one or two vertebrae (maximum about 5 mm) (Figs. 6 and 9). – 2.

2) Nose with a pronounced nose leaf (cutaneous process) (Fig. 4). Ears without a tragus (Fig. 5). Tail shorter or of same length as the hind legs (Fig. 6). Echolocation calls audible by a bat detector as long whistles. Five species in Europe. – **RHINOLOPHIDAE**.

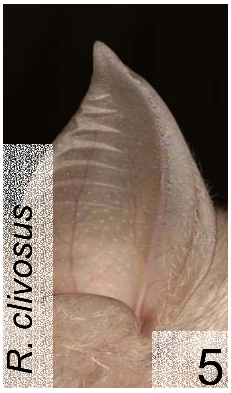
► No nose leaf (Figs. 7 and 10). Ears with a tragus (Figs. 8 and 11). Tail longer than the hind legs (Fig. 9). – 3.

3) Ears projecting beyond the top of the head (Fig. 7). Second phalanx of the third finger not specially elongated (up to about twice the length of the first phalanx, usually both are of more or less the same length). 34 Species in 9 genera in Europe. – **VESPERTILIONIDAE**.

► Ears very short and triangular, not projecting beyond the top of the head (as if cut with scissors) (Figs. 10 and 11). Second phalanx of the third finger (P3.2) about three times as long as the first phalanx (P3.1) (Fig. 12). 3rd and 4th fingers at rest folded in the joint between 1st and 2nd phalanges. Only one species in Europe. – **MINIOPTERIDAE**.



Molossidae



Rhinolophidae

Vespertilionidae

Miniopteridae

Plate 1: Characteristics of the four European bat families.

IDENTIFICATION KEY TO THE HORSESHOE BATS OF EUROPE

The identification of horseshoe bats is based mainly on the structure and characters of the nose leaf. The different parts of the nose leaf are explained in Figs. 13 and 14.

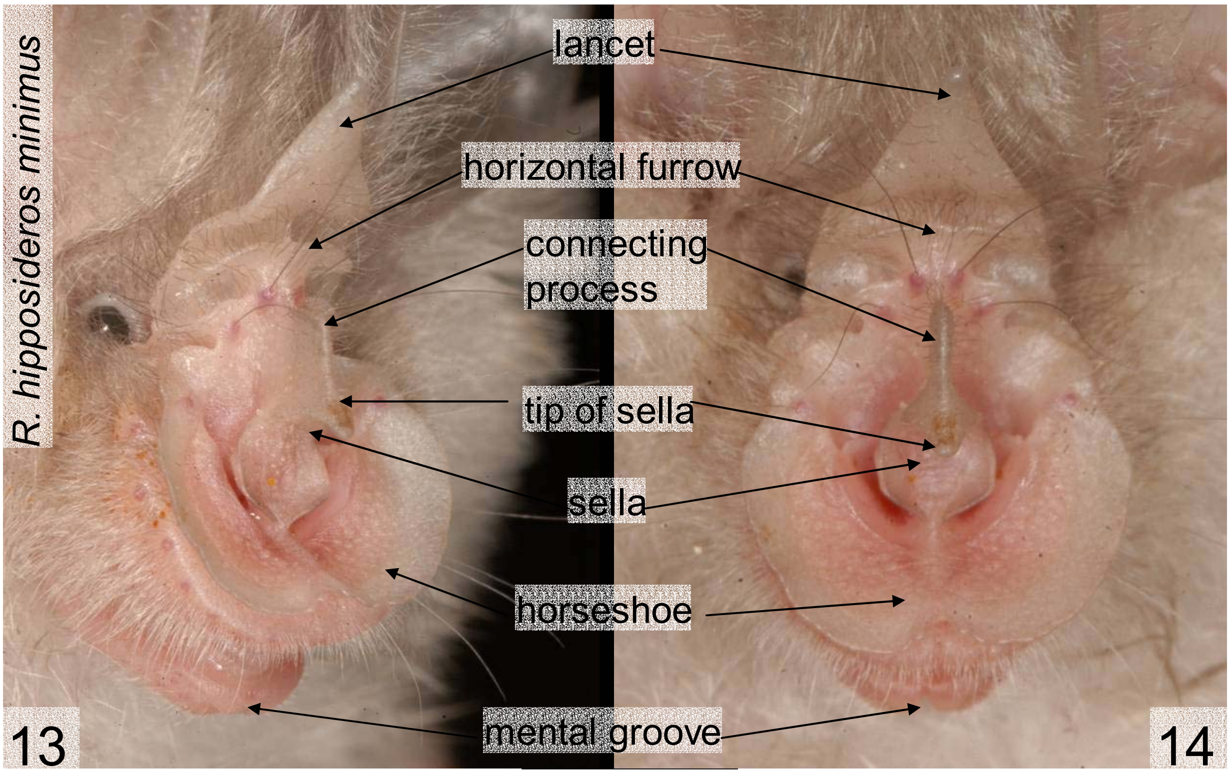


Plate 2: The different parts of the nose leaf of the family Rhinolophidae.

IDENTIFICATION KEY TO THE HORSESHOE BATS OF EUROPE

1) Connecting process (= upper saddle process, Crista) bluntly rounded in profile and shorter than the tip of the sella (= lower saddle process) (Figs. 16 and 19). – 2.

► Connecting process in profile pointed and always longer than the tip of the sella (Figs. 22, 25 and 28). – 3.

2) Biggest of the five horseshoe bats, FA > 54 mm (54.0 – 62.4 mm, lowest extreme 51.0 mm), D5: 63 – 77 mm, D3: 78 – 94 mm, P4.1: 9.5 – 13.4 mm; P4.2: 17.5 – 22.5 mm. High and bluntly rounded connecting process, the small sella is usually constricted in the middle (Fig. 30) and the lancet is long and has a slender tip. (Fig. 17). – *Rhinolophus ferrumequinum*.

> Additional characters: One or three mental grooves in the lower lip (Fig. 15) (very often the two lateral ones are reduced). Cf-frequency 79 - 84 kHz.
>
> Distribution in Europe: Occurs in southern and central Europe, northwards to southern England and Wales, the Netherlands and Poland. Present on most Mediterranean Islands.
>
> Distribution in adjacent areas: Widely distributed from Northern Africa throughout the Middle East, Ukraine and Caucasus. Missing only in Egypt.

► Smallest of the horseshoe bats, FA < 43 mm (usually 36 – 41 mm), D5: 46 – 53 mm, D3: 51 – 57 mm, P4.1: 5.7 – 7.5 mm; P4.2: 12.0 – 14.2 mm. The tip of the sella (= lower saddle process) is distinctly longer than the connecting process and in profile tapering to a point (Fig. 19). The fur is soft and sparse, grey on the back in younger individuals and brownish in older ones. – *Rhinolophus hipposideros*.

> Additional characters: The lower lip has one mental groove (Fig. 18). Cf-frequency 108 - 115 kHz.
>
> Distribution in Europe: It has the northernmost limit of distribution of all Rhinolophidae in Europe, reaching Ireland, the Netherlands, Germany and Poland. Common in the Mediterranean area and present on most islands.

Distribution in adjacent areas: Widely distributed in Northern Africa but missing in Libya and most of Egypt (present in Sinai only). Also widely distributed in Turkey, Cyprus, Ukraine, Caucasus and the Middle East.

Taxonomical note: The taxonomic position of some forms within this group is still not solved satisfyingly, especially in Asia. There are some morphological differences between the nominate form distributed over most of Europe and the populations from Northern Africa (*R. h. escalerae*), Sicily, Crete, Anatolia and the Middle East (*R. h. minimus*) and Cyprus (*R. h. midas*).

3) Second phalanx of the fourth finger (P4.2) less than twice as long as the first (P4.1) (P4.1: 7.6 – 9.2 mm; P4.2: 14.3 – 17.4 mm) (Fig. 39). Tip of the sella (= lower saddle process) narrow when viewed from the front and lower part not rounded (Figs. 23 and 37). The sella is wedge shaped when viewed from below (Fig. 37). The horizontal furrow below the lancet is usually clearly indented in the middle when viewed from the front (Fig. 23). Connecting process (= upper saddle process) relatively long and straight, never curving downwards (Fig. 22). Bases of the hair whitish (tousled parts of the pelage have therefore a very light appearance), the tips of the hair are brown or greyish, often with a yellowish tinge (Fig. 21). FA 43.9 – 50.1 mm, D5: 54 – 62 mm, D3: 63 – 74 mm. – *Rhinolophus blasii*.

Additional characters: Cf-frequency 93 – 96 kHz.

Distribution in Europe: Restricted to south-eastern Europe from the northern Adriatic coast eastwards to Romania and all over the Balkans and Greece. Found also on some Greek islands including Crete.

Distribution in adjacent areas: Northwest Africa, Turkey, Syria, Israel, Transcaucasia.

► Second phalanx of fourth finger (P4.2) more than twice as long as the first (P4.1) (Figs. 43 and 47). Tip of the sella (= lower saddle process) broad when viewed from the front and lower margin rounded (Figs. 26, 29, 41 and 45). – 4.

4) Lancet narrows more or less gradually to its tip, it has only a slight constriction above the middle and the tip is broadly rounded (Fig. 26). Connecting process (= upper saddle process) is slightly horn-shaped, being pointed in profile and forward curving (slightly downwards) (Fig. 25). FA usually < 50 mm (44.0 – 51.0 mm), D5: 52 – 63 mm, D3: 63 – 76 mm, P4.1: 5.7 – 8.2 mm; P4.2: 16.4 – 18.1 mm. Coloration of the belly more greyish-brownish (Fig. 24), not as whitish as in *R. mehelyi*. The boundary between the back and underside is indistinct. – *Rhinolophus euryale*.

Additional characters: The width of the antitragus of the ear (horizontal lobe at the base of the ear) is about equal to its height and is usually only weakly indented close to the connection to the ear (Fig. 42). Cf-frequency 102 – 107 kHz. Body mass usually around 12 g (9 – 15 g) in summer.

Distribution in Europe: Widest distributed species of the three medium-sized horseshoe bats in the whole Mediterranean area and the Balkans, extends north to central France, northern Italy, Slovakia and Romania. Present on Corsica, Sardinia and Sicily but absent from the Balearic Islands.

Distribution in adjacent areas: Northwest Africa, Turkey, Syria, Lebanon and Israel, Caucasus and Transcaucasia. Missing in Libya and Egypt.

Taxonomical note: The eastern Mediterranean form (*R. e. judaicus*) is separated by a wide gap in the species distribution in Asia Minor (Benda and Horáček 1998), but geographic variation within *R. euryale* is little known.

► Lancet is abruptly narrowed above the middle to a distinctly linear tip (Figs. 27 and 29). Connecting process (= upper saddle process) relatively blunt in profile and only slightly longer than the lower process (Fig. 28). FA usually > 49 mm (48.2 – 54.8 mm), D5: 57 – 67 mm, D3: 71 – 83 mm, P4.1: 6.5 – 9.3 mm; P4.2: 17.4 – 21.5 mm. Whitish belly coloration and clear boundary between the back and underside coloration in adult individuals. – *Rhinolophus mehelyi*.

Additional characters: The width of the antitragus of the ear (horizontal lobe at the base of the ear) is greater than the height and is often strongly indented close to the connection to the ear (Fig. 46). Cf-frequency 106 - 112 kHz. Body mass usually around 15 g (12 – 18 g) in summer.

Distribution in Europe: Distributed in the Mediterranean area from central and southern Iberia, southern France, Sardinia, Sicily to Greece, range extends in the Balkans northwards to Romania.

Distribution in adjacent areas: Widely distributed throughout Northern Africa, Turkey, Syria, Israel (here possibly extinct), Ukraine, Caucasus and Transcaucasia.

Plate 3: Characters of the five European horseshoe bats (Rhinolophidae).

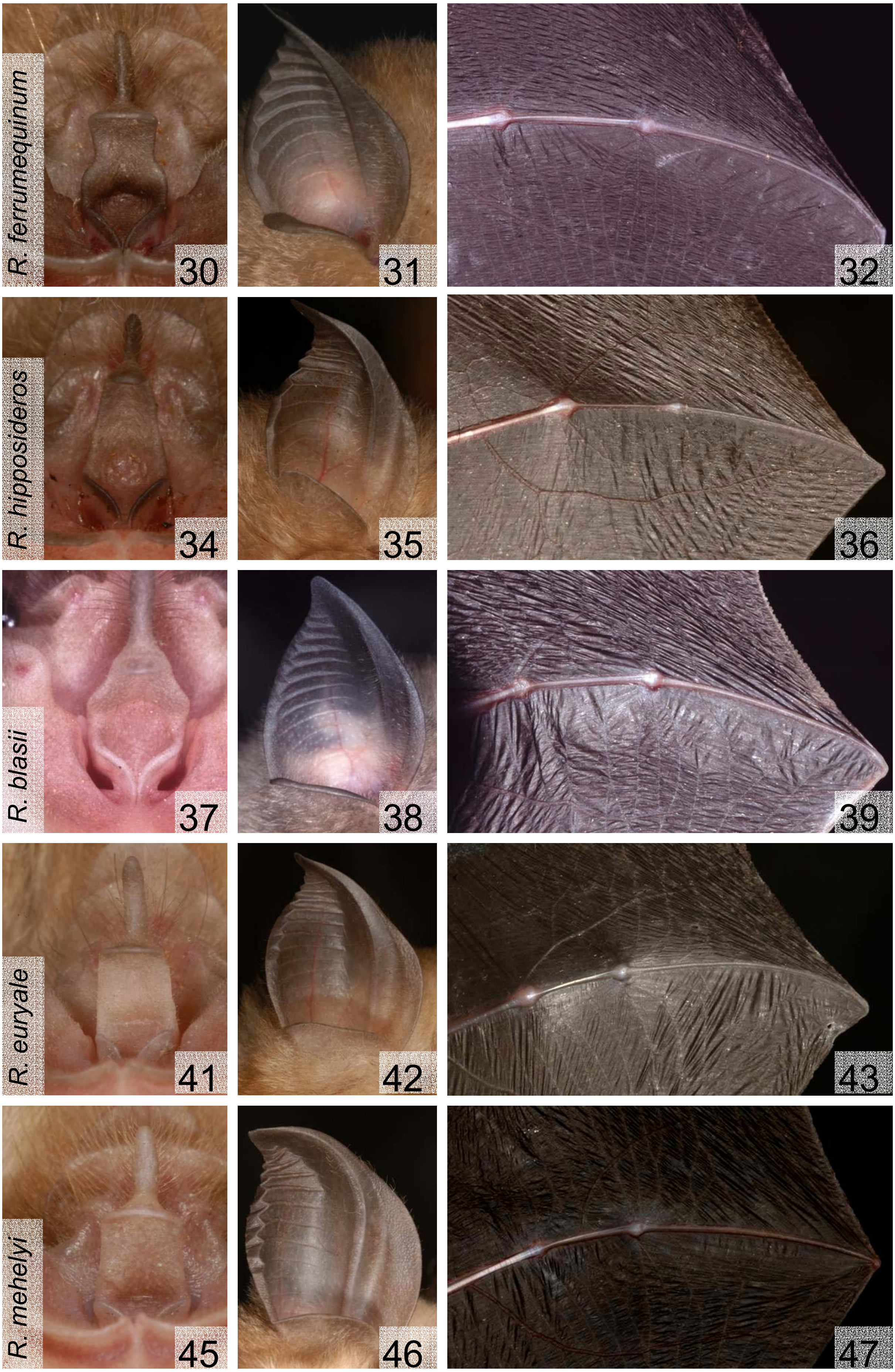


Plate 4: Characters of the five European horseshoe bats (Rhinolophidae).

FIELD TEST OF THE ID-KEY

In order to test the validity of the characters used in the ID-key, more than 7.200 horseshoe bats were identified using the characters of the nose leaf. For this bats were captured in several European countries (Bulgaria, Greece, Croatia, Italy, Spain and Portugal), in Northern Africa (Morocco, Egypt) and the Middle East (Israel, Turkey). The interindividual and interspecific variability of bats captured in the same areas was evaluated and aberrant or abnormal morphology of the nose leaf was described and documented by photographs.

The field-identification of horseshoe bats based on the nose leaf morphology alone (ignoring size characters and measurements) proved to be possible in the vast majority of bats. In fact only one out of the more than 7.200 captured bats could not be assigned to *R. euryale* or *R. mehelyi*, neither by the nose leaf morphology nor by measurements. However in 24 horseshoe bats an aberrant nose leaf morphology obscured some of the otherwise very clear characters:

- In one adult *R. blasii* the connecting process was not pointed as usual but shorter and rounded (Fig. 51), more like in *R. mehelyi*. In an other adult bat the connecting process was completely missing (Fig. 53). Both individuals could be identified by other nose leaf characteristics.

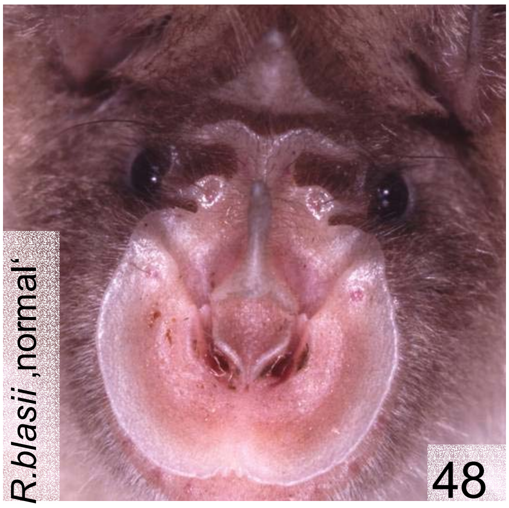
- Six adult *R. euryale* also showed deviations from the normal morphology of the connecting process: in 3 individuals big parts were missing (Fig. 55), in one individual it was directed upwards instead of curving downwards (Fig. 56) being more similar to *R. blasii*, in one individual it was deformed in a strange way (Fig. 57) and in one individual of the subspecies *R. e. judaicus* it was very short (Fig. 59), resembling the connecting process of *R. hipposideros*.

- Five adult *R. euryale* had an unusual margin of the horseshoe: the usually smooth margin was more uneven (Fig. 61).

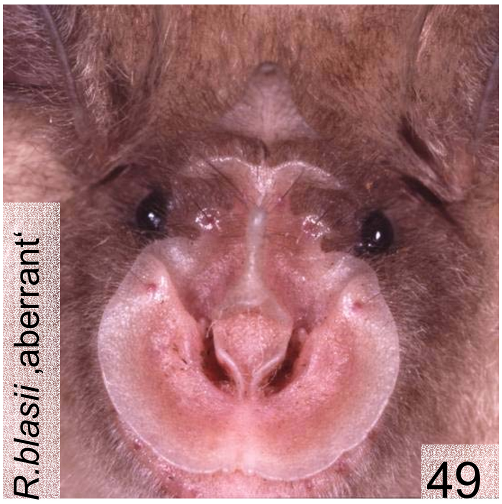
- Five other adult *R. euryale* had a missing or deformed lancet without a slender tip (Figs. 62 and 63).

- One old (possibly senescent) adult *R. ferrumequinum* had a very short lancet without a slender tip (Fig. 65), while the lancet was deformed in 5 other bats (Fig. 66).

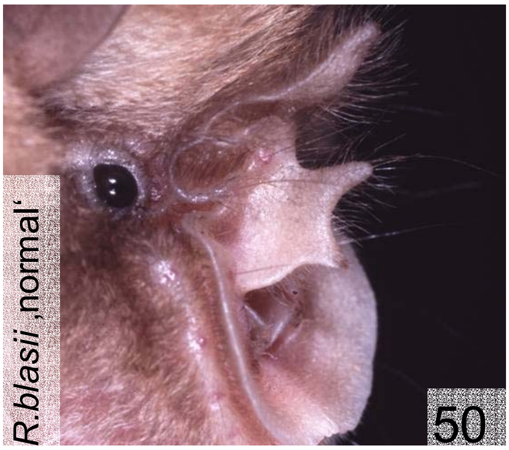
R. mehelyi showed a quite high variability in some morphological details of the nose leaf but no exceptional abnormalities were noted. In *R. hipposideros* several subspecies have been described basing on differences in nose leaf morphology and these differences were noted in bats from different parts of the distribution in the present study as well.



48



49



50

51

52

53

Plate 5: Normal and aberrant nose leaf morphology in *Rhinolophus blasii*. Fig. 48 & 50 and 49 & 51 show the same individuals respectively.

Plate 6: Normal and aberrant nose leaf morphology in *Rhinolophus euryale*.

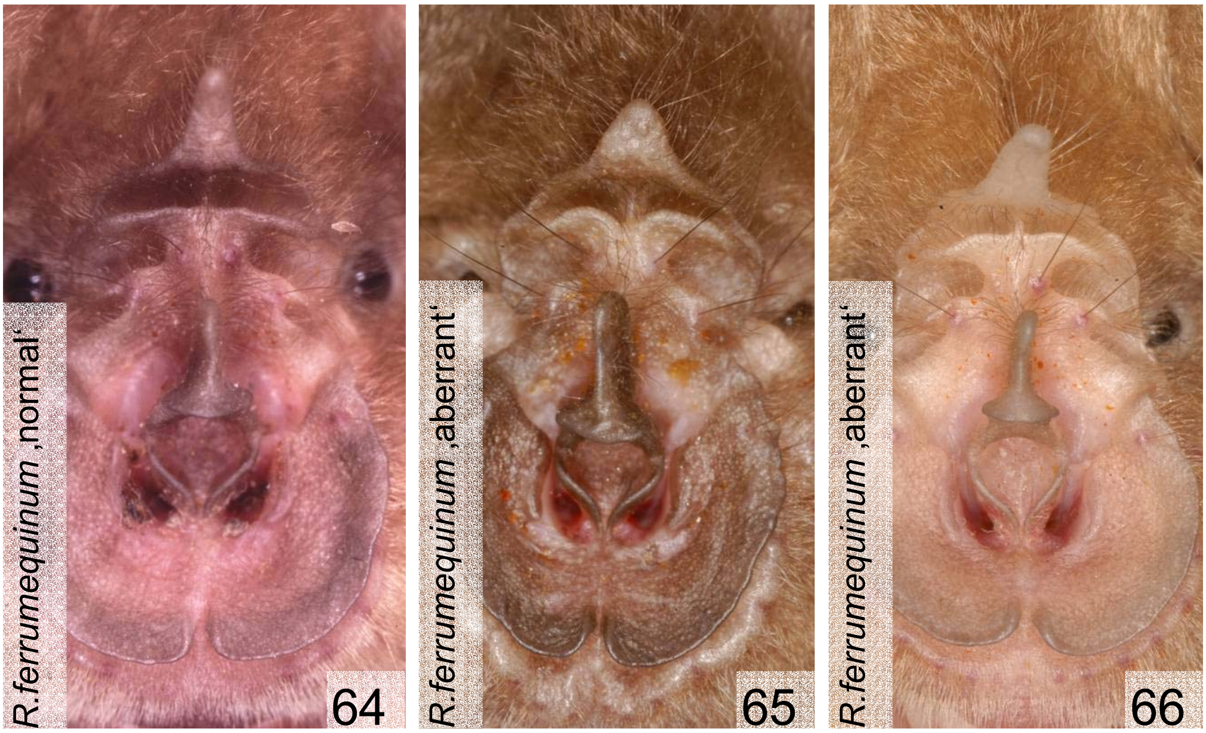


Plate 7: Normal and aberrant nose leaf morphology in *Rhinolophus ferrumequinum*.

CONCLUSIONS

The morphology of the nose leaf offers suitable characters to identify the European species throughout their distributions and enables reliable species identification. In some individuals deformations or other abnormalities may obscure some of the nose leaf characteristics, however taking other characters or measurements into account, identification is unambiguous. A possible exception are aberrant specimen of *R. euryale* or *R. mehelyi*: as echolocation call frequencies and external measurements overlap widely only skull charctersitics allow an unambiguous identification in specimen with an aberrant nose leaf. However among more than 2.000 captured bats of both species only a single one could not be identified with the necessary accuracy, most probably it was a stunted *R. mehelyi* with intermediate characters of its lancet and connecting process.

REFERENCES

BARRATT, E.M., R. DEAVILLE, T.M. BURLAND, M.W. BRUFORD, G. JONES, P.A. RACEY AND R.K. WAYNE. 1997. DNA answers the call of pipistrelle bat species. Nature 387: 138-139.

BENDA, P. AND I. HORÁČEK. 1998. Bats (Mammalia: Chiroptera) of the Eastern Mediterranean. Part 1. Review of distribution and taxonomy of bats in Turkey. Acta Soc. Zool. Bohem. 2: 255-313.

BENDA, P., M. RUEDI AND S. AULAGNIER. 2004. New data on the distribution of bats (Chiroptera) in Morocco. Vespertilio 8: 13-44.

CASTELLA, V., M. RUEDI, L. EXCOFFIER, C. IBAÑEZ, R. ARLETTAZ AND J. HAUSSER. 2000. Is the Gibraltar Strait a barrier to gene flow for the bat *Myotis myotis*? Molecular Ecology 9: 1761-1772.

DIETZ, C., O. VON HELVERSEN AND D. NILL. 2007. Handbuch der Fledermäuse Europas und Nordwestafrikas, 399 pp.; Frankh-Kosmos, Stuttgart.

DE PAZ, O. 1995. Geographic variation of the greater horseshoe bat (*Rhinolophus ferrumequinum*) in the west-half of the Palearctic region. Myotis 32/33: 33-44.

FELTEN, H., F. SPITZENBERGER AND G. STORCH. 1977. Zur Kleinsäugerfauna West-Anatoliens, Teil IIIa. Senckenbergiana biologica 58: 1-44.

HANÁK, V., P. BENDA, M. RUEDI, I. HORÁČEK AND T.S. SOFIANIDOU. 2001. Bats (Mammalia: Chiroptera) of the Eastern Mediterranean, Part 2. New records and review of distribution of bats in Greece. Acta Soc. Zool. Bohem. 65: 279-346.

HARRISON, D.L. AND P.J.J. BATES. 1991. The mammals of Arabia, 2nd edition, 354 pp.; Harrison Zoological Museum.

HELLER, K.-G. AND O. VON HELVERSEN. 1989. Resource partitioning of sonar frequency bands in rhinolophoid bats. Oecologia 80: 178-186.

HELVERSEN, O. VON. 1989. Bestimmungsschlüssel für die europäischen Fledermäuse nach äußeren Merkmalen. Myotis 27: 41-60.

HELVERSEN, O. VON, K.-G. HELLER, F. MAYER, A. NEMETH, M. VOLLETH AND P. GOMBKÖTÖ. 2001. Cryptic mammalian species: a new species of whiskered bat (*Myotis alcathoe* n.sp.) in Europe. Naturwissenschaften 88: 217-223.

HORÁČEK, I., V. HANÁK AND J. GAISLER. 2000 Bats of the Palearctic region: a taxonomic and biogeographic review. Proceedings of the 8th EBRS 1: 11-157.

IBÁÑEZ, C., J.L. GARCÍA-MUDARRA, M. RUEDI, B. STADELMANN AND J. JUSTE. 2006. The Iberian contribution to cryptic diversity in European bats. Acta Chiropterologica 8: 277-297.

KIEFER, A. AND M. VEITH. 2001. A new species of long-eared bat from Europe (Chiroptera: Vespertilionidae). Myotis 39: 5-16.

KÖNIG, C. 1959. Äußere Merkmale zur Bestimmung der lebenden Fledermäuse Europas. Säugetierkundliche Mitteilungen 7: 101-110.

LEWIS, R.E. AND D.L. HARRISON. 1962. Notes on bats from the Republic of Lebanon. Proceedings of the Zoological Society of London 138: 473-487.

MAYER, F. AND O. VON HELVERSEN. 2001. Cryptic diversity in European bats. Proceedings of the Royal Society of London B 268: 1825-1832.

MAYER, F., C. DIETZ AND A. KIEFER. 2007. Molecular species identification boosts bat diversity. Frontiers in Zoology 4: 4.

MITCHELL-JONES, A.J., G. AMORI, W. BOGDANOWICZ, B. KRYSTUFEK, P.J.H. REIJNDERS, F. SPITZENBERGER, M. STUBBE, J.B.M. THISSEN, V. VOHRALIK AND J. ZIMA. 1999. The atlas of European mammals, 484 pp.; Poyser Natural History.

MUCEDDA, M., A. KIEFER, E. PIDINCHEDDA AND M. VEITH. 2002. A new species of long-eared bat (Chiroptera, Vespertilionidae) from Sardinia (Italy). Acta Chiropterologica 4: 121-135.

QUMSIYEH, M.B. AND D.A. SCHLITTER. 1982. The bat fauna of Jabal al Akhdar, northeast Libya. Annals of the Carnegie Museum 51: 377-389.

QUMSIYEH, M.B. 1985. The bats of Egypt. Special Publications, The Museum Texas Tech University 23: 102 pp.

RACHMATULINA, I.K. 1992. Major demographic characteristics of populations of certain bats from Azerbaijan. Prague Studies in Mammalogy: 127-141; Prague.

RAKHMATULINA, I. 2001. Rare bat species of the Caucasus. Proceedings of the VIIIth EBRS 2: 143-150.

ROSSITER, S.J., P. BENDA, C. DIETZ, S. ZHANG AND G. JONES. In press. Range-wide structure and clines in genetic diversity in the greater horseshoe bat: implications for population history, taxonomy and conservation. – Molecular Evolution.

SCHOBER, W. AND E. GRIMMBERGER. 1998. Die Fledermäuse Europas, 265 pp.; Frankh-Kosmos, Stuttgart.

SIEMERS, B.M., K. BEEDHOLM, C. DIETZ, I. DIETZ AND T. IVANOVA. 2005. Is species, sex, age or individual quality conveyed by echolocation call frequency in European horseshoe bats? Acta Chiropterologica 7: 259-274.

SPITZENBERGER, F. 1979. Die Säugetierfauna Zyperns Teil II: Chiroptera, Lagomorpha, Carnivora und Artiodactyla. Annalen des Naturhistorischen Museums Wien 82: 439-465.

SPITZENBERGER, F., P. STRELKOV AND E. HARING. 2003. Morphology and mitochondrial DNA sequences show that *Plecotus alpinus* KIEFER AND VEITH, 2002 and *Plecotus microdontus* SPITZENBERGER, 2002 are synonyms of *Plecotus macrobullaris* KUZJAKIN, 1965. Nat. Croat. 12: 39-53.

SPITZENBERGER, F., P.P. STRELKOV, H. WINKLER AND E. HARING. 2006. A preliminary revision of the genus *Plecotu*s (Chiroptera, Vespertilionidae) based on genetic and morphological results. Zoologica Scripta 35: 187-230.

APPENDIX 1: LIST OF SCIENTIFIC AND ENGLISH NAMES OF THE EUROPEAN HORSESHOE BAT SPECIES

Rhinolophus ferrumequinum (Schreber, 1774) – greater horseshoe bat
    Vespertilio ferrum-equinum Schreber, Säugethiere 1: 174, pl. 62. Type locality: France.

Rhinolophus hipposideros (Bechstein, 1800) – lesser horseshoe bat
    Vespertilio hipposideros Bechstein, in Pennant, Allgemeine Uebersicht der Vierfüssigen Thiere 2: 629. Type locality: France.

Rhinolophus euryale Blasius, 1853 – Mediterranean horseshoe bat
    Rhinolophus euryale, Blasius, Arch. Naturgesch. 19, 1: 49. Type locality: Milano, Italy.

Rhinolophus blasii Peters, 1866 – Blasius' horseshoe bat
    Rhinolophus blasii Peters, Monatsber. K. Preuss. Akad. Wiss. Berlin 17. Type locality: SE-Europe (Italy)

Rhinolophus mehelyi Matschie, 1901 – Mehely's horseshoe bat
    Rhinolophus mehelyi Matschie, Sitzber. Ges. Naturf. Fr. Berlin 225. Type locality: Bucharest, Romania.

Chapter 2

Age classification and assessment of reproductive condition in female greater horseshoe bats (*Rhinolophus ferrumequinum*, Chiroptera: Rhinolophidae)

By C. Dietz and I. Dietz

The ms. is not published yet.

Age classification and assessment of reproductive condition in female greater horseshoe bats (*Rhinolophus ferrumequinum*, Chiroptera: Rhinolophidae)

By C. Dietz and I. Dietz

Animal Physiology, Zoological Institute, Tübingen University, Tübingen, Germany.

ABSTRACT

Ageing and the assessment of the reproductive condition is an important prerequisite for many ecological studies. We studied metrical and qualitative changes of characters related to age and reproduction in free ranging greater horseshoe bats, *Rhinolophus ferrumequinum* in Northern Bulgaria. 218 females were marked as juveniles within the first two months of their life at a nursery colony. 94 out of the marked individuals were recaptured 260 times. By noting the status of the epiphyseal growth plates, shape of the finger joints, colour of the pelage, state and size of thoracic and pubic nipples and if a foetus was palpable or not and by taking portraits and close-up pictures in each bat whenever it was caught we were able to establish a character matrix. This allows the age classification of female *R. ferrumequinum* up to an age of 28 months. The shape of the finger joints in combination with a less dense and light grey fur and undeveloped thoracic and pubic nipples allowed to distinguish up to 4 months old bats from older ones. Till an age of 16 months the fur remained grey in colour but was dense like in adult ones, while the nipples remained minute. Until an age of 28 months the secondary reproductive organs became fully developed in most females as most of them gave birth to their first young at an age of 24 months. However until their third hibernation (from an age of 28 months on) the pelage in the facial parts remained much darker than in older bats. After their third hibernation bats were at least 33 months old and showed the typical adult characteristics of the reproductive organs and in fur colouration.

Key-words: ageing, interspecific variability, reproduction, horseshoe bats

INTRODUCTION

Behaviour, spatial use or survival in vertebrates might differ significantly not only between sexes but also between age classes of the same species. Behavioural peculiarities can be a result of different sizes between subadults and adults, of differences in manoeuvrability or of reproductive condition as a function of age. While a similar behaviour between age classes can be expected in environments with unlimited resources, behavioural differences might be adaptive especially when they help to reduce intraspecific competition for limited resources (Tschumy 1982). Age classes may even act as ecological species and use different niches (Polis 1984; Adams 2000). In such cases a correct age classification is an important prerequisite for ecological studies and their interpretation. In most field studies ageing methods have to be applicable to living individuals. While weight and some linear dimensions are useful e.g. in many mammals (Morris 1972), they often fail in flying vertebrates as they require a rigid and stable skeleton with the onset of flight and therefore finish growth very soon (Case 1978; Forsyth 1976). This is especially true in bats: most species finish growth in an age of 6-10 weeks (Barclay 1995; Burnett and Kunz 1982; de Paz 1986; Dietz et al. 2007; Hoying and Kunz 1998; Reiter 2004; Sharifi 2004). Unusual for small mammals, bats show an extraordinary longevity and a delayed onset of sexual maturity (Gaisler 1989; Racey and Entwistle 2000) strongly increasing the time premature individuals can be found within study populations. Bats are highly specialised mammals mainly foraging on the wing in the night by using echolocation calls. The majority of bats are insectivorous, but no other order of mammals exhibits a greater diversity of dietary specialisations ranging from blood to fruits (Patterson et al. 2003). Some ecological studies could demonstrate differences in habitat use, foraging behaviour or spatial use in juveniles, subadult or adult bats (Adams 1996, 1997, 2000; Kalcounis and Brigham 1995; Kokurewicz 2004), in diet (Adams 1996; Anthony and Kunz 1977; Hamilton and Barclay 1998; Rolseth et al. 1994), or in echolocation (Jones et al. 1992; Jones and Kokurewicz 1994; Russo et al. 2001; Siemers et al. 2005), while others found differences in survival between age classes (Sendor and Simon 2003). An influence of the reproductive condition of adult bats on foraging behaviour is often suspected (e.g. Belwood and Fenton 1976) but rarely shown (Barclay 1989; Henry et al. 2002; O'Donnell 2002; Racey and Swift 1985; Ransome 1990).

The age of the studied animal can be established most precisely by marking it at birth or at an early juvenile stage. At all subsequent observations the exact age will be known and can be correlated with any ecological data. In bats the most widely applied method for marking is the use of bat bands (Barclay and Bell 1988). However, it has been shown repeatedly that the marking method can have serious impact on the studied species (Baker et al. 2001; Dietz et al. 2006; Happold and Happold 1998) and especially in long living animals like bats it is often impossible to mark enough members of the population at birth. Therefore, a need for age estimation methods exists. Most of the wide variety of methods in age classification of bats are valid only to distinguish juveniles/subadults up to an age of several months from adult ones (Anthony 1988). This applies especially for metrical characters of the wing bones (Baptista et al. 2000; Krátký 1981; Reiter 2004; Sharifi 2004; Sharifi and Akmali 2004) and the evaluation of the epiphyseal growth plates (Baagøe 1977a; Barrett-Hamilton 1910; Rybář 1969, 1971, 1972). In a very few species characteristics of fur or skin coloration provide established methods for age classification (Gaisler and Titlbach 1964; Geiger et al. 1996; Richardson 1994; Trappmann 1999), while attempts to correlate tooth abrasion and age are quite uncertain and evaluating the teeth is much more a relative method to compare several individuals (Sluiter 1954). Most other methods are invasive or can only be applied to dead animals like the analysis of dental layers or pulp cavity size (Baagøe 1977b; Batulevicius et al. 2001), incremental lines of bones (Phillips et al. 1982; Klevezal' and Kleinenberg 1967 cited in Anthony 1988), lens-weight (Perry and Herreid 1969) or dissection with inspection of the genitalia (Racey 1974; Sluiter 1954, 1960; Sluiter and Bouman 1951; Smirnov and Tsytsulina 2003). On the other hand, some of the reproductive conditions of a bat, like lactation or late stages of pregnancy, can be quite easily assessed from the state of the external reproductive organs (Racey 1988). As the onset of reproduction can be quite late in a bat's life (Ransome 1995), the reproductive condition could possibly be used as an age criterion as well (Racey 1974).

Aim of the present study was to establish reliable and non invasive classification characters for age and reproductive condition in female greater horseshoe bats (*Rhinolophus ferrumequinum*), an insectivorous heterothermic bat species with seasonal monoestry and delayed fertilization inhabiting the temperate zones of Europe, Northern Africa and Asia.

MATERIALS AND METHODS

Study area

Our study area was the hilly karst-area between the lowlands of the Danube and the Balkan mountains in Northern Bulgaria. Bats were marked in the years 2001-2003 at sites around the village Muselievo in the Osam valley (near the town of Nikopol, District Pleven), about 10 km south of the river Danube. In order to study the changes of reproductive condition and age characters we marked juvenile greater horseshoe bats (*Rhinolophus ferrumequinum*) within the first two months of their life and tried to recapture them as often as possible. To mark the bats individually we used numbered flanged nickel-chromium alloy bat rings with a size of 4.2 mm manufactured by Lambournes (Lambournes Ltd., Leominster, Herefordshire, UK; rings used in 2001) and by Porzana (Porzana Ltd., Wetland-Trust, UK; rings used in 2002-2003). Most of the bats were captured at the cave "Nanin Kamăk" inhabited by a colony of up to 1,000 bats (*R. ferrumequinum*, *R. mehelyi*, *R. euryale*, *Myotis capaccinii*, *M. emarginatus* and *Miniopterus schreibersii*). Some more greater horseshoe bats were captured and marked in the surroundings of Muselievo in alternative day roosts, in night roosts and foraging sites.

In the three years 218 juvenile female *R. ferrumequinum* were marked with individually numbered bat bands (2001: 67 juvenile females, 2002: 55 and 2003: 96). In each of the bats five standard measurements were taken with a mechanical precision caliper (Hommel-Hercules Industries, Viernheim, Germany; precision ± 0.05 mm): length of forearm including wrist, length of 5th finger excluding wrist, length of 3rd finger excluding wrist, length of 1st phalanx of 4th digit, and length of 2nd phalanx of 4th digit. Body mass was measured using an electronical balance (Soehnle 200: Leifheit AG, Nassau/Lahn, Germany; precision ± 0.1 g). The following characters were noted in each individual: status of the epiphyseal growth plates, shape of the finger joints, colour of the pelage, state and size of thoracic and pubic nipples and if a foetus was palpable or not. We also took portraits and close-up pictures of the thoracic and pubic nipples in each bat with a Nikon F100 camera and ISO-100 slide films (in the years 2001-2003) and a digital Nikon D100 camera (in the years 2004-2006) using a 105mm macro lens with close-up extension and a close-up flash (Nikon SB-29). We tried to recapture as many of the marked bats in the years 2001-2006 and the same procedure of data recording was repeated whenever we got a marked bat. In 2001-2003 bats were captured from April to October, in later years only during shorter field trips in May-July. This resulted in a total number of 260 recaptures of 94 individuals of the 218 *R. ferrumequinum* marked as juveniles. Some individuals were recaptured up to 11 times. The field work was carried out under licence of the Bulgarian authorities (15-RD-08/15.01.2001, 48-00-56/16.01.2001, 8/02.07.2004 RIOSV Pleven, RIOSV Rousse).

Figure 1: A juvenile about 6 weeks old female *R. ferrumequinum* (right) and its 25 months old mother (left). While the juvenile is characterized by its grey and sparse fur, the mother has the typical adult pelage, differing from older ones only in the darker pelage in the face; this darkened facial parts are a typical characteristic for 22-28 months old *R. ferrumequinum*.

RESULTS AND DISCUSSION

1. Age classification

Metrical characters

In juvenile female *R. ferrumequinum* the five standard measurements (lengths of forearm, 5th and 3rd finger and of the phalanges of the 4th finger) were significantly smaller than in adults until latest mid-August when they were 2 months old. From mid of August on, all bats had reached adult size (Dietz et al. 2007).

The very rapid increase in lengths of forearm and fingers and the fact that the bats reach adult size very soon limits the use of metrical characters to classify juvenile age to the first 2 or 3 months of their life (Anthony 1988; Barclay 1995; de Paz 1986; Gaisler 1960; Hoying and Kunz 1998; Hughes et al. 1995; Reiter 2004). *R. ferrumequinum* has been shown to grow to full skeletal size in about 60 days (Dietz et al. 2007; Jones et al. 1995; Ransome 1989, 1998).

Fusion of epiphyses

Until an age of 7-9 weeks the cartilaginous epiphyseal plates in the finger bones and at the distal end of the metacarpals were well visible when the bat's wing was transilluminated. The cartilaginous zones appeared lighter than the ossified parts of the bones. At an age of approximately 2 months the cartilaginous plates became no longer visible but the finger joints of the bats remained less knobbly and more evenly tapered than those of adults. This different shape proved to be a reliable criterion to distinguish young bats at least till an age of 4 months from adult ones. After hibernation in most bats the joints were very similar to those of adults, less than two fifths of the young bats still had more evenly tapered joints. From an age of 12 months on all individuals had knobbly finger joints.

The state of the ossification of the epiphyseal growth plates is a well known method to distinguish juvenile from subadult and adult bats (Andersen 1917; Anthony 1988; Baagøe 1977a, 1977b; Barrett-Hamilton 1910; Cheng and Lee 2002; Davis 1963; Davis and

Hitchcock 1965; de Paz 1986; Gaisler 1960; Kleiman 1969; Kunz and Anthony 1982; Rybář 1969, 1971; Sharifi 2004; Stebbings 1968) and our results are in accordance to those studies. However, Rybář (1971, 1972) was able to extend the period of correct age assessment to three months by using an ossification index, a method not used in our study, while Baagøe (1977b) used X-rays to distinguish between young and older bats, extending the period of correct age classification considerably until an age of approximately 10 months.

Dentition and tooth wear

The permanent teeth were fully developed with the onset of independent foraging flights in *R. ferrumequinum*, while some juveniles at their first flights still had a few remaining milk teeth. The teeth (especially the canines) were very sharply pointed in young but full-grown bats and got shorted and dulled over the years due to abrasion. However big individual differences were noted, some at least 7 years old (and possibly much older) females had still very long sharp and pointed canines, while some of the 4 or 5 years old bats had strongly eroded teeth being at least one third shorter than in less than 1 year old ones. If this is a normal difference due to different diet or prey selection or if the stronger teeth wear in some bats could be a result of biting the ring (e.g. Young 2001) remains open. However, none of the bats of 5 years age had mostly or totally worn teeth (totally to the gums) as seen in a very few most possibly very old bats captured. Dentition was considered not to be a reliable method for age classification in life *R. ferrumequinum* but it may be possible to assign bats to broad age classes with possibly low accuracy. Our results are in accordance with many published studies, the usefulness of the method for reliable age classification was shown in museum specimen with cleaned skulls only (Anthony 1988; Baagøe 1977b; Davis et al. 1962; Fenton 1970; Gaisler and Titlbach 1964; Hall et al. 1957; Jones 1967; Kleiman 1969; Kunz 1973; Perry and Herreid 1969; Sluiter 1960, 1961; Young 1975).

Body mass

When leaving the cave on their own for the first flights, juvenile female *R. ferrumequinum* had a weight of 13-16 g. Till Mid of August when being 2 months old they reached 18-20 g. In an age of 12-17 months they had a body mass of 19.5-22.5 g, while more than 24 months old bats were at least 0.5-1 g heavier. To some degree the body mass was found to be useful to assign female *R. ferrumequinum* to the three age classes: juvenile – subadult/nulliparous – adult, but only when taking the weight in a standardized way, e.g. only of bats leaving the roost in the evening. However, misclassifications might occur due to a broad overlap in body mass, mainly in autumn due to fat accumulation prior to hibernation or in starving adult bats. Other authors found body mass to be a good indicator of age within the first 2-3 months of life but not later on (e.g. Davis and Hitchcock 1965; de Paz 1986) with exception of *Rhinolophus hipposideros* (Gaisler 1965; Gaisler and Titlbach 1964) and *Rhinolophus megaphyllus* in Australia (Young 1975, 2001) with similar results to ours.

Pelage length and density

The hair length was found to differ only between juvenile stages but not between different age classes of more than 2 ½ months old female *R. ferrumequinum* (see also Klíma and Gaisler 1967). Fur density of 3-4 months old *R. ferrumequinum* is less than in older ones, a criterion that could be used in addition to others to distinguish the few months old females from at least one year old ones.

Pelage colouration

Colour differences in pelage proved to be very effective in classifying female *R. ferrumequinum*, when having at least several bats at hand to compare them (Fig. 1), while it was sometimes quite difficult to attribute a single captured bat. All juveniles up to an age of 16 months were readily distinguishable from older bats in having a grey fur being well distinguishable from the yellowish brown fur of the older ones (Plate 2). There were no indications for moult till October. In none of the recaptures a bat older than 22 months had grey fur on the back and belly and none of the bats less than 16 months had a yellowish-brown fur, so we expect the bats to moult in their second late autumn or winter from grey to yellowish-brown. All of the 22-28 months old bats had a very similar fur coloration of the back and the belly to adult ones, but the vast majority of individuals had a different colouration of the pelage surrounding the horseshoe: most had a somewhat darker, mask-like colouration (Plate 2) never observed in female *R. ferrumequinum* older than 28 months.

Pelage coloration is known to differ between juveniles and adults in many bat species, including horseshoe bats but is usually judged to be difficult for correct age classification due to strong interindividual variation (Davis 1963; Davis and Hitchcock 1965; Dietz and Helversen 2004; Mazák 1963; 1965; Pearson et al. 1952; Racey 1974; Stebbings 1968), however regarded to be reliable to distinguish up to 14 months old from older horseshoe bats (Andersen 1917; Gaisler 1960, 1966; Gaisler and Titlbach 1964; Rollinat and Trouessart 1897). In some horseshoe bat species these changes might be obscured by the occurrence of different age-independent colour phases (Young 1975).

Reproductive criteria

Reproductive criteria are of limited usefulness for age determination as they occur repeatedly during each reproductive season. However in our study population the onset of reproduction could be used to sort the bats into sexually immature (= nulliparous) and mature (= parous) individuals. As nearly all of the females gave birth for the first time in an age of approximately 24 months (see puberty), the reproductive criteria can be used to sort the females in the two age categories “more” and “less” than 24 months.

2. Reproductive classification

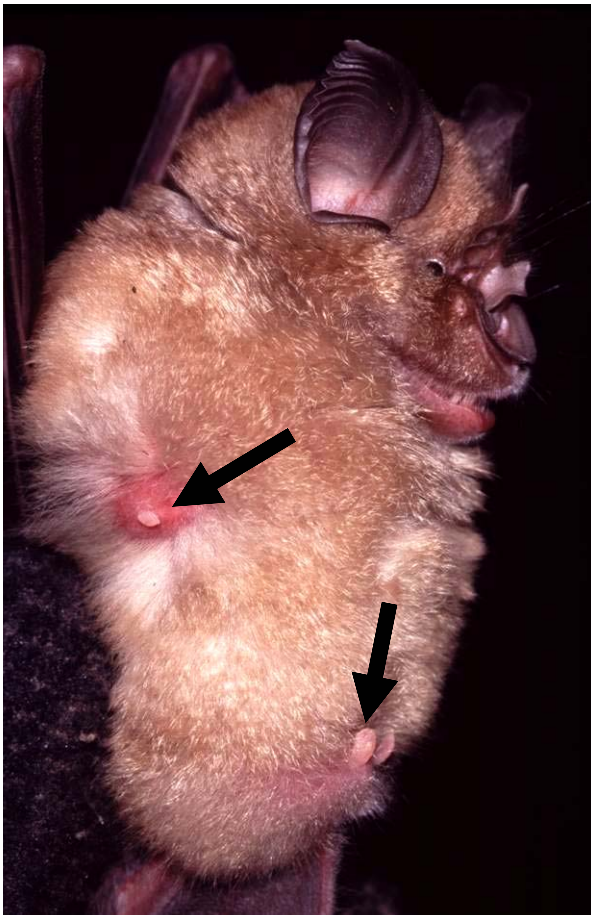


Figure 2: Adult lactating female *Rhinolophus ferrumequinum* showing one of the thoracic (upper arrow) and the pubic (lower arrow) nipples.

Thoracic nipples

In *R. ferrumequinum* thoracic nipples of nulliparous females are rudimentary (of the same size as in males) and covered by dense hair (Plate 1 and 2). They start to grow during the first pregnancy and reach nearly the size of multiparous females at first parturition, but still being much more turgid (rounded in diameter) and not being cornified (Plate 1). During the first lactation period they get more and more flattened, flaccid, and cornified and do not differ from multiparous females anymore (Plate 1). In a very few females the thoracic nipples stayed in an intermediate position between nulliparous and multiparous females and mostly had a light greyish colouration, most probably due to the loss of the juvenile. In multiparous females the nipple cornification also increases with the duration of lactation (Plate 1). Before lactation the nipples are usually greyish and get reddish with the onset of lactation due to an increased vascularization. Very often some injuries and haematomas can be found around the nipples of females with older young, most probably related to the stronger teeth. This becomes especially true during weaning, when mother and young struggle and the mother have to fend of young that were trying to suckle. Unlike in vespertilionids in *R. ferrumequinum* the mammary glands can not be seen as white areas under skin in the bats leaving the cave in the evening but they are well visible in bats returning to the roost in the morning. Soon after the end of lactation period hair start to grow around the nipples, the nipples get less reddened (as the vascularization is being reduced) and postlactation can be recognized (Plate 1). During winter the nipples of primi- or multiparous females shrink considerably to about half of their length and cornification is reduced but remains stronger than in nulliparous females.

It has been already found that the nipples remain tiny in nulliparous females until the time of first implantation (Gaisler 1960, 1966; Gopalakrishna and Rao 1977; Pearson et al. 1952; Rollinat and Trouessart 1897; Young 1975), accordingly relative nipple size has been found to differ between nulliparous and primi- or multiparous females (Racey 1988) and has been used to assess the reproductive status (Baagøe 1977b; Gaisler 1965; Matthews 1937; Pearson et al. 1952; Racey 1974; Rollinat and Trouessart 1897; Ryberg 1947; Sluiter 1954; Sluiter and Bouman 1951). Unlike in many vespertilionid species (Racey 1974, 1988; own data) but similar to rhinopomatids (own data; Levin pers. com.) the teats of *Rhinolophus ferrumequinum* did not became darkly pigmented during lactation but remain of the same colour than the surrounding skin, only getting reddened from the bites of the juveniles.

False or pubic nipples

Like all Rhinolophids also *R. ferrumequinum* posses additional “holdfast” nipples near the genitalia (Simmons 1993). The young attach to these pubic nipples when resting (Kolb 1950; Matthews 1937), but no milk is produced in the European species (Schilling in Jäckel 1860; Kuhl 1817; Matthews 1937; Rollinat and Trouessart 1895, 1897). We found the pubic nipples to be rudimentary in nulliparous female *R. ferrumequinum* and of the same minute size as in males (Plate 1 and 2). The pubic nipples start to grow only during the first pregnancy and reach at first parturition nearly the size of those of multiparous females, but still being much more rounded in diameter and not cornified (Plate 1). During the first lactation period they get more elongated, flattened and cornified and do not differ much from multiparous females anymore, reaching a mean size of 4.2 mm and a maximum of 5.0 mm (Plate 1). The pubic nipples stay in an enlarged size throughout the rest of the bat’s life. In a very few females the pubic nipples stayed in an intermediate position between nulliparous and multiparaous females, most probably due to the loss of the juvenile. In multiparous females the cornification of the pubic nipples also increased with the duration of lactation and the pubic nipples became more elongated and were often a bit injured and reddened (Plate 1). Soon after the end of the lactation period hair started to grow around the pubic nipples, the small injuries healed and postlactation could be recognized. From the end of lactation to the next birth the pubic nipple shrinked to a bit less than half of their size (from about 4.5 mm length to about 2.0 mm length). In a few multiparous females of unknown age (but mostly being older than at least four years) a strong asymmetry in pubic nipples was found with one of the pubic nipples having the normal size and the other one being very small.

Our observations on the development of the pubic nipples are in accordance with data given by several authors working on horseshoe bats (Gaisler 1960, 1965, 1966; Gopalakrishna and Rao 1977; Kolb 1950; Matthews 1937; Rollinat and Trouessart 1897; Young 1975) and the general observations by Simmons (1993).

Pregnancy

In bats captured at roost entrances during emergence in the evening foetuses were palpable as early as 2 months before birth. In bats captured later in the night the foetus may be obscured by a filled stomach. Even in such cases the foetuses are unmistakable palpable at least 30 days before giving birth. Females usually gave birth when reaching more than 30 gram body mass in the evening. The time of possible palpation of the foetuses is in accordance to the data given by Young (1975) and Ransome (1990).

Puberty

In our study most female *R. ferrumequinum* attained sexual maturity in their second autumn at ages of 15-17 months and gave birth to their first young at an age of approximately 24 months. The prepubertal period is much extended at the northern border of its distribution in England, where the age of females at the birth of their first young varies from 2 to 7 years (Ransome 1990, 1995) most probably due to a poor nutritional status (Wotton 1987). Dinale (1968) found Italian *R. ferrumequinum* to give their first births in an age of 3-4, maybe even 5 years and stated that quite surely no female litters at the age of 2 years. Issel and Issel (1960) report that all four recaptured females had not given birth in an age of 36-38 months, one of them was inseminated in an age of 42 months. Ransome (1995) showed that earlier breeding shortens life in female greater horseshoe bats but does not affect the lifetime reproductive success. He discussed that earlier breeding might be advantageous in situations when the population recovers from a climate induced crash until population stabilizes under the climatic conditions in England. We believe that the nutritional supply in Northern Bulgaria might be the reason for the early sexual maturity in the Bulgarian *R. ferrumequinum* (Wotton 1987). Possibly prey abundance is much higher than in Ransome’s (1995) study area in England leading to reduced intraspecific competition and allowing together with a more favourable and stable climate the Bulgarian bats to gain enough body reserves to reproduce early (Newton 1989). On the other hand the studies in Germany (Issel and Issel 1960) and Italy (Dinale 1968) were carried out in a time of drastically shrinking populations of the species leading to extinction in Germany (Roer 1984) and a strong population decline in most European countries (Horáček 1984). Late reproduction is characteristic for shrinking populations (Charlesworth 1980).

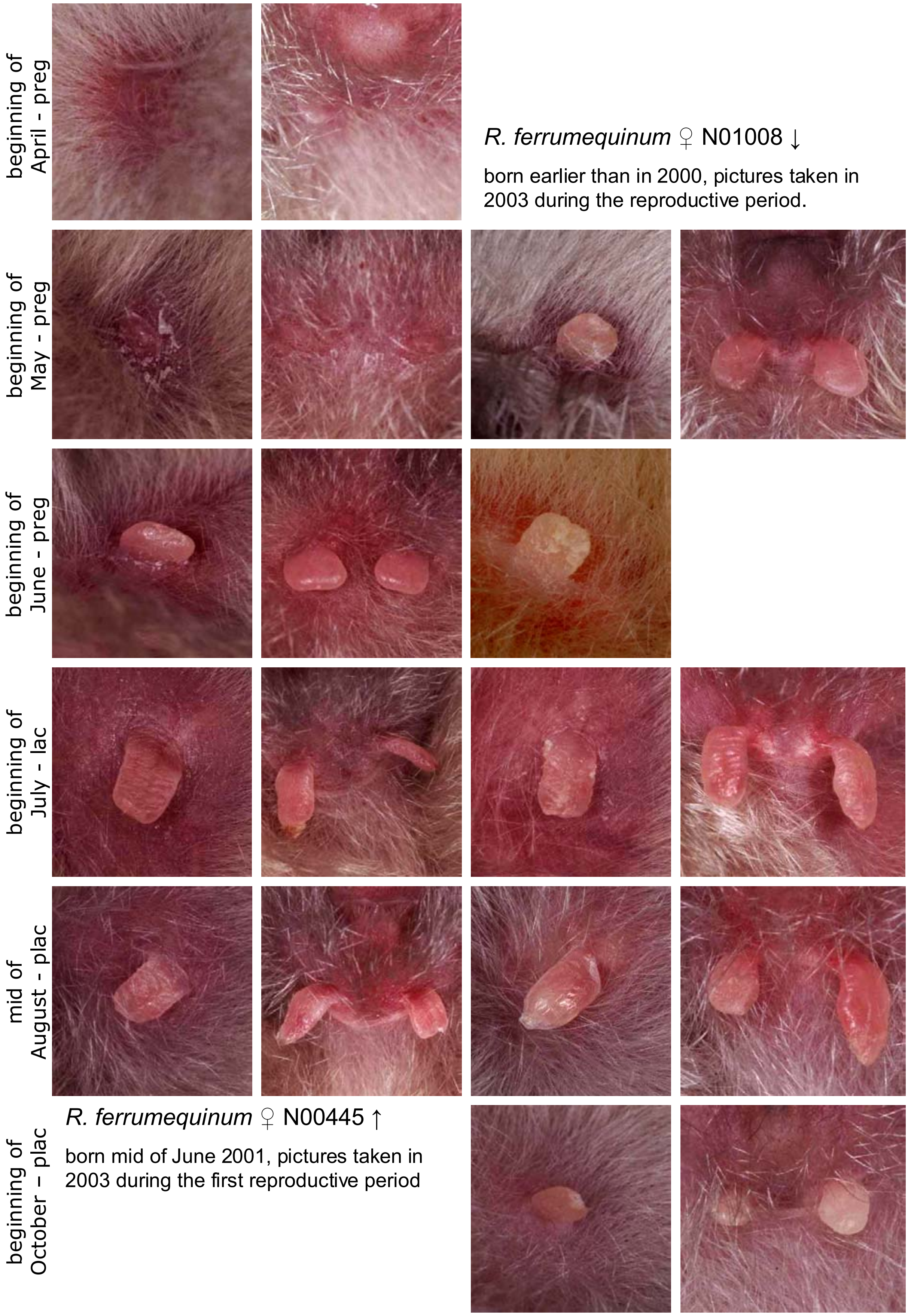
Figure 3: 37 months old adult lactating female *Rhinolophus ferrumequinum* with an approximately 23 days old young attached to the pubic nipples.

CONCLUSIONS

Our results in evaluating different characters to assign living female greater horseshoe bats to different age classes are in accordance to the experiences given by Issel and Issel (1960) and the extensive data for *R. hipposideros* by Gaisler (1960, 1966). We found a combination of characters like the shape of the finger joints, fur colouration and the size and shape of the thoracic and pubic nipples valuable to sort female *R. ferrumequinum* captured in the warm season of the year into several age- and reproductive classes (following Racey 1974; Table 1): Juvenile – a bat which has not reached adult dimensions, characterized by unfused epiphyseal growth plates, a sparse and grey pelage and minute, often hardly visible thoracic and pubic nipples. These bats are less than 2 months old. Nulliparous I – a female bat which has attained adult dimensions and is sexual immature (= subadult). Being characterized by a dense grey fur, often elongated finger joints (but with closed epiphyseal growth plates) and very small to minute thoracic and pubic nipples. These bats are more than 2 and less than 16 months old. Nulliparous II or primiparous – a female bat which has attained adult dimensions and might be sexual immature (= subadult) or has reached sexual maturity but has not given birth. This age class is characterized by a dense and yellowish-brownish fur, but most bats have a darker pelage in the facial parts. The finger joints have the same shape as adults. Size of the thoracic and pubic nipples varies from very small to growing or adult size. These females are 22-28 months old. Parous – a female bat which has given birth. It may be inseminated or not, pregnant or lactating. These bats have knobbly finger joints, a dense and yellowish-brownish fur, no darker pelage in the facial parts, and (mostly) fully developed thoracic and pubic nipples. They are more than 33 months old. Within this group bats with heavily worn teeth can be regarded as very old ones, but no detailed discrimination seems to be possible, limiting age classification to a quite short time in a bat that has been shown to live up to 30 ½ years (Caubère et al. 1984).

Table 1: Character matrix of different age classes of female *Rhinolophus ferrumequinum* inferred from recaptures of marked juveniles. The sample size gives the number of marked and recaptured individuals of the birth-cohort of 2001 only. In the years 2001-2003 a total of 218 juvenile females were marked.

Age in months (n)	**Growth plates**	**Fur and Colouration**	**Nipples**	**Pubic nipples**	**Reproduction**
Birth mostly mid of June					
< 2 months (67)	Open	Sparse and short light grey fur	Very small	Very small	None
3-4 months (40)	Fused, joints elongated	Fur is less dense than in adults and light grey	Very small	Very small	None
First hibernation					
10-11 months (9)	Fused, joints rounded, sometimes elongated	Dense but greyish fur	Very small	Very small	None
12-16 months (22)	Fused, joints rounded	Dense but greyish fur	Very small	Very small	None
Second hibernation					
22-24 months (10)	Fused, joints rounded	Dense and yellowish-brown fur but in most bats darker pelage in the facial parts	Sometimes very small, in most bats growing.	Sometimes very small, in most bats growing.	In most females first pregnancy, foetuses palpable in the field
25-28 months (21)	Fused, joints rounded	Dense and yellowish-brown fur but in most bats darker pelage in the facial parts	In most bats adult size, only in a few bats very small.	In most bats adult size, only in a few bats very small.	In most females first lactation and postlactation period
Third hibernation					
> 33 months (16)	Fused, joints rounded	Typical dense yellowish-brown fur, no darker pelage in the facial parts.	Adult size	Adult size	All females take part in reproduction



R. ferrumequinum ♀ N01008 ↓

born earlier than in 2000, pictures taken in 2003 during the reproductive period.

R. ferrumequinum ♀ N00445 ↑

born mid of June 2001, pictures taken in 2003 during the first reproductive period

Plate 1: Changes in size and shape of thoracic and pubic nipples in a 22-26 months old primiparous female *R. ferrumequinum* (left) and in an older multiparous female (right).

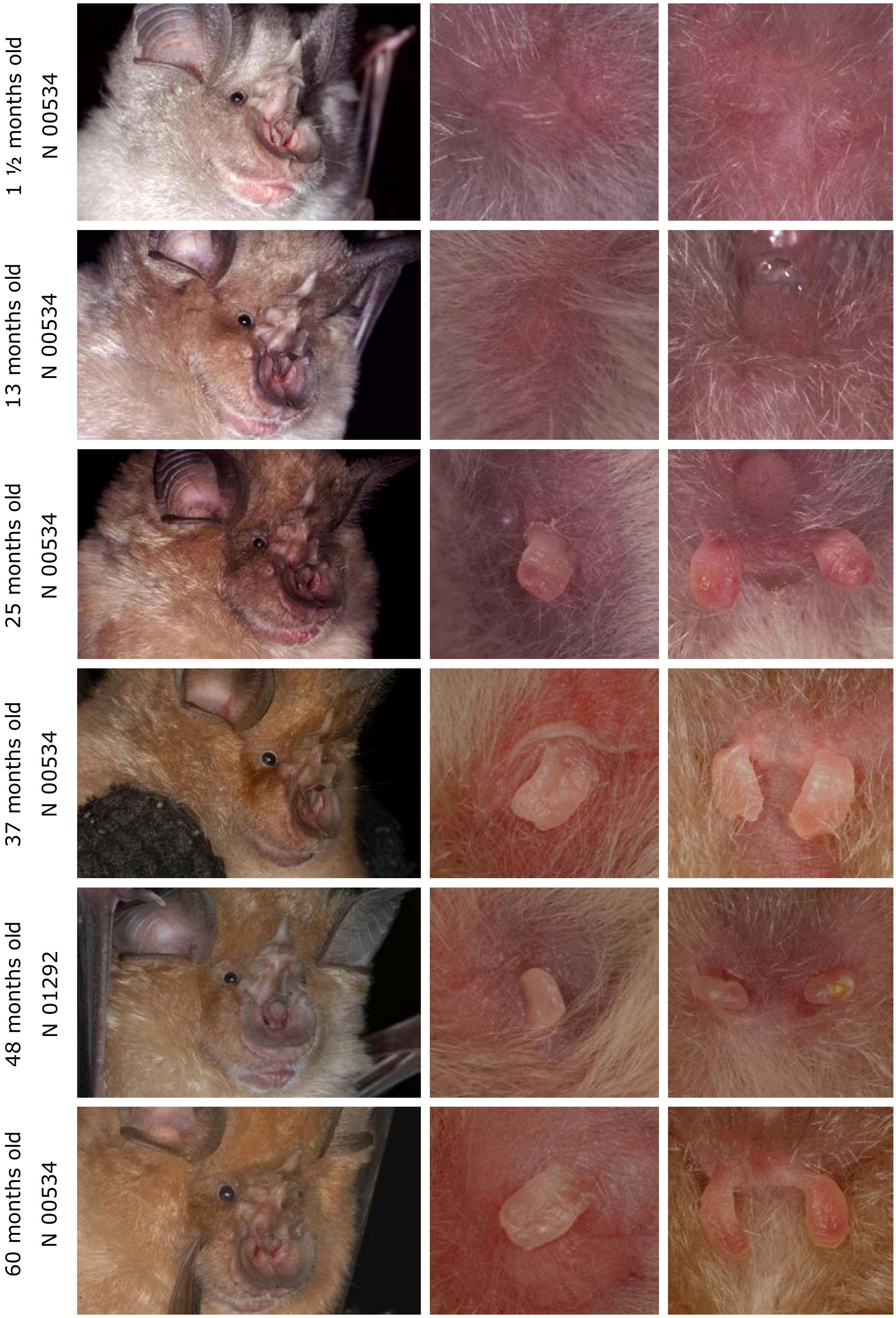


Plate 2: Changes in colouration and nipple-morphology in a female *R. ferrumequinum* marked as juvenile from an age of 1 ½ months till an age of 60 months. Note: pictures in the 5th line are from an other individual.

ACKNOWLEDGEMENTS

Our study in Bulgaria was made possible through the close cooperation with B.M. Siemers and his permanent support, sustenance and help is highly acknowledged. We are also indebted to the Bulgarian Bat Research and Protection group, especially to T. Ivanova. We are grateful for the help received in many respects of the project, for organising permits and showing the roost sites. We want to thank especially S. Merdschanov, D. Merdschanova, K. Christov, I. Borrisov and S. Staneva for spending so many nights out with us to help in catching bats, B.P. Petrov for logistical help and E. Dimanova for her kind hospitality and love.

This research was funded by grants of the Graduiertenförderung des Landes Baden-Württemberg to CD and of the Deutsche Bundesstiftung Umwelt to ID.

LITERATURE CITED

ADAMS, R.A. 1996. Size-specific resource use in juvenile little brown bats, *Myotis lucifugus* (Chiroptera: Vespertilionidae): Is there an ontogenetic shift? Canadian Journal of Zoology 74: 1204-1210.

ADAMS, R.A. 1997. Onset of volancy and foraging patterns of juvenile little brown bats, *Myotis lucifugus*. Journal of Mammalogy 78: 239-246.

ADAMS, R.A. 2000. Wing ontogeny, shifting niche dimensions, and adaptive landscapes. Pp. 275-315 in Ontogeny, functional ecology, and evolution of bats (R.A. ADAMS AND S.C. PEDERSEN, eds.); Cambridge University Press, Cambridge, United Kingdom.

ANDERSEN, K. 1917. On the determination of age in bats. Journal of the Bombay Natural History Society 25: 249-259.

ANTHONY, E.L.P. 1988. Age determination in bats. Pp. 47-58 in Ecological and Behavioral Methods for the Study of bats (T.H. KUNZ, ed.); Smithsonian Institution Press, Washington D.C., United States.

ANTHONY, E.L.P. AND T.H. KUNZ. 1977. Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. Ecology 58: 775-786.

BAAGOE, H.J. 1977a. Choice of age criteria and judgement of the attainment of full grown size in bats. Videnskabelige meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn 140: 93-110.

BAAGOE, H.J. 1977b. Age determination in bats. Videnskabelige meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn 140: 53 -92.

BAPTISTA, T.L., C.S. RICHARDSON AND T.H. KUNZ. 2000. Postnatal growth and age estimation in free-ranging bats: a comparison of longitudinal and cross-sectional sampling methods. Journal of Mammalogy 81: 709-718.

BAKER, G.B., L.F. LUMSDEN, E.B. DETTMANN, N.K. SCHEDVIN, M. SCHULZ, D. WATKINS AND L. JANSEN. 2001. The effect of forearm bands on insectivorous bats (Microchiroptera) in Australia. Wildlife Research 28: 229-237.

BARCLAY, R.M.R. 1989. The effect of reproductive condition on the foraging behavior of female hoary bats, *Lasiurus cinereus*. Behavioral Ecology and Sociobiology 24: 31-37.

BARCLAY, R.M.R. 1995. Does energy or calcium availability constrain reproduction by bats? Symposia of the Zoological Society of London 67: 245-258.

BARCLAY, R.M.R. AND G.P. BELL. 1988. Marking and observational techniques. Pp. 59-76 in Ecological and Behavioral Methods for the Study of bats (T.H. KUNZ, ed.). Smithsonian Institution Press, Washington D.C., United States.

BARRETT-HAMILTON, G.E.H. 1910. A history of British mammals I., 263 pp.; London.

BATULEVICIUS, D., N. PAUZIENE AND D.H. PAUZA. 2001. Dental incremental lines in some small species of the European vespertilionid bats. Acta Theriologica 46: 33-42.

BELWOOD, J.J. AND M.B. FENTON. 1976. Variation in the diet of *Myotis lucifugus* (Chiroptera: Vespertilionidae). Canadian Journal of Zoology 54: 1674-1678.

BURNETT, C.D. AND T.H. KUNZ. 1982. Growth rates and age estimation in *Eptesicus fuscus* and comparison with *Myotis lucifugus*. Journal of Mammalogy 63: 33-41.

CASE, T.J. 1978. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. The quarterly review of biology 53: 243-282.

CAUBÈRE, B., P. GAUCHER AND J.F. JULIEN. 1984: Un record mondial de longévité *in natura* pour un chiroptère insectivore ? – Revue d'écologie (terre et la vie) 39: 351-353.

CHARLESWORTH, B. 1980. Evolution in age-structured populations, 320 pp.; Cambridge University Press, Cambridge, United Kingdom.

CHENG, H.C. AND L.L. LEE. 2002. Postnatal growth, age estimation, and sexual maturity in the Formosan leaf-nosed bat (*Hipposideros terasensis*). Journal of Mammalogy 83: 785-793.

DAVIS, R.B., C.F. HERREID AND H.L. SHORT. 1962. Mexican free-tailed bats in Texas. Ecology Monographs 32: 311-346.

DAVIS, W.H. 1963. Aging bats in winter. Transactions of the Kentucky Academy of Sciences 24: 28-30.

DAVIS, W.H. AND H.B. HITCHCOCK. 1965. Biology and migration of the bat, *Myotis lucifugus*, in New England. Journal of Mammalogy 46: 296-313.

DE PAZ, O. 1986. Age estimation and postnatal growth of the greater mouse-eared bat *Myotis myotis* in Guadalajara, Spain. Mammalia 50: 243-251.

DIETZ, C. AND O. VON HELVERSEN. 2004. Identification Key to the Bats of Europe. 72 pp. Electronical publication, version 1.0, available at www.uni-tuebingen.de/tierphys/Kontakt/mitarbeiter_seiten/ dietz.htm.

DIETZ, C., I. DIETZ, T. IVANOVA AND B.M. SIEMERS. 2006. Effects of forearm bands on horseshoe bats (Chiroptera: Rhinolophidae). Acta Chiropterologica 8: 523-535.

DIETZ, C., I. DIETZ AND B. M. SIEMERS. 2007. Growth of horseshoe bats (Chiroptera: Rhinolophidae) in temperate continental conditions and the influence of climate. Mammalian Biology 72: 129-144.

Dinale, G. 1968. Studi sui chirotteri Italiani VII. Sul raggiungimento della maturita sessuale nei Chirotteri europei ed in particolare nei Rhinolophidae. Archivio Zoologico Italiano 53: 51-71.

Fenton, M.B. 1970. The deciduous dentition and its replacement in *Myotis lucifugus*. Canadian Journal of Zoology 48: 817-820.

Forsyth, D.J. 1976. A field study of growth and development of nestling masked shrews (*Sorex cinereus*). Journal of Mammalogy 57: 708-721.

Gaisler, J. 1960. Postnatale Entwicklung der Kleinen Hufeisennase (*Rhinolophus hipposideros*) unter natürlichen Bedingungen. Symposium Theriologicum 1960: 118-125.

Gaisler, J. 1965. The female sexual cycle and reproduction in the lesser horseshoe bat (*Rhinolophus hipposideros hipposideros*). Vestnik Ceskoslovenske Spolecnosti Zoologicke 29: 336-352.

Gaisler, J. 1966. Reproduction in the lesser horseshoe bat (*Rhinolophus hipposideros hipposideros*). Bijdragen tot de Dierkunde 36: 45-64.

Gaisler, J. 1989. The r-K selection model and life-history strategies in bats. Pp. 117-124 in European Bat Research 1987 (V. Hanák, I. Horáček and J. Gaisler, eds.); Praha.

Gaisler, J. and M. Titlbach. 1964. The male sexual cycle in the lesser horseshoe bat (*Rhinolophus hipposideros hipposideros*). Vestnik Ceskoslovenske Spolecnosti Zoologicke 28: 268-277.

Geiger, H., M. Lehnert and C. Kallasch. 1996. Zur Alterseinstufung von Wasserfledermäusen (*Myotis daubentoni*) mit Hilfe des Unterlippenflecks („chin-spot"). Nyctalus (N.F.) 6: 23-28.

Gopalakrishna, A. and K.V.B. Rao. 1977. Breeding habits and associated phenomena in some Indian bats, Part II: *Rhinolophus rouxi*. Journal of the Bombay Natural History Society 74: 213-219.

Hall, J.S., R.J. Cloutier and D.R. Griffin. 1957. Longevity records and notes on tooth wear of bats. Journal of Mammalogy 38: 407-409.

Hamilton, I.M. and R.M.R. Barclay. 1998. Diets of juvenile, yearling, and adult big brown bats (*Eptesicus fuscus*) in southeastern Alberta. Journal of Mammalogy 79: 764-771.

Happold, D.C.D. and M. Happold. 1998. Effects of bat-bands and banding on a population of *Pipistrellus nanus* in Malawi. Zeitschrift für Säugetierkunde 63: 65-78.

HENRY, M., D.W. THOMAS, R. VAUDRY AND M. CARRIER. 2002. Foraging distances and home range of pregnant and lactating little brown bats (*Myotis lucifugus*). Journal of Mammalogy 83: 767-774.

HORÁČEK, I. 1984. Remarks on the causality of population decline in European bats. Myotis 21-22: 138-147.

HOYING, K.M. AND T.H. KUNZ. 1998. Variation in size at birth and post-natal growth in the insectivorous bat *Pipistrellus subflavus.* Journal of Zoology (London) 245: 15-27.

HUGHES, P.M., J.M.V. RAYNER AND G. JONES. 1995. Ontogeny of „true" flight and other aspects of growth in the bat *Pipistrellus pipistrellus*. Journal of Zoology London 235: 291-318.

ISSEL, B. AND W. ISSEL. 1960. Beringungsergebnisse an der Großen Hufeisennase (*Rhinolophus ferrumequinum*) in Bayern. Bonner Zoologische Beiträge, Sonderheft 11/ 1960: 124-142.

JÄCKEL, A.J. 1860. Die bayerischen Chiropteren. Ein Beitrag zur Kenntnis der Lebensweise und der geographischen Verbreitung der deutschen Fledermäuse. Abhandlungen des zoologisch-mineralogischen Vereines in Regensburg 8: 1-110; Regensburg.

JONES, C. 1967. Growth, development, and wing loading in the evening bat, *Nycticeius humeralis*. Journal of Mammalogy 48: 1-19.

JONES, G., P.L. DUVERGÉ AND R.D. RANSOME. 1995. Conservation biology of an endangered species: field studies of greater horseshoe bats. Symposia of the Zoological Society of London 67: 309-324.

JONES, G., T. GORDON AND J. NIGHTINGALE. 1992. Sex and age differences in the echolocation calls of the lesser horseshoe bat, *Rhinolophus hipposideros*. Mammalia 56: 189-193.

JONES, G. AND T. KOKUREWICZ. 1994. Sex and age variation in echolocation calls and flight morphology of Daubenton`s bats *Myotis daubentonii*. Mammalia 58: 41-50.

KALCOUNIS, M.C. AND R.M. BRIGHAM. 1995. Intraspecific variation in wing loading affects habitat use by little brown bats (*Myotis lucifugus*). Canadian Journal of Zoology 73: 89-95.

KLEIMAN, D.G. 1969. Maternal care, growth rate, and development in the noctule (*Nyctalus noctula*), pipistrelle (*Pipistrellus pipistrellus*), and serotine (*Eptesicus serotinus*) bats. Journal of Zoology 157: 187-211.

KLÍMA, M. AND J. GAISLER. 1967. Study on growth of juvenile pelage in bats, II. Rhinolophidae, Hipposideridae. Zoologicke Listy 16: 343-354.

KOKUREWICZ, T. 2004. Sex and age related habitat selection and mass dynamics of Daubenton's bats *Myotis daubentonii* hibernating in natural conditions. Acta Chiropterologica 6: 121-144.

KOLB, A. 1950. Beiträge zur Biologie einheimischer Fledermäuse. Zoologische Jahrbücher (Systematik, Ökologie und Geographie) 78: 547-572.

KRÁTKY, J. 1981. Postnatale Entwicklung der Wasserfledermaus, *Myotis daubentonii* und bisherige Kenntnis dieser Problematik im Rahmen der Unterordnung Microchiroptera (Mammalia: Chiroptera). – Folia Musei Rerum Naturalium Bohemiae Occidentalis 16: 1-34.

KUHL, H. 1817.Die Deutschen Fledermäuse. Annalen der Wetterauischen Gesellschaft für die gesamte Naturkunde 4: 11-49; Hanau, Germany.

KUNZ, T.H. 1973. Population studies of the cave bat (*Myotis velifer*): reproduction, growth and development. Occasional papers of the Museum for Natural History. University of Kansas 15: 1-43.

KUNZ, T.H. AND E.L.P. ANTHONY. 1982. Age estimation and post-natal growth in the bat *Myotis lucifugus*. Journal of Mammalogy 63: 23-32.

MATHEWS, L.H. 1937. The female sexual cycle in the British horse-shoe bats, *Rhinolophus ferrum-equinum insulanus* and *R. hipposideros minutus.* Transactions of the Zoological Society of London 32: 224-266.

MAZÁK, V. 1963. Hair growth in large mouse-eared bat, *Myotis myotis myotis*, during its praenatal and early postnatal life. Acta Societatis Zoologicae Bohemoslovenicae 27: 234-242.

MAZÁK, V. 1965. Changes in pelage of *Myotis myotis* (Mammalia, Chiroptera). Vestnik Ceskoslovenske Spolecnosti Zoologicke, Acta Societatis Zoologicae Bohemoslovenicae 29: 368-376.

MORRIS, P. 1972. A review of mammalian age determination methods. Mammal Review 2: 69-104.

NEWTON, I. 1989. Lifetime reproduction in birds. Academic Press, London, United Kingdom.

O'DONNELL, C.F.J. 2002. Influence of sex and reproductive status on nocturnal activity of long-tailed bats (*Chalinolobus tuberculatus*). Journal of Mammalogy 83: 794-803.

PATTERSON, B.D., M.R. WILLIG AND R.D. STEVENS. 2003. Trophic strategies, niche partitioning, and patterns of ecological organization. Pp. 536-579 in Bat ecology (T.H. KUNZ AND M.B. FENTON, eds.); The University of Chicago Press, Chicago, United States.

PEARSON, O.P., M.R. KOFORD AND A.K. PEARSON. 1952. Reproduction of the lump-nosed bat (*Corynorhinus rafinesquei*) in California. Journal of Mammalogy 33: 273-320.

PERRY, A.E. AND C.F. HERREID. 1969. Comparison of the tooth-wear and lens-weight methods of age determination in the guano bat*, Tadarida brasiliensis mexicana*. Journal of Mammalogy 50: 357-360.

PHILIPPS, C.J., B. STEINBERG AND T.H. KUNZ. 1982. Dentin, cementum, and age determination in bats: a critical evaluation. Journal of Mammalogy 63: 197-207.

POLIS, G.A. 1984. Age structure component of niche width and intraspecific resource partitioning: can age groups function as ecological species? The American Naturalist 123: 541-564.

RACEY, P.A. 1974. Ageing and assessment of reproductive status of pipistrelle bats, *Pipistrellus pipistrellus*. Journal of Zoology 173: 264-271.

RACEY, P.A. 1988. Reproductive assessment in bats. Pp. 31-45 in Ecological and Behavioral Methods for the Study of bats (T.H. KUNZ, ed.); Smithsonian Institution Press.

RACEY, P.A. AND A.C. ENTWISTLE. 2000. Life-history and reproductive strategies of bats. Pp. 363-414 in Reproductive biology of bats (E.G. CRICHTON AND P.H. KRUTZSCH, eds.); Academic Press San Diego.

RACEY, P.A. AND S.M. SWIFT. 1985. Feeding ecology of *Pipistrellus pipistrellus* during pregnancy and lactation. I. Foraging behavior. Journal of Animal Ecology 54: 205-215.

RANSOME, R.D. 1989. Population changes of greater horseshoe bats studied near Bristol over the past twenty-six years. –Biological Journal of the Linnean Society 38: 71-82.

RANSOME, R. 1990. The natural history of hibernating bats, 235 pp.; Christopher Helm, London, United Kingdom.

RANSOME, R.D. 1995. Earlier breeding shortens life in female greater horseshoe bats. Philosophical Transactions of the Royal Society of London B 350: 153-161.

RANSOME, R.D. 1998. The impact of maternity roost conditions on populations of greater horseshoe bats. English Nature Research Reports No. 292, 80 pp. English Nature.

REITER, G. 2004. Postnatal growth and reproductive biology of *Rhinolophus hipposideros* (Chiroptera: Rhinolophidae). – Journal of Zoology (London) 262: 231-241.

RICHARDSON, P.W. 1994. A new method of distinguishing Daubenton´s bats (*Myotis daubentonii*) up to one year old from adults. Journal of Zoology London 233: 307-309.

ROER, H. 1984. Zur Bestandssituation von *Rhinolophus ferrumequinum* und *Rhinolophus hipposideros* im westlichen Mitteleuropa. Myotis 21-22: 122-131.

ROLLINAT, R. AND E. TROUESSART. 1895. Sur la reproduction des chauves-souris. Bulletin de la Societé Zoologique de France 20: 25-28.

ROLLINAT, R. AND E. TROUESSART. 1897. Sur la reproduction des chauves-souris. II. Les Rhinolophes (1). Mémoires de la Societé Zoologique de France 10: 114-138.

ROLSETH, S.L., C.E. KOEHLER AND R.M.R. BARCLAY. 1994. Differences in the diets of juvenile and adult hoary bats, *Lasiurus cinereus*. Journal of Mammalogy 75: 394-398.

RUSSO, D., G. JONES AND M. MUCEDDA. 2001. Influence of age, sex and body size on echolocation calls of Mediterranean and Mehely's horseshoe bats, *Rhinolophus euryale* and *R. mehelyi* (Chiroptera: Rhinolophidae). Mammalia 65: 429-436.

RYBÁŘ, P. 1969. Ossification of bones as age criterion in bats (Chrioptera). Prace a studie-Prir Pardubice 1: 115-136.

RYBÁŘ, P. 1971. On the problems of practical use of the ossification of bones as age criterion in the bats (Microchiroptera). Prace a studie-Prir Pardubice 3: 97-121.

RYBÁŘ, P. 1972. Eine Möglichkeit der Altersbestimmung von Fledermäusen nach der Ossifikation der Flügelknochen. Nyctalus 4: 27-34; Halle/ Saale.

RYBERG, O. 1947. Studies on bats and bat parasites. 330 pp.; Bokförlaget Svensk Natur, Stockholm.

SENDOR, T. AND M. SIMON. 2003. Population dynamics of the pipistrelle bat: effects of sex, age and winter weather on seasonal survival. Journal of Animal Ecology 72: 308-320.

SHARIFI, M. 2004. Postnatal growth and age estimation in the Mehely’s horseshoe bat (*Rhinolophus mehelyi*). Acta Chiropterologica 6: 155-161.

SHARIFI, M. AND V. AKMALI. 2006. Postnatal growth in the Lesser Mouse-eared bat, *Myotis blythii*, in captivity. Zoology in the Middle East 37: 13-20.

SIEMERS, B.M., K. BEEDHOLM, C. DIETZ, I. DIETZ AND T. IVANOVA. 2005. Is species identity, sex, age or individual quality conveyed by echolocation call frequency in European horseshoe bats? Acta Chiropterologica 7: 259-274.

SIMMONS, N.B. 1993. Morphology, function, and phylogenetic significance of pubic nipples in bats (Mammalia: Chiroptera). American Museum Novitates 3077: 37 pp.

SLUITER, J.W. 1954. Sexual maturity in bats of the genus *Myotis*. II. Females of *M. mystacinus* and supplementary data of female *M. myotis* and *M. emarginatus*. Koninklije Nederlandse Akademie van Wetenschappen, Proceedings of the Section of Sciences 57 C: 695-700.

SLUITER, J.W. 1960. Reproductive rate of the bat *Rhinolophus hipposideros*. Proceedings. Koninklije Nederlandse Akademie van Wetenschappen 63 C: 283-393.

SLUITER, J.W. 1961. Abrasion of teeth in connection with age in the bat *Myotis myotis*. – Proceedings. Koninklije Nederlandse Akademie van Wetenschappen 64 C: 424-434.

SLUITER, J.W. AND M. BOUMAN. 1951. Sexual maturity in bats of the genus *Myotis*. I. Size and histology of the reproductive organs during hibernation in connection with age and wear of the teeth in female *Myotis myotis* and *Myotis emarginatus*. Proceedings. Koninklije Nederlandse Akademie van Wetenschappen 54 C: 594-601.

SMIRNOV, D.G. AND K. TSYTSULINA. 2003. The ontogeny of the baculum in *Nyctalus noctula* and *Vespertilio murinus* (Chiroptera: Vespertilionidae). Acta Chiropterologica 5: 117-123.

STEBBINGS, R.E. 1968. Measurements, composition and behaviour of a large colony of the bat *Pipistrellus pipistrellus*. Journal of Zoology (London) 156: 15-33.

TRAPPMANN, C. 1999. Anmerkungen zur Altersbestimmung bei der Fransenfledermaus *Myotis nattereri*. Nyctalus (N.F.) 7: 121-135.

TSCHUMY, W.O. 1982. Competition between juveniles and adults in age-structured populations. Theoretical Population Biology 21: 255-268.

WOTTON, J.T. 1987. The effects of body mass, phylogeny, habitat, and trophic level on mammalian age at first reproduction. Evolution 41: 732-749.

YOUNG, R.A. 1975. Aging criteria, pelage colour polymorphism and moulting in *Rhinolophus megaphyllus* (Chiroptera) from south-eastern Queensland, Australia. Mammalia 39: 75-111.

YOUNG, R.A. 2001. The eastern horseshoe bat, *Rhinolophus megaphyllus*, in south-east Queensland, Australia: colony demography and dynamics, activity levels, seasonal weight changes, and capture-recapture analysis. Wildlife Research 28: 425-434.

Chapter 3

Effects of forearm bands on horseshoe bats (Chiroptera: Rhinolophidae)

By Christian Dietz, Isabel Dietz, Teodora Ivanova and Björn. M. Siemers

The ms. was published in:

Acta Chiropterologica 8 (2): 523-535.

Received 05.12.2005

Accepted 25.04.2006

Printed 2006

Effects of forearm bands on horseshoe bats (Chiroptera: Rhinolophidae)

Christian Dietz[1], Isabel Dietz[1], Teodora Ivanova[2], and Björn M. Siemers[1]

[1] Animal Physiology, Zoological Institute, Tübingen University, Auf der Morgenstelle 28, 72076 Tübingen; Germany. Email: Christian.Dietz@uni-tuebingen.de

[2] National Museum of Natural History, Tsar Osvoboditel Blvd. 1, Sofia 1000; Bulgaria

ABSTRACT

We assessed effects of forearm bands on three species of horseshoe bats (*Rhinolophus ferrumequinum*, *R. euryale* and *R. mehelyi*) marked for studies on regional movements and colony structure in Northern Bulgaria. Overall, more than 85% of the 580 recaptured individuals showed no negative impact of the banding. We had to note, however, slight or severe injuries in 7.6 and 6.4% of the bats, respectively. Injury rates varied greatly according to species and ring sizes. The use of the smaller of two tested ring sizes caused major injury rates of more than 60 % of the recaptured *R. mehelyi*. But even in *R. ferrumequinum*, for which we obtained the largest sample size, and for which the recommended ring size is well-established, carefully fitted forearm bands caused injuries in 9.3 % of the recaptures, an injury rate that is much higher than in most vespertilionid bat species. The main reason for the sensitivity of the horseshoe bats to ringing was that the ring rubbed raw the bats' propatagium; the resulting injuries led to growing scars and infections. We compare published and unpublished injury rates of 28 bat species with our results and discuss the use of alternative marking methods. We suggest that banding of horseshoe bats should be limited to well defined projects and only used if the study populations are in a good preservation condition and long term effects of the marking method can be monitored.

Key words: ringing, marking methods, *Rhinolophus*, Vespertilionidae

INTRODUCTION

To address research questions such as spatial movement, dispersal, longevity, social structure and mating system, reliable marking techniques are necessary to ensure the recognition of individuals over extended periods of time. In birds and bats the use of individually numbered rings is the most widespread method when it comes to the study of large-scale movements and migration (Calvo and Furness, 1992). Dating back to the studies of Eisentraut and Griffin in the beginning of the 20th century (Eisentraut, 1934, 1960; Griffin, 1934), marking bats with aluminium bands at the forearm is a standard method for studying bat migration (Barclay and Bell, 1988). In the United States, bird bands were initially placed around the bats' legs (Allen, 1921), but since the studies of Trapido and Crowe (1946) bats have been banded there around the forearm like in Europe (Eisentraut, 1934). However, bird rings have subsequently been found to cause severe injuries (Hooper and Hooper, 1956; Hitchcock, 1957; Davis, 1960, 1961; Herreid *et al.*, 1960), so special bat rings have been developed (Issel, 1951; Bels, 1952; Casteret cited in Hooper and Hooper, 1956, Herreid *et al.*, 1960). To further decrease injury rates, harder and yet lighter materials of the bat bands came into use and the edges were smoothed (Eisentraut, 1960; Zöphel and Hiebsch, 1994). Nevertheless, several authors pointed out that bats can have severe problems with bat rings (Bopp, 1958; Issel and Issel, 1960; Dinale, 1965; Richter, 1970; Sluiter *et al.*, 1971; Bradbury, 1977). From a combination with stress caused by the regular capture of bats at their roosts, their handling and disturbance together with a high risk of injuries, negative effects on the populations were noted (Dinale, 1965; Stebbings, 1969; Richter, 1970; Bork, 1972; Hiebsch, 1972; Rybář, 1973). Improper banding technique or too small rings were even shown to cause skeletal damages in juvenile bats (Perry and Beckett, 1966). The decline of the European bat populations since the 1970s (e.g. Daan *et al.*, 1980; Horáček, 1984; Stebbings, 1988) has been linked partially to the mass banding of bats. The strongest negative effects were attributed to the disturbance in mass hibernacula and nursery colonies as well as to the ringing of especially sensitive species such as the horseshoe bats (Beaucournu, 1962; Feldmann, 1967; Saint-Girons and Saint-Girons, 1968; Brosset *et al.*, 1988). Only very few authors can explicitly rule out banding as a reason for population declines (Ransome, 1989, 1990). As a consequence of the overall population decline ringing has been reduced or abandoned in the 1970s e.g. in western Germany and France (Brosset *et al.*, 1988; Kiefer and Hutterer, 2002). However, in other European countries ringing of bats continued, e.g. in the former German Democratic Republic (DDR) and Czechoslovakia (Zöphel and Hiebsch, 1994; Uhrin *et al.*, 1996). *Rhinolophus hipposideros* was generally excluded from ringing in these countries, because it was considered to be the most sensitive species (Eisentraut, 1960; Gaisler and Hanák, 1969a, b; Richter, 1970; Hiebsch, 1972; Gaisler and Chytil, 2002). Since the 1990s, a strong increase in studies involving the ringing of bats can be observed (Brockmann and Zöphel, 2004), even in regions where ringing had been abandoned for more than two decades (e.g. federal state of Baden-Württemberg, Germany). This 'renaissance' of bat ringing also included species found earlier on to be very sensitive to ringing (Eisentraut, 1960; Richter, 1970; Hiebsch, 1972; Gaisler and Chytil, 2002) like *R. hipposideros* (only low numbers under intensive control with video observation and repeated recaptures: Bontadina *et al.*, 2001; Bontadina and Märki, 2003) or *Barbastella barbastellus* (Brockmann and Zöphel, 2004). It is often emphasised that steadily improved materials, manufacturing techniques and design of the rings, training of bat workers, more sensitive capture methods and the ban of mass-ringing mainly in hibernacula have solved the former problem of severe impacts on the studied populations (e.g. Zöphel and Hiebsch, 1994; Haensel and Ohlendorf, 2004). Unfortunately, quantitative information on the influence of modern ringing methods on bats is rarely available.

Here we report data on ringing efforts, recapture rates and on a systematic evaluation of banding induced injuries that were collected during an ecological study on European horseshoe bats (genus *Rhinolophus*) in Bulgaria. Animals were banded to record regional movements and use of roost sites (Dietz *et al.*, in press), to document growth and onset of reproduction in known free-living individuals as well as to reliably individualize bats that had been radio-tracked to study habitat selection (C. Dietz and I. Dietz, unpublished data). The aim of the present manuscript is to systematically document the influence of different bat rings on the horseshoe bat species *Rhinolophus ferrumequinum, R. euryale* and *R. mehelyi*. Special attention was given to ringing effects on the latter two species, because no detailed published data are available. We ringed only a comparatively small number of individuals, using two different ring sizes that in parallel to this study were also preliminarily recommended by Eurobats (2003). Our data are the first field test for ringing in these species and thereby now provide an empirical basis for ring size suggestions. We compare our own results with an extensive review of literature data, mainly on ringing injuries in vespertilionids, and make suggestions for future marking of rhinolophids.

MATERIAL AND METHODS

Our study area was the hilly karst-area between the lowlands of the Danube and the Balkan mountains in Northern Bulgaria. Bats were marked in the years 2001-2004 at sites around the village Muselievo in the Osam valley (near the town of Nikopol, District Pleven), about 10 km south of the river Danube for ecological studies on colony structure, reproduction, regional movements, growth and habitat use. Most of the bats were captured at a single cave (cave "Nanin Kamăk") inhabited by a colony of up to 1,000 bats (*R. ferrumequinum*, *R. mehelyi*, *R. euryale*, *Myotis capaccinii*, *M. emarginatus* and *Miniopterus schreibersii*). Some more horseshoe bats were captured and marked in the surroundings of Muselievo in alternative day roosts, in night roosts and foraging sites. We used three different size classes of flanged metal bat rings (2.9, 3.5 and 4.2 mm) manufactured by Lambournes (Lambournes Ltd., Leominster, Herefordshire, UK; rings used in 2001) and by Porzana (Porzana Ltd., Wetland-Trust, UK; rings used in 2002-2004). The 3.5 mm magnesium-aluminium alloy rings (Lambournes Ltd.) were used in two colours: green for *R. mehelyi* and red for *R. euryale*. The silver 2.9 and 4.2 mm rings were incoloy bands (nickel-chromium alloy, Lambournes Ltd. in 2001, Porzana Ltd. in 2002-2004). The ring size was chosen according to recommendations of colleagues being experienced in ringing horseshoe bats and recommendations by the Mammal Society and Eurobats: 4.2 mm in *R. ferrumequinum* and 2.9 or 3.5 mm rings in *R. euryale* and *R. mehelyi* (recommendation by the Mammal Society in Mitchell-Jones and McLeish, 1999, 2004 and Eurobats, 2003). In the medium sized horseshoe bats no official recommendation has been available in the beginning of the project, accordingly it was necessary to test several ring sizes in the field. Based on own tests on museum specimen, we decided for the 2.9 and 3.5 mm rings. During our study period, Eurobats (2003) issued a preliminary recommendation of 2.9 to 4.2 mm rings for European medium sized horseshoe bats. Our data now provide an empirical field test for this preliminary recommendations, that, judging from the severe injuries that we had to note especially in *R. mehelyi*, will have to be revised in the future.

The ringing of bats has been carried out by one person (CD) only and the method had been learned in a special training workshop for bat banders held by the ringing centre of Eastern Germany (Sachsen) in 1999. Banding has been continuously practiced on several vespertilionid species in Germany and south-eastern Europe, intense discussion and exchange with several experienced European bat workers helped to improve the ringing method: rings were fitted to the bats' forearm following the instructions given by Stebbings (1978) by placing the band around the forearm and squeezing the band while turning it between thumb and index finger. The bands were closed carefully until the gap between the flanges was small enough to avoid the metacarpals getting trapped in between. Special attention was paid to avoid bents in the ring's shape and to assure that the ring could move free along the forearm.

We captured bats in regular intervals in the course of the above mentioned ecological studies. In banded recaptures, the condition of the bat's wing and skin and of the ring was noted. The recaptured bats were classified into the following groups (following Herreid *et al.*, 1960). No injuries (1): skin without scars, ring in good condition. Slight injuries (2): irritations, first signs of injuries, rawness or worn skin in the area of the ring or scar tissue around the ring and along the margin of the propatagium. If no recent inflammations were present, rings that had penetrated the wing membrane were counted as slight injuries. Severe injuries (3): holes caused by the ring in the propatagium or the arm wing, inflammations, scab and pus around the ring or ring embedded, partially or fully overgrown by skin. In every individual the injury was described and severe injuries were photographed before and after removing the ring. If the ring of a recaptured bat showed no damages it was opened, bent around a metal bar to restore its original form and placed on the bat's opposite wing. If the ring showed any damages or was deformed, a new ring was fitted to the opposite wing. Because of the high injury rate recorded (see below), from August 2003 onward we removed all 2.9 mm rings of recaptured *R. euryale* and *R. mehelyi*, whether injuries were present or not.

The field work was carried out under licence of the Bulgarian authorities (15-RD-08/15.01.2001, 48-00-56/16.01.2001, 8/02.07.2004 RIOSV Pleven, RIOSV Rousse).

RESULTS

Recaptures of marked bats revealed important data on individual movements, colony structure, the onset of reproduction in bats of known age and enabled identification of bats used in radio-tracking before. Overall, more than 85% of the 580 recaptured individuals showed no negative impact of the banding. We had to note, however, slight or severe injuries in the remainder of recaptures. As detailed below, injury rates differed strongly between species, ring-type and different cohorts of marked bats.

Effects of the Ring Size

In *R. euryale* and *R. mehelyi* we compared two ring sizes. In both species a small proportion has been marked with coloured 3.5 mm rings, while most bats received 2.9 mm bands (Table

1). In *R. euryale* the recapture proportion did not differ between both ring types (χ^2 with Haber-correction = 1.59, *d.f.* = 1, *P* = 0.21) and there were no differences of the injury rate between both ring sizes (χ^2 with Haber-correction = 0.25, *d.f.* = 1, *P* = 0.62). In *R. mehelyi* the recapture rate was also not different between both ring types (χ^2 with Haber-correction = 0.04, *d.f.* = 1, *P* = 0.83) but a significant bigger proportion of the recaptured individuals marked with the 2.9 mm bands was injured (χ^2 with Haber-correction = 3.85, *d.f.* = 1, $P < 0.05$). When comparing the total number of recaptures (including repeated recaptures of the same individuals - Table 1) between both ring types, it became even more obvious that the 2.9 mm bands caused a much higher injury rate (χ^2 with Haber-correction = 7.83, *d.f.* = 1, $P < 0.01$).

TABLE 1. Rate of band induced injuries in three species of European horseshoe bats (2001 - 2004). Columns headed with "*n*" contain the number of recaptured individuals per cohort; an individual was assigned to the highest injury stage found during repeated recaptures. Columns headed with "Total" give the total number of recaptures, including repeated recaptures per individual bat. For statistics see text.

			Recaptured bats			Severely injured bats				Slightly injured bats				Total (all injured)			
Species	Ring type (mm)	Banded *n*	*n*	%	total	*n*	%	total	%	*n*	%	total	%	*n*	**%**	total	%
R. ferrumequinum	4.2	**1211**	483	39.9	744	11	2.3	14	1.9	34	7.0	44	5.9	45	**9.3**	58	7.8
R. euryale	3.5	**28**	14	50.0	23	1	7.1	1	4.3	0	0	0	0	1	**7.1**	1	4.3
	2.9	**82**	23	28.0	30	3	13.0	3	10.0	1	4.3	1	3.3	4	**17.4**	4	13.3
R. mehelyi	3.5	**19**	11	57.9	23	1	9.1	1	4.3	0	0	0	0	1	**9.1**	1	4.3
	2.9	**93**	49	52.7	61	21	42.9	22	36.1	9	18.4	10	16.4	30	**61.2**	32	52.5

Effects of Sex or Age at Banding and Changes in Injury Rate with Time

In *R. ferrumequinum* the injury rate did neither differ between bats marked as juveniles or adults (χ^2 with Haber correction = 0.87, *d.f.* = 1, $P = 0.35$) nor between sexes (χ^2 with Haber correction = 0.00, *d.f.* = 1, $P = 1.00$ – Table 2). Bats recaptured in the year of initial banding had a significantly higher injury rate than bats recaptured in the following years (χ^2 with Haber correction = 11.04, *d.f.* = 1, $P < 0.001$). However, only the bats marked as juveniles contributed to this effect while in adults no difference in injury rates between recaptures in the year of initial banding and following years was present (χ^2 with Haber correction = 10.28, *d.f.* = 1, $P < 0.01$ for juveniles and χ^2 with Haber correction = 2.05, *d.f.* = 1, $P = 0.15$ for adults). The sample size has been too small to present statistics on the short term development of injury scores. Our qualitative observation is that injury rates have been highest about six months after initial ringing (see observations on the injury status in *R. ferrumequinum*).

TABLE 2. Recapture and injury rate in different age classes and cohorts of banded *R. ferrumequinum* including repeated recaptures. For statistics see text.

Marked as	Year	Sex	*n* bats	Recaptured same year				Recaptured following year(s)			
				Total (% of *n* marked)	Injury (% of *n* recaptured)			Total (% of *n* marked)	Injury (% of *n* recaptured)		
					No	Slight	Severe		No	Slight	Severe
Juvenile	2001	male	61	13 (21%)	5 (38%)	8 (62%)	0	5 (8%)	5 (100%)	0	0
		female	67	9 (13%)	7 (78%)	1 (11%)	1 (11%)	36 (54%)	36 (100%)	0	0
	2002	male	51	5 (10%)	4 (80%)	1 (20%)	0	2 (4%)	2 (100%)	0	0
		female	56	8 (14%)	6 (75%)	2 (25%)	0	14 (25%)	14 (100%)	0	0
	2003	male	68	12 (18%)	12 (100%)	0	0	0	0	0	0
		female	80	21 (26%)	21 (100%)	0	0	11 (14%)	11 (100%)	0	0
	Total juveniles		383	68 (18%)	55 (81%)	12 (18%)	1 (1%)	68 (18%)	68 (100%)	0	0
Adult	2001	male	4	1 (25%)	1 (100%)	0	0	0	0	0	0
		female	93	10 (11%)	8 (80 %)	2 (20%)	0	53 (57%)	50 (94%)	2 (4%)	1 (2%)
	2002	male	18	5 (28%)	4 (80%)	1 (20%)	0	1 (6%)	1 (100%)	0	0
		female	390	73 (19%)	65 (89%)	5 (7%)	3 (4%)	157 (40%)	150 (96%)	4 (3%)	3 (2%)
	2003	male	8	0	0	0	0	1 (13%)	1 (100%)	0	0
		female	223	55 (25%)	52 (95%)	3 (5%)	0	37 (17%)	34 (92%)	1 (3%)	2 (5%)
	Total adults		736	144 (20%)	130 (90%)	11 (8%)	3 (2%)	249 (34%)	236 (95%)	7 (3%)	6 (2%)
Total			1119	212 (19%)	185 (87%)	23 (11%)	4 (2%)	317 (28%)	304 (96%)	7 (2%)	6 (2%)

Interspecific Differences in Banding Vulnerability

Injury rate differed among species (χ^2 = 47.1, *d.f.* = 2, P < 0.001) with the highest rate observed in *R. mehelyi* banded with 2.9 mm bands (61.2 % - Table 1). When only considering the ring sizes with lowest injury rates for each species (i.e., those that a posteriori appear to be best suited), no differences in the injury rates between the three species were found (χ^2 = 0.05, *d.f.* = 2, P = 0.97 - Table 1). Injuries occurred in 7.1 to 9.3 % of those individuals.

Observations on the Injury Status in R. ferrumequinum

A synopsis of the noted injury status of *R. ferrumequinum* from all recaptures resulted in the following observations:

1) 90.7 % of the *R. ferrumequinum* did not show any injuries at any time (Table 1).
2) There were no injuries in recaptures up to 10 days after initial ringing.
3) First injuries occurred in recaptures several weeks after initial ringing and were usually only weak (small scars along the propatagium).
4) In repeated recaptures the proportion of injuries was highest four to six months after the initial ringing, severest injuries occurred after about six months (inflammations with pus, holes in the wing membranes).
5) All individuals recaptured several times recovered very fast from their injuries after the ring had been removed.

We observed several reasons for ring injuries:

1) Due to ringing method. We gave great care to fit the rings in the best way. Nevertheless, in a few of the recaptures we had to note that rings were oval shaped and therefore attached to the upper and lower part of the forearm where they rubbed the skin.
2) Rubbing of the ring along the margin of the propatagium. Permanent movement of the ring along the propatagium led to slight injuries in some bats. These were usually

covered by a small scar. If the scar got repeatedly rubbed it continued to grow. If the growing scar reached a certain size, the ring was fixed and could not move along the forearm anymore. In a next step, the ring either penetrated the membrane or the scar started to grow over the ring. By the tensions in the tissue the margins of the wound were permanently opened which often lead to an inflammation.

3) Biting by the animal: If the bats bit the ring, it got either closed too much or the ring received sharp edges that cut the skin. A bend in the curvature led usually to an abrasion of the skin at the margin of the propatagium and was followed by a growing scar or an inflammation. Sometimes the ring penetrated the membrane as well.
4) Dislocation of the ring: The ring moved along the forearm towards the wrist and turned in a way that the propatagium slid through the gap of the ring. By this the membranes of the propatagium and the arm wing were in the gap and the ends of the ring rubbed on both membranes. As a result the ring penetrated one or both membranes and the gap of the ring showed at the front. Sometimes inflammations followed, but usually the situation became stable without any visible problems.

All injuries could stabilize at any stage without further visible problems for the animals (in terms of injuries), but quite often severe inflammations did appear. In all injured bats rings were removed and the bats usually were marked again with a new ring at the other wing in order to follow up the healing process. This showed that after removal of the ring from the injured wing, all injuries healed very fast within one to six weeks.

DISCUSSION

Species and Ring Size

Whereas more than 85% of the 580 recaptured individuals showed no negative impact of the banding, we had to note an alarmingly high injury rate in some cohorts. The Eurobats (2003) resolution about band-size for each European species preliminarily recommended to use ring sizes between 2.9 and 4.2 mm in medium sized horseshoe bats. As shown by our experiences, 2.9 mm rings are definitively too small at least for *R. mehelyi* and caused most of the injuries observed in this species. 4.2 mm rings on the other side are too big. Own experiments on museum specimen and on life individuals (without releasing the bats with these rings) have shown that the 4.2. mm rings either can slip around the elbow or around the wrist and may cause even worse injuries. As 3.5 mm and 4.2 mm rings do not much differ in size it is mainly the shape of the ring and maybe the material also that leads to a better fit of the 3.5 mm ring at the forearm of medium sized horseshoe bats. We therefore propose to change the recommendation in the Eurobats (2003) resolution to 3.5 mm rings in medium sized horseshoe bats (but see further notes below). Further research should be undertaken to find the optimal ring size and shape for these species. It has been shown in several other species that the use of the appropriate ring size could strongly reduce the injury rate (Davis, 1960; Baker *et al.*, 2001).

The remaining injury rate of about 10 % in the other recapture cohorts is quite high, too. It is likely that some of the non-recaptured bats might have died from injuries or inflammations and hence a serious impact on the studied part of the population has to be feared. Increased mortality rates or reduced fitness of marked populations contradict conservation efforts of endangered species and limit the scientific value of recapture data (Dinale, 1965; Stebbings, 1969).

Vulnerability of Rhinolophids and Vespertilionids Compared

The injury rates during our study on horseshoe bats have been much higher than during other own studies on verspertilionid bats (Table 3). To compare banding vulnerability of rhinolophids and vespertilionids, we compiled information from the literature, unpublished data generously provided by colleagues and own data (Table 3). From this compilation, it becomes evident that the injury rate in several European vespertilionid bats (*Myotis nattereri*, *M. daubentonii*, *M. capaccinii*, *M. dasycneme*, *M. emarginatus*, *M. mystacinus*, *Nyctalus noctula*, *Pipistrellus pipistrellus*, and *Plecotus auritus*) marked with flanged metal bands since the 1990s was generally below 5 %; only *P. nathusii* showed a higher injury rate of 6.3 %. For the bat family Rhinolophidae, data on injury rates were only available for two species. In *R. megaphyllus*, injury rate varied between 45.7 % and 93.8 % of the recaptured individuals, mainly with severe injuries (Dwyer, 1965; McKean in Dwyer, 1965; Young, 2001; Baker *et al.*, 2001); a situation well comparable to our results found in the similar sized *R. mehelyi*. Sluiter *et al.* (1971) observed injury rates of 14-24 % in different recapture cohorts of *R. ferrumequinum*, a rate slightly above our results. Unfortunately no further data on ring induced injuries are available in this commonly marked bat species. In their studies on Asian bats, Kingston and Rossiter found only low injury rates in ten species of horseshoe bats (S. Rossiter, pers. com.). In contrast, a high sensitivity of horseshoe bats to ringing has been reported by most of the earlier studies in Europe (Hooper and Hooper, 1956; Issel and Issel, 1960; Dinale, 1965; Saint-Girons and Saint-Girons, 1968; Gaisler and Hanák, 1969a, b; Sluiter *et al.*, 1971), however without giving data or further details.

We could not confirm Young's (2001) observation that most injured *Rhinolophus* have a strong tooth abrasion due to biting the ring. Our observations indicate that the major reason for ring injuries in horseshoe bats was the width of their propatagium and the resulting abrasion of the skin by the ring along the edge of the propatagium. Similar observations have been made by McKean (in Dwyer, 1965) in *R. megaphyllus*. In this context, it should be noted that the *Rhinolophus* propatagium differs from the verspertilionid propatagium in being wider especially along the forearm close to the thumb. Consequently, ringed vespertilionids with their smaller propatagium in the distal parts of the forearm suffer much less from rubbing of the ring along the frontal margin of the propatagium.

TABLE 3. Reference data about band induced injuries in horseshoe bats and European vespertilionid bats.

Species	recaptures (*n*)	Injury rate	Country	Source
Ringing until 1980s				
Myotis dasycneme	118	28.5 % ring damage	Netherlands	Sluiter *et al.* 1971
Myotis dasycneme	115	10.4 % ring damage	Netherlands	Sluiter *et al.* 1971
Myotis myotis	Several thousand	≥ 1 %	Germany	Eisentraut 1960
Pipistrellus pipistrellus	1774	27.5 %	Germany	Grimmberger and Bork 1978
Rhinolophus ferrumequinum	489	14-24 % in different recapture cohorts	France	Sluiter *et al.* 1971
Rhinolophus megaphyllus	215	45.7 % (15.7 % slight, 7.1 % moderate, 22.9 % severe)	Australia	Young 2001
Rhinolophus megaphyllus	48	93.8 %	Australia	Dwyer 1965
Rhinolophus megaphyllus	29	86 %	Australia	McKean in Dwyer 1965
ringing 1990s onwards				
Myotis capaccinii	16	0 %	Bulgaria	Dietz and Dietz, own data
Myotis dasycneme	89	0 %	Germany	Labes (pers. com.)
Myotis daubentonii	257	3.5 % (1.5 % slight, 2.0 % severe)	Germany	Dietz and Dietz, own data
Myotis daubentonii	525	3.4 % (0.4 % slight, 3.0 % severe)	Germany	Labes (pers. com.)
Myotis emarginatus	29	0 %	Bulgaria	Dietz and Dietz, own data
Myotis mystacinus (cf. aurascens)	67	0 %	Bulgaria	Dietz and Dietz, own data
Myotis nattereri	322	1.2 % (0.3 % slight, 0.9 % severe)	Germany	Labes (pers. com.)
Nyctalus noctula	489	0.4 % (0.4 % severe)	Germany	Labes (pers. com.)
Pipistrellus nathusii	320	6.3 % (1.6 % slight, 4.7 % severe)	Germany	Labes (pers. com.)
Pipistrellus pipistrellus	3403	0.4 % severe, no information given on slight injuries	Germany	Sendor and Simon 2003
Pipistrellus pipistrellus	19	0 %	Germany	Labes (pers. com.)
Plecotus auritus	30	0 %	Germany	Labes (pers. com.)

Consequences of Ringing

Our observations of an increasing number of injured bats up to six months after initial ringing is in accordance with data given by Dwyer (1965), Sluiter *et al.* (1971) and Jolly (1988), and can be explained by the quite high elasticity and puncture strength of bat wings and skin that prevent severe problems for quite a long time (Studier, 1972). For *R. ferrumequinum*, our results suggest a higher sensitivity of juveniles in the first year after initial banding than in later recaptures, a fact that might lower their survival probability. While Baker *et al.* (2001) found a significantly reduced survival rate for ringed bats in three Australian species and Dinale (1965) noted a decrease in body weight and a reduced survival rate in bats with too tight bands or injured bats, Dwyer (1965), Ransome (1990) and Happold and Happold (1998) did not find any negative influence on the populations. Baker *et al.* (2001) suggested continuing ringing studies only if injury rates in recaptures are below 2 % to minimise the negative effects on populations. If one would follow their suggestion, any ringing in horseshoe bats, but also in most other European bat species (Table 3) needed to be abandoned immediately.

Alternative Marking Techniques for Horseshoe Bats?

Alternative marking techniques of bats have been proposed and tested by several authors; e.g. punch-marking (Bonaccorso and Smythe, 1972), necklaces made from beadclasp ball chains (Barcley and Bell, 1988) or self-locking cable ties (Gannon, 1993), tattoos (Griffin, 1934) and PIT-tags (Kerth, 1995; Kerth and König, 1996). The feasibility of these techniques for marking horseshoe bats remains to be studied, however. Until more appropriate marking techniques will be established for horseshoe bats, an improvement of the forearm banding method might be of some use to reduce injury rate. Bonaccorso *et al.* (1976) suggested to place the ring through a cut in the propatagium around the forearm in bats with a wide propatagium, a method tested successfully by Barclay and Bell (1988) and Jolly (1988).

Conclusion and Suggestions

We of course have to and do assume responsibility for the high injury rates caused by our ringing. We are, however, convinced that the injuries were not a consequence of carelessness or inexperience. We strived to take great care when applying rings; CD, who did all ringing is well experienced and certified by the German bat ringing centre. The aim of this publication is to share our unpleasant and superincumbent experience with all colleagues concerned to help avoiding similar experiences in the future.

Judging from the information gathered from the literature and our own experiences, the individual marking of horseshoe bats with rings remains problematic (e.g. Hooper and Hooper, 1956) even when modern banding methods are applied and intensive training of bat workers in the method of ringing has been undertaken in advance. We therefore recommend to carefully weight costs and benefits before ringing horseshoe bats and to consider and test alternative study methods. The improved handling methods and rings seem to have reduced the impact of ringing and the risk of ring induced injuries in most vespertilionid bats (but see e.g. Pierson and Fellers, 1993), but in rhinolophid bats negative effects remain high. A promising method to reduce the injury rate of horseshoe bats might be to place the ring through a cut in the propatagium around the forearm (Bonaccorso *et al.*, 1976; Barclay and Bell, 1988; Jolly, 1988) or to use PIT-tags (Kerth, 1995; Kerth and König, 1996), but both methods have to be checked carefully in experiments before using them regularly on horseshoe bats. Based on published observations (Beaucournu, 1962; Dinale, 1965; Feldmann, 1967; Saint-Girons and Saint-Girons, 1968; Sluiter *et al.*, 1971; Brosset *et al.*, 1988; Ransome, 1990) and our own data, we suggest to exclude the small to medium sized horseshoe bat species (including the three European medium sized species *R. euryale*, *R. mehelyi* and *R. blasii* and the smallest European species *R. hipposideros*) from further ringing, until studies about long-term effects and new improved ringing techniques will be available.

In general we suggest that banding of horseshoe bats should be limited to well defined projects and only used if the study populations are in a good preservation condition and long term effects of the marking method can be monitored. Most of these suggestions are already part of the licensing procedure in most Western and Central European countries and are encouraged by Eurobats (2003). However in many other countries licensing procedures do not cover all of these aspects recommended.

Finally, we would like to encourage all bat workers to note injury rates of recaptured bats carefully and to add these results in their publications. If future studies indeed would corroborate that banding effects are very small in vespertilionid bats, the acceptance and justification of the method in scientific and conservation work would be based on an appropriate body of empirical data. On the other hand, if more publish records of banding induced problems become available, the pressure to develop new marking methods will increase.

ACKNOWLEDGEMENTS

We are particularly grateful to all the people that helped to capture and recapture bats during our own studies, especially the members of the Bulgarian Bat Research and Protection Group and our field assistants (in alphabetic order): I. Borrisov, K. Christov, D. Merdschanova, S. Merdschanov, B. Petrov, N. Simov and S. Staneva. For many rewarding discussions about the pros and cons of methods in the study of the behaviour of bats and help in getting some references we are obliged to (in alphabetic order): F. Bontadina, J. Gebhard, J. Haensel, U. Häussler, I. Kaipf, G. Kerth, F. Mayer, E. Müller, A. Nagel, R. Nagel, B. Ohlendorf, E. Papadatou, G. Reiter, S. Rossiter, A. Schaub, H.-U. Schnitzler and O. von Helversen. We are specifically grateful to R. Labes who kindly provided numerous unpublished recapture data and reports about injuries.

LITERATURE CITED

Allen, A.A. 1921. Banding bats. Journal of Mammalogy, 2: 53-57.

Baker, G.B., L.F. Lumsden, E.B. Dettmann, N.K. Schedvin, M. Schulz, D. Watkins, and L. Jansen. 2001. The effect of forearm bands on insectivorous bats (Microchiroptera) in Australia. Wildlife Research, 28: 229-237.

Barclay, R.M.R., and G.P. Bell. 1988. Marking and observational techniques. Pp. 59-76 *in* Ecological and Behavioral Methods for the Study of bats (T.H. Kunz, ed.). Smithsonian Institution Press, Washington D.C., 533 pp.

Beaucournu, J.-C. 1962. Observations sur le baguage des Chiroptères: résultats et dangers. Mammalia, 26: 539-565.

Bels, L. 1952. Fifteen years of bat-banding in the Netherlands. Publicaties van het natuurhistorisch genootschap in Limburg, 5: 1-99.

Bonaccorso, F.J., and N. Smythe. 1972. Punch-marking bats: an alternative to banding. Journal of Mammalogy, 53: 389-390.

Bonaccorso, F.J., N. Smythe, and S.R. Humphrey. 1976. Improved techniques for marking bats. Journal of Mammalogy, 57: 181-182.

Bontadina, F., and K. Märki. 2003. Neues vom Forschungsprojekt “Rhippos”. Fledermaus-Anzeiger, 74: 1-2.

Bontadina, F., R. Arlettaz, T. Frankhauser, M. Lutz, E. Mühlethaler, A. Theiler, and P. Zingg. 2001. The lesser horseshoe bat *Rhinolophus hipposideros* in Switzerland: present status and research recommendations. Swiss Coordination Center for the Study and Protection of Bats, Zürich and Geneva, 24pp.

Bopp, P. 1958. Zur Lebensweise einheimischer Fledermäuse (1.Mitteilung). Säugetierkundliche Mitteilungen, 6: 11-13.

Bork, H. 1972. Selbstkritischer Bericht über Beringung von *Pipistrellus pipistrellus* in einer Riesenkolonie in Demmin. Nyctalus, 1: 11-15; Halle/ Saale.

Bradbury, J.W. 1977. Lek mating behaviour in the hammer-headed bat. Zeitschrift für Tierpsychologie, 45: 225-255.

Brockmann, D., and U. Zöphel. 2004. Fledermausmarkierung in Ostdeutschland seit 1990 – Stand und Entwicklung. Nyctalus (N.F.), 9: 197-202.

Brosset, A., L. Barbe, J.-C. Beaucournu, C. Faugier, H. Salvayre, and Y. Tupinier. 1988. La raréfaction du rhinolophe euryale (*Rhinolophus euryale*) en France. Recherche d´une explication. Mammalia, 52: 101-122.

Calvo, B., and R.W. Furness. 1992. A review of the use and the effects of marks and devices on birds. Ringing and Migration, 13: 129-151.

Daan, S., G.H. Glas, and A.M. Vôute. 1980. Long term changes in bat populations in the Netherlands. Lutra, 22: 1-118.

Davis, W.H. 1960. Band injuries. Bat Banding News, 1: 1-2.

Davis, W.H. 1961. Band injury. Bat Banding News, 2: 30.

Dietz, C., I. Dietz, T. Ivanova, and B. M. Siemers. In press. Movements of horseshoe bats (*Rhinolophus*, Chiroptera: Rhinolophidae) in Northern Bulgaria – Myotis.

Dinale, G. 1965. Studii sui chirotteri Italiani: III. Influenza dell'inanellamento sul peso e sulla probabilita' di sopravvivenza in *Rhinolophus ferrum equinum.* Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano, 104: 23-40.

Dwyer, P.D. 1965. Injuries due to bat-banding. Pp. 19-24 *in* Third and fourth annual reports on bat-banding in Australia (K.G. Simpson and E. Hamilton-Smith, eds.). Division of Wildlife Research Technical Paper, 9. Commonwealth Scientific and Industrial Research Organization, Australia, Melbourne, 24 pp.

Eisentraut, M. 1934. Markierungsversuche bei Fledermäusen. Zeitschrift für Morphologie und Ökologie der Tiere, 28: 553-560.

Eisentraut, M. 1960. Die Fledermausberingung, ihre Entwicklung, ihre Methode und ihre Bedeutung für die wissenschaftliche Forschung. Bonner Zoologische Beiträge, Sonderheft, 11: 7-21.

Eurobats. 2003. Guidelines for the issue of permits for the capture and study of captured wild bats. Eurobats.MoP4.Record.Annex 9a,9b and 9c, pp. 44-49 *in* Record of the 4th Session of the Meeting of Parties, Sofia, Bulgaria, 22-24 September 2003.

Feldmann, R. 1967. Bestandsentwicklung und heutiges Areal der Kleinhufeisennase, *Rhinolophus hipposideros*, im mittleren Europa. Säugetierkundliche Mitteilungen, 15: 43-49.

Gaisler, J., and J. Chytil. 2002. Mark-recapture results and changes in bat abundance at the cave of Na Turoldu, Czech Republic. Folia Zoologica, 51: 1-10.

Gaisler, J., and V. Hanák. 1969*a*. Summary of the results of bat-banding in Czechoslovakia, 1948-1967. Lynx, 10: 25-34.

Gaisler, J., and V. Hanák. 1969*b*. Ergebnisse der zwanzigjährigen Beringung von Fledermäusen (Chiroptera) in der Tschechoslowakei: 1948-1967. Acta scientiarum naturalium Academiae scientiarum bohemoslovacae, Brno, 3: 1-33.

Gannon, M.R. 1993. A new technique for marking bats. Bat Research News, 34: 88-89.

Griffin, D.R. 1934. Marking bats. Journal of Mammalogy, 15: 202-207.

Grimmberger, E., and H. Bork. 1978. Untersuchungen zur Biologie, Ökologie und Populationsdynamik der Zwergfledermaus, *Pipistrellus p. pipistrellus*, in einer großen Population im Norden der DDR, Teil 1. Nyctalus (N.F.), 1: 55-73.

Haensel, J., and B. Ohlendorf. 2004. Die Fledermausmarkierung – nach wie vor eine sehr aktuelle Methode der Fledermausforschung und des wissenschaftlich untersetzten Fledermausschutzes. Nyctalus (N.F.), 9: 195-196.

Happold, D.C.D., and M. Happold. 1998. Effects of bat-bands and banding on a population of *Pipistrellus nanus* in Malawi. Zeitschrift für Säugetierkunde, 63: 65-78.

Herreid, C.F., R.B. Davis, and H.L. Short. 1960. Injuries due to bat banding. Journal of Mammalogy, 41: 398-400.

Hiebsch, H. 1972. Neue Zielstellung der Fledermausforschung. Nyctalus, 4: 49-50.

Hitchcock, H.B. 1957. The use of bird bands on bats. Journal of Mammalogy, 38: 402-405.

Hooper, J.H.D., and W.M. Hooper. 1956. Habits and movements of cave-dwelling bats in Devonshire. Proceedings of the Zoological Society of London, 127: 1-26.

Horáček, I. 1984. Remarks on the causality of population decline in European bats. Myotis, 21-22: 138-147.

Issel, B., and W. Issel. 1960. Beringungsergebnisse an der Großen Hufeisennase (*Rhinolophus ferrumequinum*) in Bayern. Bonner Zoologische Beiträge, Sonderheft, 11/ 1960: 124-142.

Issel, W. 1951. Ökologische Untersuchungen an der Kleinen Hufeisennase (*Rhinolophus hipposideros*) im mittleren Rheinland und unterem Altmühltal. Zoologische Jahrbücher (Systematik, Ökologie und Geographie), 79: 71-86.

Jolly, S. 1988. A comparison of two banding methods in the common sheath-tailed bat, *Taphozous georgianus*. Macroderma, 4: 64-66.

Kerth, G. 1995. Erste Erfahrungen mit dem Einsatz von Transpondern und einer Infrarot-Videokamera zu Verhaltensuntersuchungen an der Bechsteinfledermaus (*Myotis bechsteini*) im Freiland. Pp. 383-389 *in* Methoden feldökologischer Säugetierforschung, Band 1 (M. Stubbe, A. Stubbe and D. Heidecke, eds.). Martin Luther Universität Halle-Wittenberg, 396 pp.

Kerth, G., and B. König. 1996. Transponder and infrared-videocamera as methods used in a fieldstudy on the social behavior of Bechstein´s bats (*Myotis bechsteini*). Myotis, 34: 27-34.

Kiefer, A., and R. Hutterer. 2002. Fledermausmarkierung in der Bundesrepublik Deutschland: Beispiele für die Auswertung von Beringungsdaten mit Hilfe der Datenbank BatRing. Pp. 259-266, *in* Ökologie, Wanderungen und Genetik von Fledermäusen in Wäldern. Untersuchungen als Grundlage für den Fledermausschutz (A. Meschede, K.-G. Heller, and P. Boye, eds.). Schriftenreihe für Landschaftspflege und Naturschutz, 71. Bundesamt für Naturschutz, Bonn, 288 pp.

Mitchell-Jones, A.J., and A.P. McLeish. 1999. The bat workers' manual. Joint Nature Conservation Committee, Peterborough, 138 pp.

Mitchell-Jones, A.J., and A.P. McLeish. 2004. Bat workers' manual. 3rd edition. Joint Nature Conservation Committee, Peterborough, 178 pp.

Perry, A.E., and G. Beckett. 1966. Skeletal damage as a result in band injury in bats. Journal of Mammalogy, 47: 131-132.

Phillips, W.R. 1985. The use of bird bands for marking tree-dwelling bats, a preliminary appraisal. Macroderma, 1: 17-21.

Pierson, E.D., and G.M. Fellers. 1993. Injuries to *Plecotus townsendii* from lipped wing bands. Bat Research News, 34: 89-91.

Ransome, R.D. 1989. Population changes of greater horseshoe bats studied near Bristol over the past twenty-six years. Biological Journal of the Linnean Society, 38: 71-82.

Ransome, R. 1990. The natural history of hibernating bats. Christopher Helm, London, 235 pp.

Richter, H. 1970. Kritische Bemerkungen zur Markierungstätigkeit an Fledermäusen. Nyctalus, 2: 18-24.

Rybář, P. 1973. Remarks on banding and protection of bats. Periodicum Biologorum, 75: 177-179.

Saint-Girons, H., and M.-C. Saint-Girons. 1968. Le Baguage des chauves-souris par les spéléologues. Spelunca-Bulletin, 1968: 19-21.

Sendor, T., and M. Simon. 2003. Population dynamics of the pipistrelle bat: effects of sex, age and winter weather on seasonal survival. Journal of Animal Ecology, 72: 308-320.

Sluiter, J.W., P.F. van Heerdt, and M. Gruet. 1971. Paramètres de population chez le grand rhinolophe fer-a-cheval (*Rhinolophus ferrum-equinum*), estimes par la méthode des reprises après baguages. Mammalia, 35: 254-272.

Stebbings, R.E. 1969. Observer influence on bat behaviour. Lynx, 10: 93-100.

Stebbings, R.E. 1978. Marking bats. Pp. 81-94, *in* Animal Marking (B. Stonehouse, ed.). The Macmillan Press, London, 243 pp.

Stebbings, R.E. 1988. The conservation of European Bats. Christopher Helm, London, 246 pp.

Studier, E.H. 1972. Some physiological properties of the wing membranes of bats. Journal of Mammalogy, 53: 623-625.

Trapido, H., and P.E. Crowe. 1946. The wing banding method in the study of the travels of bats. Journal of Mammalogy, 27: 224-226.

Uhrin, M., S. Danko, J. Obuch, I. Horáček, S. Pacenovsky, P. Pjencak, and M. Fulin. 1996. Distributional patterns of bats in Slovakia. Part 1, horseshoe bats (Rhinolophidae). Acta societatis Zoologicae Bohemoslovenicae, 60: 247-279.

Young, R.A. 2001. The eastern horseshoe bat, *Rhinolophus megaphyllus*, in south-east Queensland, Australia: colony demography and dynamics, activity levels, seasonal weight changes, and capture-recapture analysis. Wildlife Research, 28: 425-434.

Zöphel, U., and H. Hiebsch. 1994. Fledermausmarkierung in Ostdeutschland, Erfahrungen und Perspektiven. Nyctalus (N.F.), 5: 27-36.

Chapter 4

Movements of horseshoe bats (*Rhinolophus*, Chiroptera: Rhinolophidae) in northern Bulgaria

By Christian Dietz, Isabel Dietz, Teodora Ivanova

and Björn. M. Siemers

The ms. was submitted to:

Myotis; Bonn.

Received 05.10.2005

Accepted 02.12.2005

Ms. is in press and will be printed in the forthcoming issue.

Movements of horseshoe bats (*Rhinolophus*, Chiroptera: Rhinolophidae) in northern Bulgaria

Christian Dietz[1)], Isabel Dietz[1)], Teodora Ivanova[2)] & Björn M. Siemers[1)]

[1)] Animal Physiology, Zoological Institute, Tübingen University, Auf der Morgenstelle 28, 72076 Tübingen; Germany. Email: Christian.Dietz@uni-tuebingen.de

[2)] National Museum of Natural History, Tsar Osvoboditel Blvd. 1, Sofia 1000; Bulgaria

ABSTRACT

We studied the movements of three species of horseshoe bats (*Rhinolophus ferrumequinum*, *R. euryale* and *R. mehelyi*) in northern Bulgaria in the years 2001-2004. More than 1,500 horseshoe bats could be marked mostly at a single cave roost used as maternity colony. Most recaptures were done at the ringing site or at a few alternative roosting sites in the close surroundings. The greater horseshoe bats (*R. ferrumequinum*) moved in autumn and winter to other caves in mean distances of 57 km and a maximum of 90 km towards the Balkan mountains. No differences in the mean distances of hibernacula from the nursery colony were found between males and females or adult and subadult females. In the two other horseshoe bat species several long distance movements could be detected, too. The Mediterranean horseshoe bat (*R. euryale*) changed roosts in distances of up to 60 km, while in the little studied Mehely's horseshoe bat (*R. mehelyi*) long distance movements of more than 90 km could be documented for the first time.

Key words: *Rhinolophus ferrumequinum*, *Rhinolophus euryale*, *Rhinolophus mehelyi*, seasonal movements, recapture probability.

INTRODUCTION

Five species of horseshoe bats (Rhinolophidae) occur in Europe. Two of them, the greater (*Rhinolophus ferrumequinum*) and the lesser (*R. hipposideros*) horseshoe bat are or have been distributed over most parts of southern and central Europe, while the other three species (*R. euryale*, *R. mehelyi, R. blasii*) are confined within Europe to the South, mainly to the Mediterranean (Mitchell-Jones et al. 1999). All five species are relatively common in Bulgaria and greater and lesser horseshoe bats belong to the most abundant bat species of the country (Benda et al. 2003).

While greater and lesser horseshoe bats are well studied in most respects of their ecology (Gaisler 1960a, 1960b, 1963, 1965, Gaisler & Titlbach 1964, Ransome 1968, 1971, 1973, 1989, 1998, 1999, McAney & Fairley 1988a, 1988b, 1989, Ransome & Hutson 2000, Bontadina et al. 2002), the biology of the three medium-sized species is much less known. The Mediterranean horseshoe bat (*R. euryale*) has been studied mainly in Italy and the Iberian peninsula (Dinale 1963, 1967, Russo et al. 2001, 2002, Aihartza 2003, Goiti et al. 2003). Numerous observations on seasonal movements of *R. ferrumequinum*, *R. hipposideros* and *R. euryale* were collected by the pioneers of bat banding (Mislin 1945, Issel 1951, Bels 1952, Hooper & Hooper 1956, Issel & Issel 1960, Kepka 1960, Beaucournu 1963, Dinale 1963) and many scientists have contributed to improve the knowledge since. All three species are regarded as mostly sedentary (Gaisler & Hanak 1969a, 1969b, Roer 1995). However very few observations deal with Mehely's (*R. mehelyi*) and Blasius' (*R. blasii*) horseshoe bats (e.g. Paunovic 1997a, 1997b). There are hardly any data available on movements of horseshoe bats from the Balkans, the only part of Europe where all five species occur in sympatry (Dulic 1957, Paunovic 1997a, 1997b, 1998).

The aim of our study was to obtain data on movements of one of the most abundant Bulgarian bat species, *R. ferrumequinum* and two of its congeners *R. euryale* and *R. mehelyi*.

MATERIAL AND METHODS

Our study site was the hilly karst-area between the lowlands of the Danube and the Balkan mountains in Northern Bulgaria (fig. 1). Bats were marked in the years 2001-2004 at sites around the village Muselievo in the Osam valley (near the town Nikopol, District Pleven, 43°37' N, 24°51' E), about 10 km south of the river Danube. Most of the bats were captured at a single cave ("Nanin Kamăk") inhabited by a colony of up to 1,000 bats (*R. ferrumequinum*, *R. mehelyi*, *R. euryale*, *Myotis capaccinii*, *M. emarginatus* and *Miniopterus schreibersii*). Some more bats were marked in the surroundings of Muselievo in alternative roosting sites of the colony in several small caves or in night roosts and foraging sites.

At the main study site (cave "Nanin Kamăk") and in its close surroundings bats were captured during 128 capture nights by mist nets, harp traps (Palmeirim & Rodrigues 1993) and by the eastern-German so called "doll-hair nets" at the roost entrances and at a few occasions by hand-nets inside the roosts. Caves, buildings and night roost in a 15 km radius around the study site were checked regularly for the presence of bats and if possible marked bats were captured. During 45 excursions caves in a distance of up to 100 km were visited during the summer season and checked for marked bats. In addition all known colony sites of horseshoe bats have been inspected during transition time end of September/beginning of October in a 100 km radius around the study site. The Bulgarian Bat Research and Protection Group carried out winter censuses and a survey for marked bats in all hibernacula used by high numbers of horseshoe bats.

Captured bats were identified by characters of the nose-leaf and the lower lip. To mark the bats individually, we used three different size classes of flanged metal bat rings (2.9, 3.5 and 4.2 mm) manufactured by Lambournes (Lambournes Ltd., Leominster, Herefordshire, UK; rings used in 2001) and by Porzana (Porzana Ltd., Wetland-Trust, UK; rings used in 2002-2004). The 3.5 mm magnesium-aluminium alloy rings were used in two colours: green for *R.*

mehelyi and red for *R. euryale*. The silver 2.9 and 4.2 mm rings were nickel-chromium alloy bands (incoloy). Effects of the banding method on the bats (ring injuries) will be discussed in a separate publication (Dietz et al. in prep.).

Field work was carried out under licence of the Bulgarian authorities (15-RD-08/15.01.2001, 48-00-56/16.01.2001, 8/02.07.2004 RIOSV Pleven, RIOSV Ruse).

RESULTS AND DISCUSSION

Influences on recapture rate

The horseshoe bats learnt quickly how to avoid nets and traps. While it has been very easy to capture large numbers at the roost entrances with two-framed harp-traps or normal mist nets within the first two months of the study period, it got more and more complicated to capture any bats toward the end of the study. To prevent horseshoe bats from simply crushing through the harp-trap we had to use six frames in the end and it was impossible to catch bats with mist nets anymore. The use of the eastern-German “doll-hair nets” improved capture success for several instances, but the horseshoe bats quickly learned to avoid them, too. While in the beginning 85–90 % of the horseshoe bats leaving the entrance were trapped, in the end only 1–5 % of the approaching bats became entangled in nets or the trap, paralleled by a steady increase of bat activity in front of the nets. The horseshoe bats hovered in front of the capture devices and escaped through holes in the nets and through broken wires of the harp trap (the capture success in *Myotis spp*. and *Miniopterus* was also reduced, but to a lesser degree). In 2003 and 2004 after having marked approximately 1,500 bats, about 70-80 % of the adult horseshoe bats in the colony at cave Nanin Kamăk carried rings (counted from photographs in the colony); however, the proportion of marked bats in captures at the two entrances of the cave never exceeded 44.2 % and averaged at 32 %. So the capture probability was very much biased towards individuals never captured before, while “experienced” bats were captured in lower numbers.

Recapture success was also low in sites other than the ringing place: Only about 50 % of the observed bats with rings could be captured in night-roosts and alternative day roost. At other colony- and breeding sites ringed bats could be observed in many instances by binoculars, but usually we could not read the ring numbers and we were unable to catch the bats either because of the height of the roosting site (up to 30 m above the ground) or because they were roosting within huge mixed clusters of several thousand bats (especially *R. euryale* and *R. mehelyi*). This applies especially for reproducing females: a total of 14 marked bats was observed together with attached young in caves of the Osam-valley (caves Devetaškata Peštera, Mandrata and Uruška Maara) 40-45 km south of the ringing place without having a possibility to capture them, in only four bats the first part of the ring number could be read on photographs. In early spring, autumn and winter recapture success in torpid *R. ferrumequinum* was quite high; more than 90 % of the observed bats could be captured. But in autumn and sometimes also in winter the medium-sized horseshoe bats formed very densely packed clusters of torpid bats, a so called “wall-carpet” or “tapestry”. It was impossible (without irresponsible disturbance) to search such dense clusters of many hundred to several thousand medium-sized horseshoe bats for rings, because most of the forearms and even most of the wrists were not visible.

Despite the attempt to visit all known large colony sites in a hundred kilometre radius around the ringing site there was a heavy bias in the probability to recapture bats: no sites in Romania have been checked for ringed bats (no colonies are known within the radius of focus), the Bulgarian sites have been checked quite irregularly, many colony sites (especially smaller ones) might be unknown and no systematic search could be done outside the 100 km radius at all. The strong bias of surveyed possible recapture sites, the observed interactions between many colony sites (see recaptures) and the low recapture rate in *R. euryale* and *R. mehelyi* forbid any conclusions about population size. Favoured direction, mean distance of movements, survival and return probability can not be derived from our data as recapture sites were not evenly distributed but predefined by known roost sites, furthermore individual recapture probability has been biased. Especially the bias in low individual recapture probability due to high agility and quick learning of how to avoid getting trapped seems to be specific for horseshoe bats, at least comparable problems have not been found neither in published nor in our own studies on vespertilionid bats.

Recaptures

The number of marked and recaptured bats is given in table 1. Recapture rates vary strongly between the species, both sexes and age classes. Of 1,254 marked greater horseshoe bats 511 have been recaptured between one to eight times, in total 807 times: 570 recaptures at the banding site, 160 in a 15 km radius and 77 long distance recaptures (tab. 1). Mediterranean (n = 110) and Mehely's (n = 112) horseshoe bats have been marked in much lower numbers and we got only a few recaptures at other sites than the ringing place (tab. 1).

In *R. ferrumequinum* 383 juveniles were marked in 2001-2003. While the proportion of marked juvenile males and females and of the recaptures in the same year did not differ significantly from an equal distribution, recapture rate of females was highly significantly bigger in the following years [180 marked juvenile males and 203 juvenile females (180:203): $Chi^2 = 1.3812$, $p = 0.2399$, same year recaptures (30:38): $Chi^2 = 0.9412$, $p = 0.3320$, following years recaptures (7:61): $Chi^2 = 42.8824$, $p < 0.0001$, comparison of marked bats and same year recaptures: Chi^2 with Haber-correction = 0.1566, $p = 0.6923$, comparison of marked bats and following years recaptures: Chi^2 with Haber-correction = 31.4641, $p < 0.0001$]. While the recapture rate of juveniles and adults in the same year did not differ significantly, recapture rate of juveniles in the following years was much lower than of adults [Chi^2 with Haber-correction = 18.6459, $p < 0.0001$]. In *R. euryale* (30 juveniles marked, 8 recaptures in the same and 3 in the following years) and *R. mehelyi* (7 juveniles marked, 2 recaptures in the same and 1 in the following years) sample sizes were too small for statistical analysis.

Table 1: Marked and recaptured horseshoe bats (Rhinolophidae - *Rhinolophus*) in northern Bulgaria.

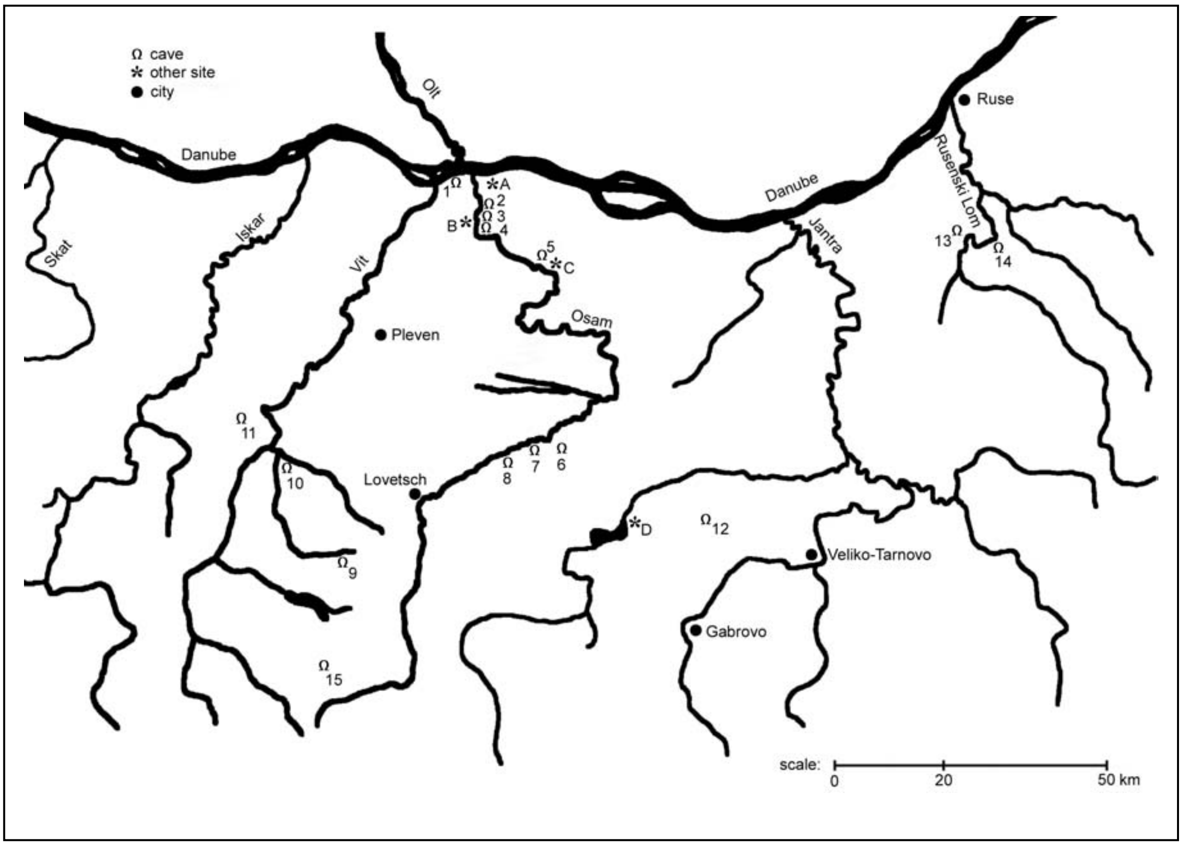
	n banded (♂♂, ♀♀)	n individuals recaptured (♂♂, ♀♀)	n total recaptures	max individual recaptures	n recaptures at banding site	n short distance recaptures (< 15 km)	n long distance recaptures (> 15 km)
R. ferrumequinum	1254 (213,1041)	511 (47,464)	807	8	570	160 (119 individuals)	77 (57 individuals)
R. euryale	110 (26,84)	39 (8,31)	55	4	34	12 (8 individuals)	9 (8 individuals)
R. mehelyi	112 (50,62)	60 (25,35)	86	4	66	17 (11 individuals)	3 (3 individuals)

Movements

Most of the bats were recaptured at the initial ringing site or in its close surroundings within a 15 km radius (tab. 1). Telemetry studies on all three species have shown that the bats use alternative roosts and foraging sites within this radius; home-ranges and core foraging areas extended usually up to 10-15 km around the roosts (own data). Of the short distance recaptures, a high proportion concerns movements between two alternative roost sites: *R. ferrumequinum* and *R. euryale* alternatively roosted in a small cave system ("twin cave") 1.8 km to the south and *R. mehelyi* in a different one (cave Morenitza) 0.6 km to the north of cave Nanin Kamăk. Accordingly, 138 movements could be documented between these alternative roosts in *R. ferrumequinum*, 5 in *R. euryale* and 16 in *R. mehelyi*. The other short distance movements were between night roosts, foraging habitats and day roosts during transition time in spring and autumn. The use of the two alternative roosts in horseshoe bats was paralleled by partial movements of other bat species inhabiting the same cave roost. The *M. emarginatus*-colony likewise moved between the same two caves used by *R. ferrumequinum* and *R. euryale* (own observations of several marked *M. emarginatus* and recapture of the female A 03262). The roost changes in *R. mehelyi* were followed by the partial movements of the *M. capaccinii*-colony (20 movements recorded by recaptures, own data). In the years 2001 and 2004, a small nursery colony of *R. ferrumequinum* was established in the basement of a school-building in the village of Sanadinovo, 15.5 km south of the cave Nanin Kamăk. It was used by a maximum of 13 breeding females in 2001, yet no bats were present in 2002 and 2003. In 2004, two out of the three breeding adult females carried rings and had been banded in the previous years at cave Nanin Kamăk, so the small colony could be regarded as a temporary satellite roost of the main colony.

A relatively small number of individuals was recaptured in distances of more than 15 km and up to 100 km; all records are given in appendices 1, 3 and 4. In addition, two bats marked by other people have been captured (appendix 2); unfortunately it was not possible to get any information about the initial ringing sites and dates. In figure 1 the sites of the long-distance recaptures are given. They spread over a considerable part of the north-Bulgarian lowland towards the Balkan mountains. The longest movements recorded are 89.6 km in *R. ferrumequinum*, 58.8 km in *R. euryale* and 94.1 km in *R. mehelyi*. The shortest observed duration for a long distance translocation were recorded in a nonreproducing nulliparous *R. euryale* (E 411102) between the caves Nanin Kamăk and Mandrata within 6 days (43.8 km in straight line, but more than 80 km according to telemetry data) and in a pregnant female *R. mehelyi* (E 411318) caught on 07.05.2003 at cave Nanin Kamăk and 19 days later, still pregnant, 94.1 km to the west at cave Zorovica Peštera. This bat had also been tagged by a radio-transmitter and left the cave Nanin Kamăk shortly after the initial marking. Since it did not come back within the following two weeks, it might have changed the roost quite fast to the cave Zorovica Peštera, inhabited by a colony of more than 5,000 *R. mehelyi*. Both bats reproduced in the same or in the following years within other colonies than the one were they have been marked. In addition, the female *R. euryale* (E 411102) mentioned above, changed from the cave Mandrata to the cave Urushka Maara 5 km away in 2002: while the cave Mandrata was inhabited by a colony of 50-200 *R. euryale* from 1999 to 2001 (Benda et al. 2004, own data), the colony disappeared in 2002 due to the start of mushroom growing by villagers inside the cave paralleled by an increase in the number of *R. euryale* in the cave Urushka Maara to a maximum of about 1,000 individuals. Judging from the recapture of the banded *R. euryale* (E 411102) and the similar movement of a marked female *M. emarginatus* (A 03144), the disturbance by mushroom growing made at least parts of the Mandrata colony move to cave Urushka Maara.

Figure 1: Map of the study site in northern Bulgaria showing the main river systems and the recapture sites of three species of horseshoe bats. Numbers refer to caves, letters to other recapture sites: 1 - underground gallery near Somovit, 2 – cave Morenitza, 3 - cave Nanin Kamăk, 4 - cave (twin cave) near Muselievo, 5 - small mine near Sanadinovo, 6 - Uruška Maara cave, 7 - Mandrata cave, 8 - Devetaškata Peštera cave, 9 - Mikrenska Peštera cave, 10 - Parnitcite cave, 11 - Sedlarkata cave, 12 - Emenskata Peštera cave, 13 - Orlova Čuka cave, 14 - Zorovica Peštera cave, 15 – cave of Mt. Vasilyov, Shipkovo, A - bridge near Nikopol, B - farm building near Muselievo, C - building in Sanadinovo, D – dam of Alexander Stamboliiski reservoir.



A high proportion of the long-distance recaptures occurred during autumn (end of September, beginning of October) or winter in caves. If the bats were already torpid and if the roosts were occupied by the same species in winter for hibernation, we counted these recaptures as movements to hibernacula, the distances between the nursery colony and the hibernacula are given in table 2. In *R. ferrumequinum,* the distances covered towards the hibernacula were not significantly different between males and females [Man-Whitney-U-test, U = 39.5, p = 0.4000] and between subadult and adult females [Man-Whitney-U-test, U = 194.0, p = 0.4515]. It is quite obvious that most of the long distance recaptures were made in caves situated in the same or in neighbouring river systems of the initial ringing site. Our telemetry data also support the hypothesis that horseshoe bats use valleys and rivers as major flight paths to commute between different parts of their annual home range.

Table 2: Distances of movements of horseshoe bats (Rhinolophidae - *Rhinolophus*) between the nursery colony and hibernation sites. Abbreviations: f – female, m – male, ad – adult, subad - subadult. Statistics are given in the text.

Species	Sex	distance of hibernacula from summer roost (km) mean +/- SD (n) min – max
R. ferrumequinum	m	61.8 +/- 5.5 (3) 57.2 – 67.9
	f	56.6 +/- 11.2 (37) 41.9 – 89.6
	f ad	55.2 +/- 10.9 (20) 41.9 – 67.9
	f subad	58.1 +/- 11.6 (17) 44.9 – 89.6
R. euryale	f	44.9 - 58.8 km (2)
R. mehelyi	f	89.9 km (1)

The greater horseshoe bat is regarded as a sedentary species that rarely migrates longer distances (Roer 1995). The longest movements of the species have so far been reported from Hungary (320 km: Dobrosi 1996, cited in Schober & Grimmberger 1998) and Spain (180 km: de Paz et al. 1986 cited in Serra-Cobo & Balcells 1991). Our recorded distances are far below these records, but the proportion of relatively far travelled individuals in the hibernacula and the mean distance between nursery and hibernacula are much higher than usually found in the species (e.g. Hooper & Hooper 1956, Issel & Issel 1960, Brosset & Poillet 1985). However, like in other facultative migrant bats the distance of movements might depend mainly on the availability of suitable roosts for hibernation. E.g. in *Myotis dasycneme* populations from the plains of the Netherlands and Northern Germany migrate 200 km (up to 330 km) to the south to reach the caves and mines of the mountains (Sluiter et al. 1971), in contrast populations in Denmark are quite sedentary and move only small distances between their summer roosts and limestone caves (Egsbaek et al. 1971). In our study area, the main site of the nursery colony could be regarded as possible hibernacula as well, however all the bats left this place to hibernate somewhere else. Bats prefer to hibernate in caves with stable and low temperatures to spend the winter with lowest possible energy expenditure (Ransome 1968, Ransome 1971, Nagel & Nagel 1991, Webb et al. 1996), a fact that might explain, that horseshoe bats migrate to caves at higher altitudes and avoid hibernating in the Danube plain at low altitudes with relatively high roost temperatures. Due to the absence of caves in the Romanian part of the Danube plain, we expect those populations also to migrate to the caves of the Bulgarian Prebalkan. Most probably there exists a high gene-flow between horseshoe bats of different colonies inhabiting the lowland of northern Bulgaria: The bats spread over a considerably large area of several thousand square-kilometres for hibernation and copulations occurred regularly in late autumn in caves used for hibernation (own data), so a more or less panmictic population structure can be expected. During our study the knowledge of the whole territory used by the studied subpopulations increased strongly with the number of recapture data, accordingly we do not believe that a separation of several populations based on a limited number of recapture data is meaningful (contra Bihari 2001).

In *R. euryale* and *R. mehelyi,* the recapture rate was too small to draw further conclusions, but the recorded distances clearly show that both species can cover large distances even within a short time. While movements of *R. euryale* of up to 134 km in France (Heymer 1964) and 83 km in Italy (Dinale 1967) have been already reported, our Bulgarian recaptures of three *R. mehelyi* in distances up to 94.1 km represent the new record for this species.

Longest movements recorded

The longest movements recorded of the five horseshoe bat species in Europe are so far: *R. ferrumequinum* – 320 km (Dobrosi 1996, cited in Schober & Grimmberger 1998) and 180 km (de Paz et al. 1986 cited in Serra-Cobo & Balcells 1991), *R. hipposideros* – 152 km (Heymer 1964), 150 km (Bels 1952) and 146 km (Harmata 1992), *R. euryale* – 134 km (Heymer 1964) and 83 km (Dinale 1967), *R. mehelyi* – 94 km (this study) and *R. blasii* – 6.4 km (Paunovic 1997a, 1997b).

Conclusions

All three studied species spread over a considerable part of the north-Bulgarian lowland in the course of annual movements. While the majority of female *R. ferrumequinum* came back to the banding site for reproduction, several *R. meheyli* and *R. euryale* changed the roosts and reproduced in other colonies. Based on similar observations in *R. euryale* Andera & Horaček (1982) assumed panmictic assemblies of several colonies. Our data show that the subpopulations of all three species seem to be well connected and a high gene-flow is likely. For conservation it is important to maintain the interchange of the colonies to guarantee a high gene flow between subpopulations. Protection measures should therefore also include migration routes, especially along rivers and the main hibernacula as meeting points and mating sites.

ACKNOWLEDGEMENTS

We are particularly grateful to all the people that helped to capture and recapture bats during our studies, especially the members of the Bulgarian Bat Research and Protection Group and our field assistants (in alphabetic order): I. Borrisov, K. Christov, D. Merdschanova, S. Merdschanov, B. Petrov, T. Troanski, N. Simov, S. Staneva and P. Zehtinsubadiev.

ZUSAMMENFASSUNG

Ergebnisse einer vierjährigen Beringungsstudie an drei Hufeisennasen-Fledermäusen (*Rhinolophus ferrumequinum*, *R. euryale* and *R. mehelyi*) werden vorgestellt. Über 1500 Hufeisennasen-Fledermäuse wurden größtenteils an einer als Wochenstube genutzten Höhle markiert. Der Großteil der Wiederfänge erfolgte am Beringungsort oder an nahe gelegenen Ausweichhangplätzen. Zur Überwinterung wanderten die Großen Hufeisennasen im Mittel 57 km und maximal 90 km in Richtung Balkan-Gebirge. Es konnten keine signifikanten Unterschiede in der Entfernung der Winterquartiere vom Sommerhangplatz zwischen Männchen und Weibchen oder Adulten und Jungtieren gefunden werden. Für die beiden anderen Hufeisennasen-Fledermäuse wurden ebenfalls weite Überflüge verzeichnet. Die Mittelmeer-Hufeisennase wechselte Quartier in Entfernungen von bis zu 60 km. Bei der bislang wenig untersuchten Mehely-Hufeisennase konnten erstmals Wanderungen von über 90 km dokumentiert werden.

References

Aihartza, J.R., I. Garin, U. Goiti, J. Zabala & I. Zuberogoita (2003): Spring habitat selection by the Mediterranean horseshoe bat (*Rhinolophus euryale*) in the Urdaibai Biosphere Reserve (Basque Country). – Mammalia 67: 25-32.

Andera, M. & I. Horaček (1982): Poznavame nase savce, 254 pp.; Praha.

Beaucournu, J.C. (1963): Observations sur le baguage des Chiroptères: résultats et dangers. – Mammalia 26: 539-565.

Bels, L. (1952): Fifteen years of bat-banding in the Netherlands. – Publicaties van het natuurhistorisch genootschap in Limburg 5: 1-99.

Benda, P., T. Ivanova, I. Horaček, V. Hanak, J. Cerveny, J. Gaisler, A. Gueorguieva, B. Petrov & V. Vohralik (2003): Bats (Mammalia: Chiroptera) of the Eastern Mediterranean. Part 3. Review of bat distribution in Bulgaria. – Acta Soc. Zool. Bohem. 67: 245-357.

Bihari, Z. (2001): Characteristics of the northernmost population of *Rhinolophus ferrumequinum* in the Carpathian Basin. – Acta Theriologica 46: 13-21.

Bontadina, F., H. Schofield & B. Naef-Daenzer (2002): Radio-tracking reveals that lesser horseshoe bats (*Rhinolophus hipposideros*) forage in woodland. – Journal of Zoology 258: 281-290.

Brosset, A. & A. Poillet (1985): Structure d´une population hibernante de grands rhinolophes *Rhinolophus ferrumequinum* dans l´est de la France. – Mammalia 49: 221-233.

Dinale, G. (1963): Studi sui chirotteri Italiani I. – Osservazioni sul *Rhinolophus euryale* in Liguria e nel Lazio. – Annali del Museo Civico di Storia Naturale Giacomo Doria 74: 1-29.

Dinale, G. (1967): Studii sui chirotteri italiani: VIII. Spostamenti di *Rhinolophus euryale* inanellati in Liguria. – Atti della Società Italiana di Science Naturali e del Museo Civico di Storia Naturale in Milano 106: 275-282.

Dulić, B. (1957): Report on the first bat banding and recoveries in Croatia. – Larus 9-10: 183-189.

Egsbaek, W., K. Kirk & H. Roer (1971): Beringungsergebnisse der Wasserfledermaus (*Myotis daubentoni*) und der Teichfledermaus (*Myotis dasycneme*) in Jütland. – Decheniana-Beihefte 18: 51-55.

Gaisler, J. (1960a): Ökologische Beobachtungen in einer Kolonie der Kleinen Hufeisennase (*Rhinolophus hipposideros*). – Acta Musei Reginae Hradecensis S.A., Scientiae naturales 1960: 83-99.

Gaisler, J. (1960b): Postnatale Entwicklung der Kleinen Hufeisennase (*Rhinolophus hipposideros*) unter natürlichen Bedingungen. – Symposium Theriologicum 1960: 118-125.

Gaisler, J. (1963): Nocturnal activity in the lesser horseshoe bat, *Rhinolophus hipposideros.* – Zoologicke Listy-Folia Zoologica 12: 223-230.

Gaisler, J. (1965): The female sexual cycle and reproduction in the lesser horseshoe bat (*Rhinolophus hipposideros hipposideros*). – Vest. Cesk. Spol. Zool. 29: 336-352.

Gaisler, J. & M. Titlbach (1964): The male sexual cycle in the lesser horseshoe bat (*Rhinolophus hipposideros hipposideros*). – Vest. Cesk. Spol. Zool. 28: 268-277.

Gaisler, J. & V. Hanak (1969a): Summary of the results of bat-banding in Czechoslovakia, 1948-1967. – Lynx 10: 25-34.

Gaisler, J. & V. Hanak (1969b): Ergebnisse der zwanzigjährigen Beringung von Fledermäusen (Chiroptera) in der Tschechoslowakei: 1948-1967. – Acta Sc. Nat. Brno 3: 1-33.

Goiti, U., J.R. Aihartza, I. Garin & J. Zabala (2003): Influence of habitat on the foraging behaviour of the Mediterranean horseshoe bat, *Rhinolophus euryale.* – Acta Chiropterologica 5: 75-84.

Harmata, W. (1992): Movements and migrations of lesser horseshoe bat, *Rhinolophus hipposideros* in south Poland. – Prace Zoologiczne 39: 47-60.

Heymer, A. (1964): Résultats du baguage de chauves-souris dans les Pyrénées-orientales de 1945 à 1959. – Vie et Milieu A 15: 765-799.

Hooper, J.H.D. & W.M. Hooper (1956): Habits and movements of cave-dwelling bats in Devonshire. – Proceedings of the Zoological Society of London 127: 1-26.

Issel, W. (1951): Ökologische Untersuchungen an der Kleinen Hufeisennase (*Rhinolophus hipposideros*) im mittleren Rheinland und unterem Altmühltal. – Zoologische Jahrbücher (Systematik, Ökologie und Geographie) 79: 71-86.

Issel, B. & W. Issel (1960): Beringungsergebnisse an der Großen Hufeisennase (*Rhinolophus ferrumequinum*) in Bayern. – Bonner Zoologische Beiträge, Sonderheft 11/ 1960: 124-142.

Kepka, O. (1960): Die Ergebnisse der Fledermausberingung in der Steiermark vom Jahr 1949 bis 1960. – Bonner Zoologische Beiträge, Sonderheft 11/ 1960: 54-76.

McAney, C.M. & J.S. Fairley (1988a): Habitat preference and overnight and seasonal variation in the foraging activity of lesser horseshoe bats. – Acta Theriologica 28: 393-402.

McAney, C.M. & J.S. Fairley (1988b): Activity patterns of the lesser horseshoe bat *Rhinolophus hipposideros* at summer roosts. – Journal of Zoology 216: 325-338.

McAney, C.M. & J.S. Fairley (1989): Analysis of the diet of the lesser horseshoe bat *Rhinolophus hipposideros* in the West of Ireland. – Journal of Zoology London 217: 491-498.

Mislin, H. (1945): Zur Biologie der Chiroptera III. Erste Ergebnisse der Fledermausberingung im Jura (Beobachtungen in den Winterquartieren 1940/45). – Revue Suisse de Zoologie 52: 371-376.

Mitchell-Jones, A.J., G. Amori, W. Bogdanowicz, B. Krystufek, P.J.H. Reijnders, F. Spitzenberger, M. Stubbe, J.B.M. Thissen, V. Vohralik & J. Zima (1999): The atlas of European mammals, 484 pp.; Poyser Natural History.

Nagel, A. & R. Nagel (1991): How do bats choose optimal temperatures for hibernation? – Comparative Biochemistry and Physiology 99A: 323-326.

Palmeirim, J.M. & L. Rodrigues (1993): The 2-minute harp trap for bats. – Bat Research News 34: 60-64.

Paunovic, M. (1997a): The history, results and problems of bat ringing in FR of Yugoslavia. V Naucno-strucni skup o prirodnim vrednostima I zastiti zivotne sredine. – *Zbornik radova*: 360-365. (in Serbian).

Paunovic, M. (1997b): First results of bat ringing in Zlotska Klisura Gorge. V Naucno-strucni skup o prirodnim vrednostima I zastiti zivotne sredine. – *Zbornik radova*: 366-371. (in Serbian).

Paunovic, M. (1998): New results on bats marking in eastern Serbia. – VI Ekoloska istina, Negotin: 243-246.

Ransome, R.D. (1968): The distribution of the greater horse-shoe bat, *Rhinolophus ferrum-equinum*, during hibernation, in relation to environmental factors. – Journal of Zoology 154: 77-112.

Ransome, R.D. (1971): The effect of ambient temperature on the arousal frequency of the hibernating greater horseshoe bat, *Rhinolophus ferrumequinum*, in relation to site selection and the hibernation state. – Journal of Zoology 164: 353-371.

Ransome, R.D. (1973): Factors affecting the timing of births of the greater horse-shoe bat (*Rhinolophus ferrumequinum*). – Period. Biol. 75: 169-175.

Ransome, R.D. (1989): Population changes of greater horseshoe bats studied near Bristol over the past twenty-six years. – Biological Journal of the Linnean Society 38: 71-82.

Ransome, R.D. (1998): The impact of maternity roost conditions on populations of greater horseshoe bats. – English Nature Research Reports No. 292, 80 pp.

Ransome, R.D. & A.M. Hutson (2000): Action plan for the conservation of the greater horseshoe bat in Europe (*Rhinolophus ferrumequinum*). – Nature and environment 109: 56 pp.

Roer, H. (1995): 60 years of bat-banding in Europe - Results and tasks for future research. – Myotis 32/33: 251-261.

Russo, D., G. Jones & A. Migliozzi (2002): Habitat selection by the Mediterranean horseshoe bat, *Rhinolophus euryale* (Chiroptera: Rhinolophidae) in a rural area of southern Italy and implications for conservation. – Biological Conservation 107: 71-81.

Russo, D., G. Jones & M. Mucedda (2001): Influence of age, sex and body size on echolocation calls of Mediterranean and Mehely's horseshoe bats, *Rhinolophus euryale* and *R. mehelyi* (Chiroptera: Rhinolophidae). – Mammalia 65: 429-436.

Schober, W. & E. Grimmberger (1998): Die Fledermäuse Europas; Kosmos-Naturführer, 265 Seiten; Stuttgart.

Serra-Cobo, J. & E. Balcells (1991): Migraciones de quiroptéros en España. – In: J. Benzal & O. de Paz (Eds.): Los murciélagos de España y Portugal: 183-209; Colección Técnica ICONA.

Sluiter, J.W., P.F. van Heerdt & A.M. Voûte (1971): Contribution to the population biology of the pond bat, *Myotis dasycneme.* – Decheniana-Beihefte 18: 1-44.

Webb, P.I., J.R. Speakman & P.A. Racey (1996): How hot is a hibernaculum? A review of the temperature at which bats hibernate. – Canadian Journal of Zoology 74: 761-765.

Appendix 1: Long distance recaptures of *Rhinolophus ferrumequinum* in Northern Bulgaria.

Abbreviations: f – female, m – male, ad – adult, juv - juvenile.

ring	sex	age	date	locality	N	E	distance	direction
N 00288	f	ad	18.06.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			27.06.2001	Mandrata cave, Aleksandrovo	43°14′	24°58′	43.8 km	169°
			12.07.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′	43.8 km	349°
N 00389	f	ad	06.07.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			24.08.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′	-	-
			12.01.2002	Parnitcite cave, Bežanovo	43°12′	24°26′	58.8 km	218°
			09.08.2003	Nanin Kamăk cave, Muselievo	43°38′	24°51′	58.8 km	38°
N 00399	f	ad	06.07.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			29.09.2002	small mine near Sanadinovo	43°33′	25°00′	15.1 km	128°
N 00401	f	juv	12.07.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			03.08.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′	-	-
			14.08.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′	-	-
			12.01.2002	Parnitcite cave, Bežanovo	43°12′	24°26′	58.8 km	218°
			16.05.2003	cave (twin cave) near Muselievo	43°37′	24°51′	58.0 km	42°
			12.07.2003	Nanin Kamăk cave, Muselievo	43°38′	24°51′	1.8 km	339°
			09.08.2003	Nanin Kamăk cave, Muselievo	43°38′	24°51′	-	-
			28.06.2004	Nanin Kamăk cave, Muselievo	43°38′	24°51′	-	-
N 00418	f	juv	03.08.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			30.09.2002	Emenskata Peštera cave, Emen	43°08′	25°22′	68.8 km	144°
N 00441	f	juv	09.08.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			12.01.2002	Uruška Maara cave, Krušuna	43°15′	25°02′	44.9 km	160°
N 00444	f	ad	09.08.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			29.09.2002	small mine near Sanadinovo	43°33′	25°00′	15.1 km	128°
N 00448	f	ad	09.08.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			12.01.2002	Parnitcite cave, Bežanovo	43°12′	24°26′	58.8 km	218°
			10.05.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′	58.8 km	38°
			14.06.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′	-	-
			27.09.2002	underground gallery near Somovit	43°41′	24°46′	9.9 km	322°
			09.08.2003	Nanin Kamăk cave, Muselievo	43°38′	24°51′	9.9 km	42°
N 00476	f	ad	13.08.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			12.01.2002	Parnitcite cave, Bežanovo	43°12′	24°26′	58.8 km	218°

N 00497	f	juv	14.08.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			12.01.2002	Parnitcite cave, Bežanovo	43°12′	24°26′	58.8 km	218°
N 00498	f	juv	14.08.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			12.01.2002	Parnitcite cave, Bežanovo	43°12′	24°26′	58.8 km	218°
N 00511	f	ad	06.07.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			16.05.2003	cave (twin cave) near Muselievo	43°37′	24°51′	1.8 km	159°
			03.10.2003	Devetaškata Peštera cave, Devetaki	43°14′	24°53′	41.9 km	182°
N 00535	f	juv	12.07.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			12.01.2002	Parnitcite cave, Bežanovo	43°12′	24°26′	58.8 km	218°
			12.07.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′	58.8 km	38°
			02.07.2004	Nanin Kamăk cave, Muselievo	43°38′	24°51′	-	-
N 00580	f	juv	22.08.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			12.01.2002	Parnitcite cave, Bežanovo	43°12′	24°26′	58.8 km	218°
N 00581	f	juv	22.08.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			12.01.2002	Parnitcite cave, Bežanovo	43°12′	24°26′	58.8 km	218°
			03.08.2003	Nanin Kamăk cave, Muselievo	43°38′	24°51′	58.8 km	38°
			09.08.2003	Nanin Kamăk cave, Muselievo	43°38′	24°51′	-	-
N 00590	f	ad	22.08.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			14.06.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′	-	-
			29.09.2002	small mine near Sanadinovo	43°33′	25°00′	15.1 km	128°
N 00591	f	juv	22.08.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			12.01.2002	Parnitcite cave, Bežanovo	43°12′	24°26′	58.8 km	218°
N 00592	m	juv	24.08.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			02.10.2002	Mikrenska Peštera cave, Mikre	43°04′	24°31′	67.9 km	205°
N 00603	f	ad	24.08.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			12.01.2002	Parnitcite cave, Bežanovo	43°12′	24°26′	58.8 km	218°
			22.05.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′	58.8 km	38°
N 00605	f	juv	24.08.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			12.01.2002	Parnitcite cave, Bežanovo	43°12′	24°26′	58.8 km	218°
N 00608	m	juv	01.09.2001	farm building near Muselievo	43°38′	24°50′		
			12.01.2002	Parnitcite cave, Bežanovo	43°12′	24°26′	57.2 km	218°
			19.06.2002	farm building near Muselievo	43°38′	24°50′	57.2 km	38°
N 00614	f	juv	02.09.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			12.01.2002	Uruška Maara cave, Krušuna	43°15′	25°02′	44.9 km	160°
			22.05.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′	44.9 km	340°

N 01001	f	ad	10.05.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			22.05.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′	-	-
			29.09.2002	small mine near Sanadinovo	43°33′	25°00′	15.1 km	128°
N 01008	f	ad	17.05.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			06.07.2003	Nanin Kamăk cave, Muselievo	43°38′	24°51′	-	-
			18.08.2003	Nanin Kamăk cave, Muselievo	43°38′	24°51′	-	-
			01.10.2003	Mikrenska Peštera cave, Mikre	43°04′	24°31′	67.9 km	205°
N 01012	f	ad	17.05.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			02.10.2002	Mikrenska Peštera cave, Mikre	43°04′	24°31′	67.9 km	205°
N 01027	f	ad	17.05.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			30.09.2002	Uruška Maara cave, Krušuna	43°15′	25°02′	44.9 km	160°
N 01033	f	ad	17.05.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			14.06.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′	-	-
			28.09.2002	Devetaškata Peštera cave, Devetaki	43°14′	24°53′	43.7 km	178°
N 01045	f	ad	17.05.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			05.05.2003	Nanin Kamăk cave, Muselievo	43°38′	24°51′	-	-
			03.10.2003	Uruška Maara cave, Krušuna	43°15′	25°02′	44.9 km	160°
			29.06.2004	Nanin Kamăk cave, Muselievo	43°38′	24°51′	44.9 km	340°
N 01098	f	ad	22.05.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			01.10.2003	Mikrenska Peštera cave, Mikre	43°04′	24°31′	67.9 km	205°
N 01122	f	ad	10.06.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			29.09.2002	small mine near Sanadinovo	43°33′	25°00′	15.1 km	128°
			02.07.2004	Nanin Kamăk cave, Muselievo	43°38′	24°51′	15.1 km	308°
N 01126	f	ad	10.06.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			06.07.2004	building in Sanadinovo	43°32′	25°00′	15.5 km	131°
N 01136	f	ad	10.06.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			12.06.2002	telemetry data: range extends to Muselievo, valley 1	-	-	3.1 km	280°
			17.04.2003	Uruška Maara cave, Krušuna	43°15′	25°02′	44.9 km	160°
N 01145	f	ad	14.06.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			29.09.2002	small mine near Sanadinovo	43°33′	25°00′	15.1 km	128°
N 01167	f	ad	14.06.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			12.07.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′	-	-
			30.09.2002	Uruška Maara cave, Krušuna	43°15′	25°02′	44.9 km	160°

N 01169	f	ad	14.06.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			03.07.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′	-	-
			28.09.2002	Devetaškata Peštera cave, Devetaki	43°14′	24°53′	43.7 km	178°
N 01176	f	ad	14.06.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			15.06.2002 – 20.06.2002	telemetry data: range extends to	-	-		
				Muselievo, valley 1			3.0 km	280°
				Muselievo, valley 2			3.4 km	315°
				Čerkvica			8.0 km	360°
				Romania			9.7 km	5°
				homerange: MCP 100%: 2005 ha				
				minimum rangespan 9,8 km				
			12.07.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′	-	-
			15.08.2002	bridge near Čerkvica	43°42′	24°51′	8.1 km	357°
			14.04.2003	small mine near Sanadinovo	43°33′	25°00′	21.1 km	145°
			15.04.2003	Cave (twin cave) near Muselievo	43°37′	24°51′	13.6 km	305°
			16.05.2003	Cave (twin cave) near Muselievo	43°37′	24°51′	-	-
			01.08.2003	Cave (twin cave) near Muselievo	43°37′	24°51′	-	-
N 01184	f	ad	28.06.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			29.09.2002	small mine near Sanadinovo	43°33′	25°00′	15.1 km	128°
			12.05.2003	Nanin Kamăk cave, Muselievo	43°38′	24°51′	15.1 km	308°
N 01227	f	ad	28.06.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			28.09.2002	Devetaškata Peštera cave, Devetaki	43°14′	24°53′	43.7 km	178°
N 01330	f	ad	12.07.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			08.02.2003	Devetaškata Peštera cave, Devetaki	43°14′	24°53′	43.7 km	178°
			06.07.2003	Nanin Kamăk cave, Muselievo	43°38′	24°51′	43.7 km	358°
			20.07.2003	Nanin Kamăk cave, Muselievo	43°38′	24°51′	-	-
			03.08.2003	Nanin Kamăk cave, Muselievo	43°38′	24°51′	-	-
			18.08.2003	Nanin Kamăk cave, Muselievo	43°38′	24°51′	-	-
N 01352	f	ad	12.07.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			02.10.2002	Mikrenska Peštera cave, Mikre	43°04′	24°31′	67.9 km	205°
			06.06.2004	Nanin Kamăk cave, Muselievo	43°38′	24°51′	67.9 km	25°
N 01370	f	ad	12.07.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			29.09.2002	small mine near Sanadinovo	43°33′	25°00′	15.1 km	128°
N 01401	f	juv	10.08.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			30.09.2002	Uruška Maara cave, Krušuna	43°15′	25°02′	44.9 km	160°
			01.08.2003	cave (twin cave) near Muselievo	43°37′	24°51′	43.0 km	342°

N 01410	m	juv	10.08.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			02.10.2002	Sedlarkata cave, Rakita	43°17′	24°18′	60.3 km	230°
N 01412	f	juv	10.08.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			30.09.2002	Uruška Maara cave, Krušuna	43°15′	25°02′	44.9 km	160°
			16.05.2003	cave (twin cave) near Muselievo	43°37′	24°51′	43.0 km	342°
N 01484	f	juv	16.08.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			01.10.2003	Mikrenska Peštera cave, Mikre	43°04′	24°31′	67.9 km	205°
N 01522	f	juv	27.09.2002	cave (twin cave) near Muselievo	43°37′	24°51′		
			26.02.2003	Orlova Čuka cave, Pepelina	43°35′	25°58′	89.6 km	92°
N 01523	f	juv	27.09.2002	cave (twin cave) near Muselievo	43°37′	24°51′		
			03.10.2003	Uruška Maara cave, Krušuna	43°15′	25°02′	44.9 km	160°
			06.06.2004	Nanin Kamăk cave, Muselievo	43°38′	24°51′	44.9 km	340°
N 01532	f	ad	14.04.2003	small mine near Sanadinovo	43°33′	25°00′		
			07.05.2003	Nanin Kamăk cave, Muselievo	43°38′	24°51′	15.1 km	308°
N 01578	f	ad	16.05.2003	cave (twin cave) near Muselievo	43°37′	24°51′		
			01.10.2003	Mikrenska Peštera cave, Mikre	43°04′	24°31′	66.4 km	206°
N 01595	f	ad	16.05.2003	cave (twin cave) near Muselievo	43°37′	24°51′		
			01.08.2003	cave (twin cave) near Muselievo	43°37′	24°51′	-	-
			01.10.2003	Mikrenska Peštera cave, Mikre	43°04′	24°31′	66.4 km	206°
N 01799	f	juv	09.08.2003	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			01.10.2003	Mikrenska Peštera cave, Mikre	43°04′	24°31′	67.9 km	205°
N 01828	f	juv	09.08.2003	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			01.10.2003	Mikrenska Peštera cave, Mikre	43°04′	24°31′	67.9 km	205°
			06.06.2004	Nanin Kamăk cave, Muselievo	43°38′	24°51′	67.9 km	25°
N 01876	f	juv	18.08.2003	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			02.07.2004	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			01.03.2005	Parnitcite cave, Bežanovo	43°12′	24°26′	58.8 km	218°
N 0xxxx	?	?	2001-2003	Lower Osăm valley (around Nanin Kamăk cave, Muselievo)	≈43°38′	≈24°51′		
			29.07.2003	Mikrenska Peštera cave, Mikre	43°04′	24°31′	≈ 68 km	≈ 205°
N 0xxxx	f	?	2001-2002	Lower Osăm valley (around Nanin Kamăk cave, Muselievo)	≈ 43°38′	≈ 24°51′		
			02.07.2002	Devetaškata Peštera cave, Devetaki	43°14′	24°53′	≈ 43 km	≈ 178°
N 0xxxx	f	?	2001-2004	Lower Osăm valley (around Nanin Kamăk cave, Muselievo)	≈ 43°38′	≈ 24°51′		
			06.07.2004	building in Sanadinovo	43°32′	25°00′	≈ 15 km	≈ 131°

N 0xxxx	f	?	2001-2002	Lower Osam valley (around Nanin Kamăk cave, Muselievo)	≈ 43°38′	≈ 24°51′		
			03.07.2002	Uruška Maara cave, Krušuna	43°15′	25°02′	≈ 45 km	≈ 160°

Appendix 2: Recaptures of *Rhinolophus ferrumequinum* in Northern Bulgaria marked with bands of unknown origin. Abbreviations see Appendix 1.

ring	sex	age	date	locality	N	E	distance	direction
Sofia D 2428		?	?	?	?	?		
	m	ad	06.07.2004	Mandrata cave, Aleksandrovo	43°14′	24°58′	?	?
Sofia D 2?62		?	?	?	?	?		
	f	ad	14.06.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′	?	?
	new ring N 01146		20.07.2003	Nanin Kamăk cave, Muselievo	43°38′	24°51′	-	-

Appendix 3: Long distance recaptures of *Rhinolophus euryale* in Northern Bulgaria. Abbreviations see Appendix 1.

ring	sex	age	date	locality	N	E	distance	direction
A 03006	f	ad	22.05.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			06.08.2002	Uruška Maara cave, Krušuna	43°15′	25°02′	44.9 km	160°
A 03030	f	ad	14.04.2003	small mine near Sanadinovo	43°33′	25°00′		
			07.10.2003	Nanin Kamăk cave, Muselievo	43°38′	24°51′	15.1 km	308°
A 03033	f	ad	07.05.2003	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			02.08.2003	Uruška Maara cave, Krušuna	43°15′	25°02′	44.9 km	160°
E 411102	f	ad	19.06.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			19.06.2001-22.06.2001	telemetry data: range extends to south of Trănčovica	-	-	20.4 km	150°
			25.06.2001	Mandrata cave, Aleksandrovo	43°14′	24°58′	43.8 km	169°
			27.06.2001	Mandrata cave, Aleksandrovo	43°14′	24°58′	-	-
			03.07.2002	Uruška Maara cave, Krušuna	43°15′	25°02′	5.1 km	85°

E 411103	f	ad	23.06.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			23.06.2001 - 25.06.2001	telemetry data: range extends to Osăm near Trănčovica and South of Trănčovica	-	-	19.8 km	130-150°
			29.06.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′	-	-
			30.06.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′	-	-
			01.07.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′	-	-
			02.07.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′	-	-
			02.08.2003	Uruška Maara cave, Krušuna	43°15′	25°02′	44.9 km	160°
			07.10.2003	Nanin Kamăk cave, Muselievo	43°38′	24°51′	44.9 km	340°
E 411117	f	juv	03.08.2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			13.01.2002	Parnitcite cave, Bežanovo	43°12′	24°26′	58.8 km	218°
A 030xx	f		2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			03.07.2002	Uruška Maara cave, Krušuna	43°15′	25°02′	44.9 km	160°
E 4111xx	f		2001	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			03.07.2002	Uruška Maara cave, Krušuna	43°15′	25°02′	44.9 km	160°

Appendix 4: Long distance recaptures of *Rhinolophus mehelyi* in Northern Bulgaria.

Abbreviations see Appendix 1.

ring	sex	age	date	locality	N	E	distance	direction
A 03215	f	ad	25.09.2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			06.02.2003	Orlova Čuka cave, Pepelina	43°35′	25°58′	89.9 km	94°
E 411318	f	ad	07.05.2003	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			26.05.2003	Zorovica Peštera cave, Červen	43°36′	26°01′	94.1 km	93°
A 03xxx	?	?	2002	Nanin Kamăk cave, Muselievo	43°38′	24°51′		
			27.09.2002	Zorovica Peštera cave, Červen	43°36′	26°01′	94.1 km	93°

Chapter 5

Growth of horseshoe bats (Chiroptera: Rhinolophidae) in temperate continental conditions and the influence of climate

By C. Dietz, Isabel Dietz and B. M. Siemers

The ms. was published in:

Mammalian Biology 72 (3): 129-144.

Receipt of Ms. 19.11.2005

Acceptance of Ms. 09.07.2006

Printed 2007

Growth of horseshoe bats (Chiroptera: Rhinolophidae) in temperate continental conditions and the influence of climate

By C. Dietz, Isabel Dietz and B. M. Siemers

Animal Physiology, Zoological Institute, Tübingen University, Tübingen, Germany

ABSTRACT

Growth characteristics of three species of horseshoe bats (*Rhinolophus ferrumequinum*, *R. euryale* and *R. mehelyi*) were studied in northern Bulgaria, and measurements of cohorts born there in different years were compared interannually. Bulgarian horseshoe bats are usually born in the first 3 weeks of June and start to leave the roost at an age of about 3 weeks. Young horseshoe bats of all three species had attained more than 95 % of the adult dimensions at the time when they started to regularly leave the cave to forage on their own in mid of July. Individually marked juvenile *R. ferrumequinum* reached adult dimensions in most external wing measurements in the first half of August. Accordingly the pooled measurements of all juveniles did not differ anymore from those of adult bats in the second half of August. The same pattern was found in *R. mehelyi* and *R. euryale*.

We found clear relationship between the climatic conditions prevailing in each year and the final size of individuals born respectively in those years. Whereas previous studies have addressed climatic effects only on several bat species along their northern limits of distribution, these data provide the first evidence for an influence of climate on the growth of individuals in the centre of the species' distributions.

Key words: *Rhinolophus ferrumequinum*, *R. euryale*, *R. mehelyi*, growth, climate.

INTRODUCTION

Growth and development of juveniles is an important life-history trait in terrestrial vertebrates (Case 1978; Ricklefs 1979; Peters 1983; Read and Harvey 1989; Promislov and Harvey 1990). This physical growth depends primarily on nutrition (Tuttle 1976; Case 1978; Kunz and Stern 1995; Bennett 1999; McAdam and Boutin 2003), but may also be affected by other intrinsic and extrinsic factors which modulate both growth rates and the final size of the individuals (Tuttle 1976; Case 1978; Henry and Ulijaszek 1996; Ochoa-Acuna et al. 1998; Lindstrom 1999; Kunz and Hood 2000; Hood et al. 2002).

Temperate zone bat species have only one breeding season a year (Tuttle and Stevenson 1982) and their parturition, lactation and weaning cycles coincide with maximum food availability in summer (Racey 1982; Kurta et al. 1989; Racey and Entwistle 2000; Arlettaz et al. 2001; Barclay and Harder 2003). As with all small mammals, postnatal growth rates are high. The juveniles are weaned after a short time and reach adult size quickly (Forsyth 1976; Case 1978). Parental care is usually limited to only a few weeks (Wilde et al. 1995; Kunz and Hood 2000).

The juveniles must deposit fat reserves quickly before the onset of their first winter (Boyce 1979; Tuttle and Stevenson 1982; Kunz et al. 1998). However, food availability in the form of insect density varies considerably from year to year, mainly as a function of climate (Williams 1940, 1961; Rautenbach et al. 1988). For example, lower temperatures and strong precipitation decrease insect densities (Taylor 1963). Since energy costs for endothermic animals like bats increase with lower temperatures (Stones and Wiebers 1965a, b, 1966), unfavourable years and/or lower insect densities may reduce the growth rates of bats, particularly at more northerly latitudes. This can lead in the extreme case to stunted growth and increased juvenile mortality (Roer 1973; Jones et al. 1995; Masson 1999).

However, the growth of juvenile bats is not affected by nutrition alone. Since bats are heterothermic, their body temperature and physiological activities are also strongly affected by changes in their roost temperature. Several studies have shown a clear correlation between birth time, prevailing climate temperatures and the size of juvenile bats, especially of horseshoe bats (Rhinolophidae), along the respective species' northern distribution ranges (Ransome 1989, 1998; McOwat and Andrews 1995; Hoying and Kunz 1998; Koehler and Barclay 2000; Kunz and Hood 2000; Hood et al. 2002; Reiter 2004).

Sustained foraging flight in bats requires a mature, rigid skeleton (Burnett and Kunz 1982), and their wing bone growth takes place during the first few weeks of life. As a consequence bats can not "catch up" later if their nutritional support is limited during the juvenile growth period. Such stunted growth may well lead to a shortened life expectancy and lower reproductive success in bats (Ransome 1998) while also influencing flight performance and habitat use (Kalcounis and Brigham 1995; Adams 1996).

Accordingly, wing measurements are a suitable measure of growth conditions during the major growth phase of bats and can be compared between years. The wing measurement that can be taken most accurately in the field is the forearm length. It is therefore commonly used to measure bat size. The lengths of the fifth and third fingers are important for describing the flight capabilities of bats (Findley et al. 1972; Norberg and Rayner 1987) and the lengths of the fourth finger phalanges in horseshoe is believed to influence their manoeuvrability (Dietz et al. 2006a).

Although intraspecific size differences in horseshoe bats in relation to climate have been found along the northern edge of their distribution, no data exist regarding the influence of climate on their growth rates farther south (e.g., in the Mediterranean area) or in extreme continental regions. The only studies concerning intraspecific size differences in bats at lower latitudes (e.g., southern Europe or the Mediterranean) have compared bats from different geographical areas only (e.g., Iliopoulou-Georgudaki 1986) rather than bats born in different years in the same region.

We investigated the influence of climatic factors on the achieved size of five external wing measurements in three sympatric species of horseshoe bats (*Rhinolophus ferrumequinum*, *R. mehelyi* and *R. euryale*) in the continental lowlands of northern Bulgaria.

MATERIAL AND METHODS

Study area

Our study was conducted in Northern Bulgaria in a hilly karst area between the lowlands of the Danube and the Balkan mountains. This region has a temperate continental climate with hot summers and cold dry winters. Mean annual temperature is around 12°C with an amplitude of about 23°C, winter minima of -35°C and summer maxima of +45°C. Precipitation is around 500 mm and highest in the months of May and June due to frequent strong, short thunderstorms. In summer extensive periods of dryness are common, and the overall summer climate is quite similar to that of the Mediterranean region (Grunewald and Stoilov 1998; Galabov 1953; Dimitrov 1966).

Bats were captured from April to October in the years 2001-2004 at colony sites and maternity roosts in natural caves. The main study sites were around the village of Muselievo in the Osam valley (caves Nanin Kamăk, Morenitza and twin cave, 43°37' N, 24°51' E), along the slope of the Devetaško plateau (caves Devetaškata Peštera, Mandrata and Uruška Maara), in the area of the Roussenski Lom (caves Zorovica Peštera and Orlova Čuka) and in further caves of the Pre-Balkan (Emenskata Peštera, Mikrenska Peštera, Sedloarkata and Parnitcite). Recapture of marked bats in the region has shown that these colony sites are inhabited by the same population of horseshoe bats (Dietz et al. 2006b). Bats were captured at 5-day intervals at the sites around Muselievo and at 2- week intervals at other sites by mist nets or harp traps at the entrances of the caves or by hand nets inside the roost. Captured horseshoe bats were kept individually in cloth bags until they were processed.

Field work was carried out under licence of the Bulgarian authorities (15-RD-08/15.01.2001, 48-00-56/16.01.2001, 8/02.07.2004 RIOSV Pleven, RIOSV Rousse).

Age classification and measurements

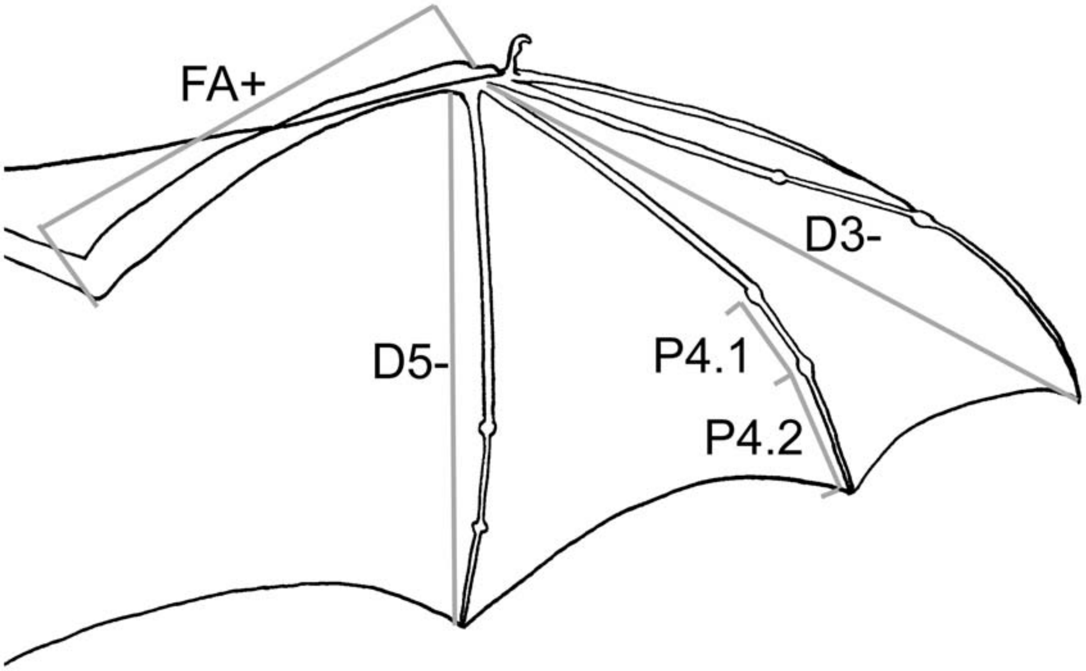
Horseshoe bats were identified by characters of the nose-leaf and the lower lip (Schober and Grimmberger 1998; Dietz and von Helversen 2004). Individuals were sexed by inspecting the genitalia and the age class was determined by the degree of closure of epiphyseal growth plates of the phalanges and by comparing fur colouration and –structure with those of ringed bats of known age (using characters described by Rollinat and Trouessart 1897; Matthews 1937; Gaisler 1960, 1965; Gaisler and Titlbach 1964). We used the following age classes for females: (1) unweaned juveniles born in the parturition season and characterised by the presence of unfused epiphyses; (2) weaned sub-adults born in the parturitions season (corresponding to yearlings), with greyer, sparser fur and not yet fully closed epiphyseal growth plates; (3) nulliparous adult females which have not given birth after their 1st winter or later (pubic nipples undeveloped, nipples small), including primigravid females early in pregnancy; (4) parous adult females which had given birth or were in an easily visible stage of their first pregnancy.

Studies on the reproductive biology of *R. ferrumequinum* in Bulgaria have shown that females give birth to their first young at an age of 2 years (own data). Similar timing can be assumed for the other two smaller-sized species as well. The vast majority of nulliparous females are therefore in their first year of life, belong to the cohort born in the previous year, and can be expected to show the size characteristics of that cohort. The adult population is an assemblage of bats born in many different years and represents the mean size characteristics of the population.

In males we distinguished only three groups: (1) juvenile: same characteristics as in females; (2) sub-adult (= yearling): immature males with a nearly invisible scrotum and a thinner penis combined with grey, sparse fur; (3) adult: full grown males with a normal-sized penis, visible scrotum, testes and epididymides (including males with adult dimensions and are more than one year old but possibly with no previous spermatogenesis).

The following measurements were taken with a mechanical precision calliper (Hommel-Hercules Industries, Viernheim, Germany, precision ± 0.1 mm): length of forearm including wrist (FA+), 5th finger excluding wrist (D5-), 3rd finger excluding wrist (D3-), 1st phalange of 4th digit (P4.1) and 2nd phalange of 4th digit (P4.2). At the sites around the village of Muselievo all captured horseshoe bats were marked individually by numbered flanged metal bat rings (but see Dietz et al. 2006c for a cautionary note on ringing horseshoe bats that was derived from experiences gathered during the present study).

Figure 1: Outstretched wing of a greater horseshoe bat. Measurements used in the text are indicated. Abbreviations: FA+: forearm length, D5-: length of fifth finger, D3-: length of third finger, P4.1: length of the first phalanx of the fourth finger, P4.2: length of the second phalanx of the fourth finger.



Time of birth and recording of growth

The time of birth was assed by noting the date of the first capture of lactating females and by daily inspection of the roosts by night to check for juveniles. To avoid unnecessary disturbance of the study colonies during several parallel projects (Dietz et al. 2006a, b, c), we neither marked newborn bats nor carried out repeated measurements of juveniles inside the roost. We also gathered data of juveniles only after the onset of flight when they could be captured at the roost entrances when leaving the cave together with adults.

Climatic data

Data on the climatic conditions in the region, in foraging areas in the surroundings, and in the main roosts were obtained by data-loggers for temperature and by counting the days on which precipitation occurred each month. Temperatures were recorded with Tinytag data-loggers (Gemini LTD, UK) with a recording range from -40 °C to 75 °C and a temperature-depending resolution of about 0.5 °C. Measurements were taken automatically every 40 minutes and the readings stored. Outside temperature loggers were deployed in shady locations 5 metres above ground and those in the main roost sites at the cave ceiling. Since outside temperatures between different foraging sites did not differ significantly, data are given only for the village of Muselievo (Tab. 6).

Statistics

To increase sample size and for better comparison, measurements were pooled for the 2-week periods at the beginning and end of each month. The aquired data were used to find the mean, the standard deviation (SD), the standard error of the mean (SEM) and the minimum (min) and maximum (max) sizes within the different groups. We used ANOVA and *t*-statistics for data analysis and the Dunnett-test for post-hoc comparisons, with the data of all adult bats as a control group. In post-hoc *t*-statistics, Bonferroni correction was applied by multiplying the *P*-

values by the number of pair-wise comparisons. Analyses were performed with Excel 2002 (Microsoft), Jump 5.1 (SAS) and Systat 11 (SPSS).

RESULTS

Time of birth

Births in the three species of horseshoe bats (*R. ferrumequinum*, *R. mehelyi* and *R. euryale*) peaked in the first three weeks of June in the years 2001 to 2003 Latest births of a few individuals occurred at the beginning of July, especially in the year 2004. The majority of births took place in a 10-day period each year.

Growth after the onset of flight

The first juveniles left the roost at about 3 weeks after the first newborn bats were observed in the colonies. We were able to compare the data of 41 individually marked *R. ferrumequinum* bats at different stages of growth when they were recaptured as adults in the following years (Tab. 1). In a paired two-sample *t*-test FA+, D5- and P4.2 were significant smaller in juveniles in the first half of July than the individualized adult measurements (paired two-sample *t*-test, $P<0.01$, Tab. 1). In the first half of August measurements of FA+, D5-, D3- and P4.1 in juveniles no longer differed from those of adults, whereas P4.2 reached adult values only at the end of August (paired two-sample *t*-test, $P>0.05$, Tab. 1).

Measurements of juveniles (including previously captured and individually marked juveniles) were pooled per 2 week intervals, and compared with all adult values. In *R. ferrumequinum* FA+, D5-, D3- and P4.2 were significantly smaller in juveniles until mid-August (*t*-test, $P<0.0001$), but similar to adult values from that time on (*t*-test, $P>0.11$, Tab. 2). Juvenile *R. euryale* and *R. mehelyi* bats captured in the second half of August were found to have attained adult dimensions, too; in fact, most *R. mehelyi* individuals had reached adult dimensions in the first half of August (two-sample *t*-test, $P>0.05$, Tabs. 3 and 4).

Table 1: Growth of juvenile *Rhinolophus ferrumequinum*: comparison of individual measurements (mean ± SD (n)) of marked bats and results of paired two-sample t-test (data sets with $n<5$ per 2-week interval not shown). Abbreviations: Juv = juveniles, Ad = adults, FA+ = forearm-length, D5- = length of 5th finger, D3- = length of 3rd finger, P4.1 = 1st phalange of the 4th finger, P4.2 = 2nd phalange of the 4th finger, numbers refer to the month, B = beginning, first 2 weeks of the month, E = end, last 2 weeks of the month.

Time	class	FA+ (mm)	D5- (mm)	D3- (mm)	P4.1 (mm)	P4.2 (mm)
B 07	Juv	56.4 ± 1.03 (9)	68.1 ± 1.75 (9)	-	11.1 ± 0.43 (9)	18.6 ± 0.73 (9)
	Ad	58.0 ± 1.07 (9)	70.9 ± 1.51 (9)	-	11.4 ± 0.57 (9)	19.9 ± 0.71 (9)
	Test	$t = 6.33$,	$t = 4.88$,	-	$t = 1.73$,	$t = 5.57$,
		$P = 0.0002$	$P = 0.0012$		$P = 0.1228$	$P = 0.0005$
B 08	Juv	57.8 ± 1.31 (23)	70.2 ± 2.50 (23)	81.6 ± 1.21 (3)	11.3 ± 0.63 (23)	19.3 ± 0.90 (23)
	Ad	58.3 ± 1.31 (23)	71.2 ± 2.32 (23)	86.6 ± 1.91 (3)	11.3 ± 0.61 (23)	19.7 ± 0.76 (23)
	Test	$t = 2.69$,	$t = 2.34$,	$t = 3.12$,	$t = 0.33$,	$t = 3.15$,
		$P = 0.0134$	$P = 0.0286$	$P = 0.0894$	$P = 0.7438$	$P = 0.0046$
E 08	Juv	58.7 ± 1.41 (12)	71.7 ± 1.89 (12)	86.9 ± 1.64 (8)	10.8 ± 0.55 (12)	19.8 ± 0.73 (12)
	Ad	58.9 ± 1.30 (12)	71.9 ± 2.08 (12)	87.5 ± 2.35 (8)	10.9 ± 0.46 (12)	19.8 ± 0.65 (12)
	Test	$t = 0.93$,	$t = 1.84$,	$t = 1.13$,	$t = 0.74$,	$t = 0.26$,
		$P = 0.3717$	$P = 0.0924$	$P = 0.2969$	$P = 0.4773$	$P = 0.8030$
All	Ad	58.3 ± 1.36 (41)	71.4 ± 2.11 (41)	87.5 ± 2.26 (16)	11.2 ± 0.51 (41)	19.8 ± 0.70 (41)

Table 2: Growth of juvenile *Rhinolophus ferrumequinum* until beginning of September: mean values of size parameters per 2 week intervals (mean ± SD (*n*)) and results of *t*-tests (Bonferroni adaptation p*8) in comparison to adult values in the last row: Abbreviations as in table 1.

Time	Class	FA+ (mm)	D5- (mm)	D3- (mm)	P4.1 (mm)	P4.2 (mm)
E 06	Juv	37.4 +/ 13.7 (8)	40.8 /- 15.3 (7)	-	7.3 ± 2.6 (6)	12.5 ± 4.4 (6)
	Test	t = 4.28,	t = 5.34,	-	t = 3.74,	t = 0.238,
		P = 0.0291	P = 0.0141		P = 0.1072	P = 0.0657
B 07	Juv	56.5 ± 2.2 (89)	67.4 ± 3.9 (88)	73.7 ± 7.1 (16)	10.8 ± 0.7 (89)	18.8 ± 0.9 (89)
	Test	t = 6.76,	t = 10.39,	t = 6.99,	t = 6.06,	t = 12.05,
		P < 0.0001	P < 0.0001	P < 0.0001	P < 0.0001	P < 0.0001
E 07	Juv	53.9 ± 2.3 (22)	63.4 ± 3.6 (22)	74.3 ± 5.8 (12)	10.5 ± 0.6 (22)	17.6 ± 1.1 (22)
	Test	t = 8.81,	t = 10.82,	t = 7.15,	t = 6.37,	t = 10.89,
		P < 0.0001	P < 0.0001	P = 0.0001	P < 0.0001	P < 0.0001
B 08	Juv	57.6 ± 1.4 (223)	70.4 ± 2.2 (224)	83.5 ± 3.3 (92)	11.2 ± 0.6 (224)	19.7 ± 0.8 (224)
	Test	t = 5.13,	t = 8.15,	t = 7.55,	t = 3.49,	t = 6.62,
		P < 0.0001	P < 0.0001	P < 0.0001	P = 0.0044	P < 0.0001
E 08	Juv	58.1 ± 1.4 (113)	71.4 ± 1.9 (110)	85.8 ± 2.4 (62)	11.1 ± 0.6 (110)	19.9 ± 0.8 (110)
	Test	t = 0.08,	t = 1.32,	t = 1.40,	t = 4.04,	t = 1.58,
		P = 1.0000	P = 1.0000	P = 1.0000	P = 0.0007	P = 0.1174
B 09	Juv	57.6 ± 1.6 (11)	70.3 ± 1.7 (11)	85.2 ± 2.8 (4)	11.5 ± 0.5 (11)	19.6 ± 0.9 (11)
	Test	t = 1.13,	t = 2.76,	t = 0.74,	t = 0.88,	t = 1.68,
		P = 1.0000	P = 0.1578	P = 1.0000	P = 1.0000	P = 0.9948
All	Ad	58.1 ± 1.4 (1127)	71.7 ± 1.9 (1124)	86.2 ± 2.4 (514)	11.3 ± 0.6 (1121)	20.1 ± 0.8 (1122)

Table 3: Growth of juvenile *Rhinolophus euryale* until beginning of September: comparison of mean values per 2 week intervals (mean ± SD (n)) and results of t-tests (Bonferroni adaptation p*7) in comparison to adult values: Abbreviations as in table 1.

Time	Class	FA+ (mm)	D5- (mm)	D3- (mm)	P4.1 (mm)	P4.2 (mm)
B 07	Juv	29.3 ± 10.3 (4)	33.1 ± 11.5 (4)	36.6 (1)	4.3 ± 1.4 (4)	9.9 ± 3.4 (4)
	Test	$t = 3.60$,	$t = 4.36$,	-	$t = 3.64$,	$t = 4.86$,
		$P = 0.2582$	$P = 0.1563$		$P = 0.2493$	$P = 0.1166$
E 07	Juv	46.8 +/ 0.8 (27)	56.7 ± 1.1 (27)	-	7.2 ± 0.4 (27)	17.7 ± 0.5 (27)
	Test	$t = 6.14$,	$t = 6.31$,	-	$t = 3.36$,	$t = 4.05$,
		$P < 0.0001$	$P < 0.0001$		$P = 0.0164$	$P = 0.0026$
B 08	Juv	47.0 ± 1.3 (57)	56.2 ± 2.1 (57)	67.2 ± 3.2 (3)	7.1 ± 0.4 (56)	17.4 ± 0.9 (56)
	Test	$t = 4.29$,	$t = 6.70$,	$t = 2.02$,	$t = 3.79$,	$t = 5.94$,
		$P = 0.0005$	$P < 0.0001$	$P = 1.0000$	$P = 0.0003$	$P < 0.0001$
E 08	Juv	47.9 ± 1.1 (38)	58.3 ± 1.3 (38)	70.8 ± 2.3 (9)	6.9 ± 0.4 (38)	18.3 ± 0.4 (38)
	Test	$t = 1.28$,	$t = 1.07$,	$t = 0.13$,	$t = 0.52$,	$t = 3.64$,
		$P = 1.0000$	$P = 1.0000$	$P = 1.0000$	$P = 1.0000$	$P = 0.0049$
B 09	Juv	47.5 ± 1.0 (7)	57.9 ± 0.7 (7)	68.6 (1)	6.8 ± 0.3 (7)	18.0 ± 0.6 (7)
	Test	$t = 0.58$,	$t = 0.80$,	-	$t = 1.14$,	$t = 0.22$,
		$P = 1.0000$	$P = 1.0000$		$P = 1.0000$	$P = 1.0000$
All	Ad	47.7 ± 1.0 (911)	58.1 ± 1.4 (911)	70.9 ± 1.8 (431)	6.9 ± 0.4 (909)	18.1 ± 0.6 (909)

Table 4: Growth of juvenile *Rhinolophus meheyli* until beginning of September: comparison of mean values per two week intervals (mean ± SD (n)) and results of t-tests (Bonferroni adaptation p*8) in comparison to adult values: Abbreviations as in table 1.

Time	Class	FA+ (mm)	D5- (mm)	D3- (mm)	P4.1 (mm)	P4.2 (mm)
E 06	Juv	39.2 +/ 14.0 (7)	45.0 /- 17.8 (7)	-	6.5 ± 1.9 (6)	15.0 ± 4.3 (6)
	Test	$t = 2.29$, $P = 0.4988$	$t = 2.56$, $P = 0.3457$	-	$t = 1.68$, $P = 1.0000$	$t = 2.66$, $P = 0.3605$
B 07	Juv	35.2 ± 7.2 (5)	38.2 ± 7.6 (5)	43.2 ± 0.8 (2)	5.6 ± 0.9 (5)	11.7 ± 2.3 (5)
	Test	$t = 5.02$, $P = 0.0591$	$t = 7.08$, $P = 0.0168$	$t = 61.79$, $P = 0.0680$	$t = 5.59$, $P = 0.0399$	$t = 7.67$, $P = 0.0123$
E 07	Juv	50.4 ± 1.2 (4)	59.8 ± 1.5 (4)	74.2 ± 2.9 (4)	8.0 ± 0.5 (4)	18.8 ± 1.1 (4)
	Test	$t = 1.61$, $P = 1.0000$	$t = 3.25$, $P = 0.3744$	$t = 2.34$, $P = 0.8023$	$t = 0.70$, $P = 1.0000$	$t = 1.56$, $P = 1.0000$
B 08	Juv	51.0 ± 1.0 (53)	61.2 ± 1.7 (53)	77.2 ± 1.3 (3)	8.1 ± 0.4 (53)	19.3 ± 0.7 (53)
	Test	$t = 2.57$, $P = 0.1008$	$t = 4.08$, $P = 0.0011$	$t = 0.20$, $P = 1.0000$	$t = 5.18$, $P < 0.0001$	$t = 3.64$, $P = 0.0047$
E 08	Juv	51.0 ± 1.3 (119)	62.2 ± 1.6 (119)	77.7 ± 2.1 (47)	7.9 ± 0.5 (119)	19.6 ± 0.6 (119)
	Test	$t = 2.49$, $P = 0.1122$	$t = 0.24$, $P = 1.0000$	$t = 0.40$, $P = 1.0000$	$t = 2.71$, $P = 0.0603$	$t = 0.77$, $P = 1.0000$
All	Ad	51.3 ± 1.0 (766)	62.2 ± 1.5 (766)	77.5 ± 1.9 (473)	7.8 ± 0.4 (765)	19.7 ± 0.7 (765)

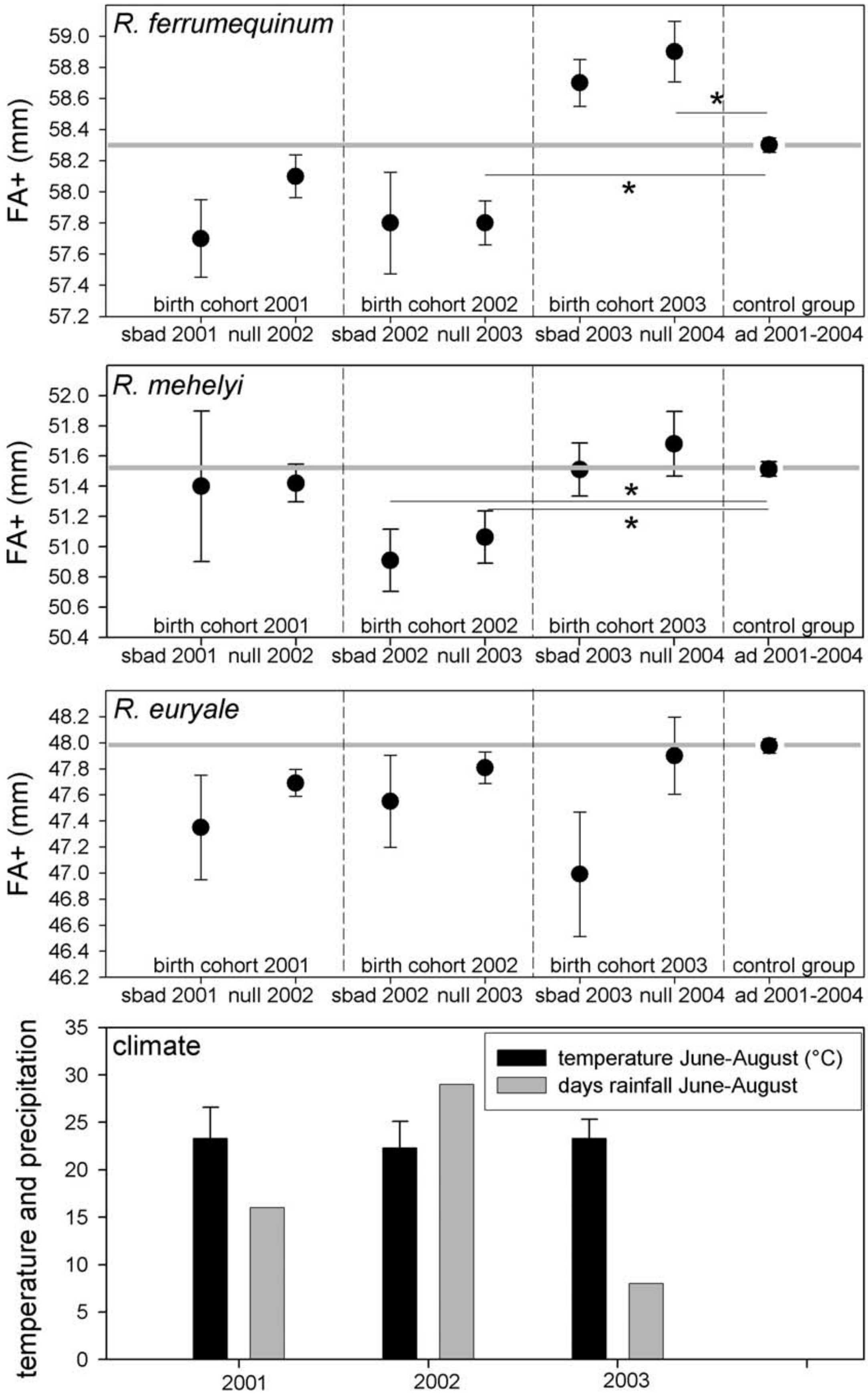
In the first, clumsily flying juveniles captured at the cave entrances, FA+ was approximately 60 % of the mean adult size; from the end of July onwards, FA+ had reached 97-98 % of mean adult size in juveniles of all three species leaving the cave regularly to forage on their own (Tabs. 1-4). With the exception of D3- in *R. ferrumequinum* (85 % of adult mean size), the other four measurements were close to adult dimensions (around 95 %) when the bats started to forage on their own.

Climatic conditions and growth

Climatic conditions in the study area during the period from 2001 to 2003 are shown in table 6. Summer temperatures in 2002 averaged 1 °C lower than in the other 2 years; there was a strong increase in the number of days with rainfall, precipitation was much higher than usual for these continental summers. On the other hand, the year 2003 was exceptionally dry (Tab. 6). Temperatures at the main roosting site remained constant during reproductive periods in all 3 years (Tab. 6). Insect densities were 3-14 times lower in the year 2002 than in the years 2003 and 2004 (depending on the respective insect order; I. Dietz, unpublished data from car-trap transects).

We found pronounced differences between the size and growth of cohorts of juveniles born in different years in two out of the three studied species. The clearest deviations from mean adult size were found in in *R. ferrumequinum* and *R. mehelyi* born in 2002 and in *R. ferrumequinum* born in 2003: the former were smaller, the latter were larger. Specifically, the measurement results were as follows. Wing dimensions (FA+, D5-, D3-, P4.1, P4.2) of bats born in different years differed significantly in *R. ferrumequinum* and *R. mehelyi* (ANOVA, $P<0.05$), but not in *R. euryale* (ANOVA, $P>0.05$). *R. ferrumequinum* born in 2003 (sub-adults in 2003 and nulliparous females in 2004) were significantly larger than those born in 2002 and 2004 (Tukey-test, $P<0.05$) (Fig. 2).

Figure 2: Comparison of the forearm length (FA+) between different birth cohorts in females of three species of horseshoe bats and climatic data during the corresponding reproduction period. Abbreviations: sbad = sub-adult (bats born in the year), null = nulliparous (bats born in the previous year), ad = adult (bats born in many years, serving as reference group). Data are given by their mean and the standard error of the mean. Results of an ANOVA and post-hoc Dunnett-test are shown: * = significant differences ($P<0.01$). Temperature is given by the mean of 40-min-interval measurements within 3 months (June-August), precipitation by the days with rainfall within 3 months (June-August).


R. ferrumequinum
FA+ (mm)
59.0
58.8
58.6
58.4
58.2
58.0
57.8
57.6
57.4
57.2
*
*
birth cohort 2001
birth cohort 2002
birth cohort 2003
control group
sbad 2001
null 2002
sbad 2002
null 2003
sbad 2003
null 2004
ad 2001-2004
R. mehelyi
FA+ (mm)
52.0
51.8
51.6
51.4
51.2
51.0
50.8
50.6
50.4
*
*
birth cohort 2001
birth cohort 2002
birth cohort 2003
control group
sbad 2001
null 2002
sbad 2002
null 2003
sbad 2003
null 2004
ad 2001-2004
R. euryale
FA+ (mm)
48.2
48.0
47.8
47.6
47.4
47.2
47.0
46.8
46.6
46.4
46.2
birth cohort 2001
birth cohort 2002
birth cohort 2003
control group
sbad 2001
null 2002
sbad 2002
null 2003
sbad 2003
null 2004
ad 2001-2004
climate
temperature and precipitation
35
30
25
20
15
10
5
0
temperature June-August (°C)
days rainfall June-August
2001
2002
2003

An even more significant influence of the birth-year on achieved size was found by comparing the wing dimensions of bats born in different years with the data of all adult bats, analyzed separately for males and females (Tab. 5 and Fig. 2). Comparison of different birth cohorts either in their year of birth (sub-adults) or in the following year (nulliparous females) revealed a significant influence of the birth year on size could be found in *R. ferrumequinum* and *R. mehelyi* (ANOVA, all $P<0.05$) but not in *R. euryale* (ANOVA, all $P>0.05$). In post-hoc tests using the adult bats of the same sex as control group, the nulliparous female *R. ferrumequinum* in 2003 (birth cohort of 2002) were significantly smaller while sub-adult males in 2003 and the nulliparous females in 2004 (birth cohort of 2003) were significantly larger than the pooled adults (Dunnett-test, $P<0.05$). In *R. mehelyi* the sub-adult females and males in 2002 and the nulliparous females in 2003 (birth cohort of 2002) were significantly smaller than the adults (Dunnett-test, $P<0.05$). In *R. euryale* no clear pattern could be detected, differences were not consistent in yearlings of both sexes (Tab. 5).

The differences were most pronounced in the measurements of FA+ and D5- (D3- was excluded due to low sample size). Judging from these data, factors in the year 2002 had a negative influence on growth of *R. ferrumequinum* and *R. mehelyi* in northern Bulgaria while factors of the year 2003 favoured growth in juvenile *R. ferrumequinum* only.

Table 5: Measurements (mean ± SD (*n*)) of different age cohorts of females in three species of *Rhinolophus*. Abbreviations: Sbad = sub-adults (= yearlings = animals born in the year, measurements from mid of August to beginning of October each year); Null = nulliparous (= full grown individuals without signs of reproduction); Rep = reproductive (= adult individuals showing signs of reproduction).

Species	Cohort	FA+ (mm)	D5- (mm)	P4.1 (mm)	P4.2 (mm)
R. ferrumequinum	Sbad 2001	57.7 ± 1.4 (31)	71.2 ± 1.9 (31)	11.3 ± 0.5 (31)	19.8 ± 0.7 (31)
	Sbad 2002	57.8 ± 1.7 (26)	71.1 ± 2.4 (25)	11.4 ± 0.5 (24)	20.1 ± 0.9 (24)
	Sbad 2003	58.7 ± 1.2 (59)	71.9 ± 1.6 (59)	11.1 ± 0.7 (59)	20.1 ± 0.7 (59)
	Null 2001	58.0 ± 1.4 (39)	71.8 ± 1.5 (39)	11.3 ± 0.5 (39)	20.1 ± 0.7 (39)
	Null 2002	58.1 ± 1.3 (96)	71.7 ± 1.9 (96)	11.5 ± 0.5 (96)	20.0 ± 0.7 (96)
	Null 2003	57.8 ± 1.3 (85)	71.1 ± 2.3 (85)	11.2 ± 0.6 (85)	19.9 ± 0.9 (85)
	Null 2004	58.9 ± 1.3 (46)	72.7 ± 1.5 (46)	11.3 ± 0.6 (46)	20.2 ± 0.6 (46)
	Rep 2001-2004	58.3 ± 1.2 (730)	71.9 ± 1.8 (727)	11.4 ± 0.6 (724)	20.1 ± 0.8 (725)
R. euryale	Sbad 2001	47.4 ± 1.1 (8)	58.1 ± 1.7 (8)	7.0 ± 0.4 (8)	18.1 ± 0.6 (8)
	Sbad 2002	47.6 ± 1.5 (18)	58.4 ± 1.6 (18)	7.0 ± 0.4 (18)	18.5 ± 0.4 (18)
	Sbad 2003	47.0 ± 1.6 (11)	55.9 ± 1.7 (11)	6.8 ± 0.4 (11)	17.2 ± 0.6 (11)
	Null 2001	48.2 ± 0.8 (24)	58.8 ± 1.0 (24)	6.9 ± 0.3 (24)	18.2 ± 0.5 (24)
	Null 2002	47.7 ± 0.9 (68)	58.0 ± 1.1 (68)	7.0 ± 0.4 (68)	18.1 ± 0.5 (68)
	Null 2003	47.8 ± 1.0 (65)	58.0 ± 1.5 (65)	6.9 ± 0.3 (65)	18.2 ± 0.6 (65)
	Null 2004	47.9 ± 1.2 (16)	58.5 ± 1.3 (16)	6.7 ± 0.3 (16)	18.1 ± 0.6 (16)
	Rep 2001-2004	48.0 ± 1.0 (325)	58.4 ± 1.4 (325)	6.9 ± 0.4 (323)	18.2 ± 0.6 (323)
R. mehelyi	Sbad 2001	51.4 ± 1.4 (8)	62.7 ± 0.9 (8)	8.0 ± 0.2 (8)	19.3 ± 0.5 (8)
	Sbad 2002	50.9 ± 1.3 (38)	61.7 ± 1.6 (38)	8.1 ± 0.4 (38)	19.6 ± 0.7 (38)
	Sbad 2003	51.5 ± 1.1 (36)	62.4 ± 1.5 (36)	7.6 ± 0.4 (36)	19.6 ± 0.6 (36)
	Null 2001	51.5 ± 1.0 (5)	62.4 ± 1.3 (5)	7.7 ± 0.5 (5)	19.0 ± 0.6 (5)
	Null 2002	51.4 ± 0.8 (44)	62.6 ± 1.3 (44)	8.0 ± 0.4 (44)	19.8 ± 0.6 (44)
	Null 2003	51.0 ± 1.1 (38)	61.7 ± 1.5 (38)	7.6 ± 0.6 (38)	19.6 ± 0.8 (38)
	Null 2004	51.6 ± 1.1 (26)	62.4 ± 1.3 (26)	7.6 ± 0.4 (26)	19.9 ± 0.6 (26)
	Rep 2001-2004	51.5 ± 1.0 (420)	62.5 ± 1.4 (420)	7.8 ± 0.4 (420)	19.7 ± 0.6 (420)

Table 6: Precipitation and temperature at the main study site Muselievo (northern Bulgaria) and at the main colony site in the vertical shaft of Nanin Kamăk cave 2001-2003.

	precipitation (n days with rain)	precipitation June-August (n days with rain)	maximum monthly temperature (°C)	minimum monthly temperature (°C)	mean monthly maximum temperature (°C)	mean monthly minimum temperature (°C)	mean monthly temperature (°C) ± SD	mean temperature (°C) ± SD	mean roost temperature (°C)	mean daily roost amplitude (°C)
June 2001	9	16	37.5	9.3	27.3	14.6	20.3 ± 2.8	23.3 ± 3.3	22.8	2.9
July 2001	5		37.0	15.3	31.6	18.3	24.4 ± 2.1			
August 2001	2		37.8	9.3	32.6	18.4	25.3 ± 2.5			
June 2002	9	29	34.9	9.9	27.0	16.2	21.7 ± 3.2	22.3 ± 2.8	22.5	2.4
July 2002	8		36.9	14.5	29.2	19.0	23.9 ± 2.6			
August 2002	12		30.7	11.3	26.4	16.8	21.4 ± 1.9			
June 2003	2	8	32.2	10.6	27.8	17.2	22.7 ± 2.0	23.3 ± 2.0	23.2	3.1
July 2003	5		32.6	12.8	28.1	17.2	22.7 ± 1.7			
August 2003	1		36.1	11.7	31.0	18.0	24.6 ± 1.8			
2001-2004	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**11.4 ± 10.1**	**11.9**	**-**

DISCUSSION

Bat flight requires a mature skeleton which is ossified enough to remain stable while the bats are catching insects in flight. Most bat species show a linear physical growth until a certain age, after which the growth rate decreases dramatically, and adult size is then reached in asymptotic growth (Burnett and Kunz 1982). Roost temperature seems to be the factor with most influence on the growth rate of neonatal bats during the first three weeks of life (McNab 1982; Tuttle and Stevenson 1982; Hood et al. 2002). However, roost temperature was not likely to have a major impact on final size during the second growth period, with its decreased growth rate. Growth at this stage may be affected mainly by nutrition which depends on the foraging skills of the volant young and prey availability.

Size at the onset of flight

Juveniles of all three horseshoe bats began to leave their roosts after attaining 95% or more of adult skeletal size. This accords with findings for other bat species (de Paz 1986; Barclay 1995; Hoying and Kunz 1998).

End of growth

Most wing measurements taken in juveniles of the three horseshoe bat species were indistinguishable from those of adult values from mid of August onward, corresponding to an approximated age of 6-7 weeks. In *R. mehelyi*, the earlier end of growth is probably explained by earlier births. Our measurements of sub-adult horseshoe bats in south-eastern Europe from mid-August onward can therefore be considered as adult values. Wing shape and size in the greater horseshoe bat is fixed when growth of forearm stops at after 40 days and of the 5th finger after 60 days (Ransome 1989, 1998). Gaisler (1960) found *R. hipposideros* reaches final size at an age of about 10 weeks.

Influence of climate

Most probably climate affects the horseshoe bats' growth via insect densities; a correlation found in many studies before (Williams 1940, 1961; Taylor 1963; Rautenbach et al. 1988; Hoying and Kunz 1998).

Conclusions

The observation time of three years in our study was too short for a well-supported statistic, but we think it likely that the stunted growth in two species of horseshoe-bats in the year 2002 resulted from depleted prey densities caused by the unusual wet and cold conditions during this years' reproduction time. Conversely, the data suggest that the very dry weather in 2003 favoured growth in *R. ferrumequinum*. Since roost temperature remained constant during all 3 years, this factor cannot explain the observed size differences. The relationship between size differences in *R. ferrumequinum* cohorts born in different years and climatic effects is thus a phenomenon which is present not only at the northern limit of the species' distribution (Ransome 1989, 1998; McOwat and Andrews 1995), but also exists in the centre of its European distribution in the Balkans. That is, climate has an influence on the final achieved body size of bats in temperate areas with a Mediterranean summer and a continental winter.

From an individuals point of view growing in unfavourable circumstances is only possible with a reduced growth rate. A slow-down in growth rate results in a lesser adult size and as a consequence in a shortened live expectation and reduced fitness (Ransome 1998). On the other hand, lower growth rates might be adaptive under averse conditions, because a constant and high growth rate might lead to a higher risk of infant mortality (Roer 1973; Jones et al. 1995; Masson 1999). Prey density as a function of climate can be regarded as the main factor for adjustment of an optimal individual growth rate within the limits of genetical, physical and physiological possibilities of the species (Case 1978).

In summary, climate has a major influence on the regulation of growth in bats. It thereby affects the survival and reproductive success of different birth cohorts in most parts of species' distribution and should be taken into account when comparing populations.

ACKNOWLEDGEMENTS

Our study in Bulgaria was made possible through the cooperation with the Bulgarian Bat Research and Protection group, especially with T. Ivanova. We are grateful for the help received in many respects of the project, for organising permits and showing the Bulgarian roost sites. We are indebted to S. Merdschanov, D. Merdschanova, K. Christov, I. Borrisov and S. Staneva for their continuous support and help in catching bats, to B.P. Petrov for logistical help and to the people of the village of Museliveo for their hospitality and their sympathy with our "odd" studies, especially to Eleonora Dimanova (Lelja Nora = aunt Nora) for her kind hospitality and love. We are very grateful to A. Tsoar, T. Rice and an anonymous reviewer for many helpful comments and improvements on an earlier version of the manuscript.

This research was funded by grants of the Graduiertenförderung des Landes Baden-Württemberg to CD and of the Deutsche Bundesstiftung Umwelt to ID. Further support was given by the Reinhold-und-Maria-Teufel-Stiftung to CD and ID and the German Research Foundation to BMS.

ZUSAMMENFASSUNG

Wachstum von Hufeisennasen-Fledermäusen (Chiroptera: Rhinolophidae) unter temperat-kontinentalen Bedingungen und der Einfluss des Klimas

Wir untersuchten das Wachstum dreier Arten von Hufeisennasen-Fledermäusen (*Rhinolophus ferrumequinum*, *R. euryale* und *R. mehelyi*) in Bulgarien und verglichen Messwerte verschiedener Geburtsjahrgänge. Bulgarische Hufeisennasen-Fledermäuse werden in der Regel in den ersten drei Juni-Wochen geboren und verlassen das Quartier erstmals in einem Alter von etwa drei Wochen. Mit dem Beginn des selbstständigen Beuteerwerbs ab Ende Juli erreichen die Jungtiere aller drei Arten bereits mehr als 95% der adulten Flügelmaße in vier Meßstrecken. Individuell markierte Jungtiere der Großen Hufeisennase (*R. ferrumequinum*) erreichten in den meisten Flügelmaßen Adultdimensionen in der zweiten Augusthälfte. Entsprechend wichen dann auch die gemittelten Maße aller Jungtiere ab Ende August nicht mehr von denen adulter Tiere ab. Ein vergleichbares Muster wurde auch bei *R. mehelyi* und *R. euryale* gefunden.

Wir konnten auch eindeutige Größenunterschiede zwischen verschiedenen Geburtsjahrgängen nachweisen, die mit Klimabedingungen während der Wachstumsphase in Zusammenhang zu bringen sind. Anhand dieser Daten kann erstmals ein Einfluss des Klimas auf das Wachstum von Individuen im Zentrum ihres Verbreitungsgebietes gezeigt werden. Bisherige Untersuchungen konnten solch einen Einfluss lediglich auf Population an den nördlichen Verbreitungsgrenzen der Arten nachweisen.

REFERENCES

Adams, R.A. (1996): Size-specific resource use in juvenile little brown bats, *Myotis lucifugus* (Chiroptera: Vespertilionidae): Is there an ontogenetic shift? Can. J. Zool. **74**, 1204-1210.

Arlettaz, R.; Christe, P.; Lugon, A.; Perrin, N.; Vogel, P. (2001): Food availability dictates the timing of parturition in insectivorous mouse-eared bats. Oikos **95**, 105-111.

Barclay, R.M.R. (1995): Does energy or calcium availability constrain reproduction by bats? Symp. Zool. Soc. Lond. **67**, 245-258.

Barclay, R.M.R.; Harder, L.D. (2003): Life histories of bats: life in the slow lane. In: Bat Ecology. Ed. by T.H. Kunz and M.B. Fenton. Chicago: University of Chicago Press. Pp. 209-253.

Bennett, R.P. (1999): Effects of food quality on growth and survival of juvenile Columbian ground squirrels (*Spermophilus columbianus*). Can. J. Zool. **77**, 1555-1561.

Boyce, M.S. (1979): Seasonality and patterns of natural selection for life histories. Am. Nat. **114**, 569-583.

Burnett, C.D.; Kunz, T.H. (1982): Growth rates and age-estimation in *Eptesicus fuscus* and comparison with *Myotis lucifugus*. J. Mammalogy **63**, 33-41.

Case, T.J. (1978): On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. Q. Rev. Biol. **53**, 243-282.

de Paz, O. (1986): Age estimation and postnatal growth of the greater mouse-eared bat *Myotis myotis* in Guadalajara, Spain. Mammalia **50**, 243-251.

Dietz, C.; von Helversen, O. (2004): Identification Key to the Bats of Europe. 72 pp. Electronical publication, version 1.0, available at www.uni-tuebingen.de/tierphys/Kontakt/mitarbeiter_seiten/dietz.htm.

Dietz, C.; Dietz, I.; Siemers, B.M. (2006a): Wing measurement variations in the five European horseshoe bat species (Chiroptera: Rhinolophidae). J. Mammalogy **87** (in press).

Dietz, C.; Dietz, I.; Ivanova, T.; Siemers, B.M. (2006b): Movements of horseshoe bats (*Rhinolophus*, Chiroptera: Rhinolophidae) in Northern Bulgaria. Myotis (in press).

Dietz, C.; Dietz, I.; Ivanova, T.; Siemers, B.M. (2006c): Effects of forearm bands on horseshoe bats (Chiroptera: Rhinolophidae). Acta Chiropterologica (in press).

Dimitrov, D. (1966): Klimatična podjalba v Bălgarija, Geografija na Bălgarija 1, Fizičeska geografija. Sofia: Bulgarian Academy of Sciences.

Findley, J.S.; Studier, E.H.; Wilson, D.E. (1972): Morphological properties of bat wings. J. Mammalogy **53,** 429-444.

Forsyth, D.J. (1976): A field study of growth and development of nestling masked shrews (*Sorex cinereus*). J. Mammalogy **57,** 708-721.

Gaisler, J. (1960): Postnatale Entwicklung der Kleinen Hufeisennase (*Rhinolophus hipposideros*) unter natürlichen Bedingungen. Symp. Theriol. **1960**, 118-125.

Gaisler, J. (1965): The female sexual cycle and reproduction in the lesser horseshoe bat (*Rhinolophus hipposideros hipposideros*). Vestn. Cesk. Spol. Zool. **29**, 336-352.

Gaisler, J.; Titlbach, M. (1964): The male sexual cycle in the lesser horseshoe bat (*Rhinolophus hipposideros hipposideros*). Vestn. Cesk. Spol. Zool. **28**, 268-277.

Galabov, S. (1953): Mjastoto na geomorphologiijata v krăga na geologo-geografskite nauki. Proc. Bulg. Geograph. Soc. **1**, 1-273.

Grunewald, K.; Stoilov, D. (1998): Natur- und Kulturlandschaften Bulgariens. Bulgarische Bibliothek (N.F.) **3**, 1-179 pp.

Henry, C.J.K.; Ulijaszek, S.J. (1996): Long-term consequences of early environment. Cambridge: University press.

Hood, W.R.; Bloss, J.; Kunz, T.H. (2002): Intrinsic and extrinsic sources of variation in size at birth and rates of postnatal growth in the big brown bat *Eptesicus fuscus* (Chiroptera: Vespertilionidae). J. Zool. (London) **258**, 355-363.

Hoying, K.M.; Kunz, T.H. (1998): Variation in size at birth and post-natal growth in the insectivorous bat *Pipistrellus subflavus.* J. Zool. (London) **245**, 15-27.

Hughes, P.M.; Ransome, R.D.; Jones, G. (1989): Aerodynamic constrains on flight ontogeny in free-living greater horseshoe bats, *Rhinolophus ferrumequinum*. In: European Bat Research 1987. Ed. by V. Hanak, I. Horacek and J. Gaisler. Pp. 255-262.

Iliopoulou-Georgudaki, J. (1986): The relationship between climatic factors and forearm length of bats: evidence from the chiropterofauna of Lesvos island (Greece – East Aegean). Mammalia **50**, 475-482.

Jones, G.; Duvergé, P.L.; Ransome, R.D. (1995): Conservation biology of an endangered species: field studies of greater horseshoe bats. Symp. Zool. Soc. Lond. **67**, 309-324.

Kalcounis, M.C.; Brigham, R.M. (1995): Intraspecific variation in wing loading affects habitat use by little brown bats (*Myotis lucifugus*). Can. J. Zool. **73**, 89-95.

Koehler, C.E.; Barclay, R.M.R. (2000): Post-natal growth and breeding biology of the hoary bat (*Lasiurus cinereus*). J. Mammalogy **81**, 234-244.

Kunz, T.H.; Hood, W.R. (2000): Parental care and postnatal growth in the Chiroptera. In: Reproductive Biology of Bats. Ed. by E.G. Crichton and P.H. Krutzsch. San Diego: Academic Press. Pp. 415-468.

Kunz, T.H.; Stern, A.A. (1995): Maternal investment and post-natal growth in bats. Symp. Zool. Soc. London **67**, 123-138.

Kunz, T.H.; Wrazen, J.A.; Burnett, C.D. (1998): Changes in body mass and fat reserves in pre-hibernating little brown bats (*Myotis lucifugus*). Ecoscience **5**, 8-17.

Kurta, A.; Bell, G.P.; Nagy, K.A.; Kunz, T.H. (1989): Energetics of pregnancy and lactation in free-ranging little brown bats (*Myotis lucifugus*). Physiol. Zool. **62**, 804-818.

Lindstrom, J. (1999): Early development and fitness in birds and mammals. TREE **14**, 343-348.

Masson, D. (1999): Histoire naturelle d'une colonie de parturition de Rhinolophe euryale, *Rhinolophus euryale*, (Chiroptera) du sud-ouest de la France. Arvicola **11**, 41-50.

Mathews, L.H. (1937): The female sexual cycle in the British horse-shoe bats, *Rhinolophus ferrum-equinum insulanus* and *R. hipposideros minutus.* Trans. Zool. Soc. (London) **32**, 224-266.

McAdam, A.G.; Boutin, S. (2003): Effects of food abundance on genetic and maternal variation in the growth rate of juvenile red squirrels. J. Evol. Biol. **16**, 1249–1256.

McNab, B.K. (1982): Evolutionary alternatives in the physiological ecology of bats. In: Ecology of Bats. Ed. by T.H. Kunz. New York: Plenum Publishing Corporation. Pp. 151-200.

McOwat, T.P.; Andrews, P.T. (1995): The influence of climate on the growth rate of *Rhinolophus ferrumequinum* in West Wales. Myotis **32/33**, 69-79.

Norberg, U.M.; Rayner, J.M.V. (1987): Ecological morphology and flight in bats: wing adaptations, flight performance, foraging strategy and echolocation. Phil. Trans. R. Soc. Lond. **316,** 335-427.

Ochoa-Acuna, H.; Francis, J.M.; Boness, D.J. (1998): Interannual variation in birth mass and postnatal growth rate of Juan Fernández fur seals. Can. J. Zool. **76**, 978-983.

Peters, R.H. (1983): The Ecological Implications of Body Size.Cambridge: University Press. Pp. 329.

Promislov, D.E.L.; Harvey, P.H. (1990): Living fast and dying young: a comparative analysis of life-history variation among mammals. J. Zool. (London) **220**, 417-437.

Rautenbach, I.L.; Kemp, A.C.; Scholtz, C.H. (1988): Fluctuations in availability of arthropods correlated with microchiropteran and avian predator activities. Koedoe **31**, 77-90.

Racey, P.A. (1982): Ecology of bat reproduction. In: Ecology of bats. Ed. by T.H. Kunz. New York: Plenum Publishing Corporation. Pp. 57-104.

Racey, P.A.; Entwistle, A.C. (2000): Life-history and reproductive strategies of bats. In: Reproductive Biology of Bats. Ed. by E.G. Crichton and P.H. Krutzsch. San Diego: Academic Press. Pp. 363-414.

Ransome, R.D. (1989): Population changes of greater horseshoe bats studied near Bristol over the past twenty-six years. Biol. J. Linn. Soc. **38**, 71-82.

Ransome, R.D. (1995): Earlier breeding shortens life in female greater horseshoe bats. Philos. Trans. R. Soc. Lond. B **350**, 153-161.

Ransome, R.D. (1998): The impact of maternity roost conditions on populations of greater horseshoe bats. English Nature Research Reports No. 292, 80 pp. English Nature.

Read, A.F.; Harvey, P.H. (1989): Life history differences among the eutherian radiations. J. Zool. (London) **219**, 329-353.

Reiter, G. (2004): Postnatal growth and reproductive biology of *Rhinolophus hipposideros* (Chiroptera: Rhinolophidae). J. Zool. (London) **262**, 231-241.

Ricklefs, R.E. (1979): Adaptation, constraint, and compromise in avian postnatal development. Biol. Rev. **54**, 269-290.

Roer, H. (1973): Über die Ursachen hoher Jugendmortalität beim Mausohr, *Myotis myotis*. Bonn. Zool. Beitr. **24**, 332-341.

Rollinat, R.; Trouessart, E. (1897): Sur la reproduction des chauves-souris. II. Les Rhinolophes (1). Mem. Soc. Zool. Fr. **10**, 114-138.

Sano, A. (2000): Postnatal growth and development of thermoregulative ability in the Japanese greater horseshoe bat, *Rhinolophus ferrumequinum nippon*, related to maternal care. Mammal Study **25**, 1-15.

Schober, W.; Grimmberger, E. (1998): Die Fledermäuse Europas. 265 pp. Stuttgart: Kosmos-Naturführer. Pp. 1-265.

Stones, R.C.; Wiebers, J.E. (1965a): Seasonal changes in food consumption of little brown bats held in captivity at a „neutral“ temperature of 92° F. J. Mammalogy **46**, 18-22.

Stones, R.C.; Wiebers, J.E. (1965b): A review of temperature regulation in bats (Chiroptera). Am. Midl. Nat. **74** 155-167.

Stones, R.C.; Wiebers, J.E. (1966): Body weight and temperature regulation of *Myotis lucifugus* at a low temperature of 10°C. J. Mammalogy **47**, 520-521.

Taylor, L.R. (1963): Analysis of the effect of temperature on insects in flight. J. Anim. Ecol. **32**, 99-117.

Tuttle, M.D. (1976): Population ecology of the gray bat (*Myotis grisescens*): factors influencing growth and survival of newly volant young. Ecology **57**, 587-595.

Tuttle, M.D.; Stevenson, D. (1982): Growth and survival of bats. In: Ecology of bats. Ed. by T.H. Kunz. New York: Plenum Publishing Corporation. Pp.105-150.

Wilde, C.J.; Kerr, M.A.; Knight, C.H.; Racey, P.A. (1995): Lactation in vespertilionid bats. Symp. Zool. Soc. Lond. **67**, 139-149.

Williams, C.B. (1940): An analysis of four years captures of insects in a light trap. Part II. The effect of weather conditions on insect activity; and estimation and forecasting of changes in the insect population. Trans. R. Entomol. Soc. Lond. **90**, 227-306.

Williams, C.B. (1961): Studies in the effect of weather conditions on the activity and abundance of insect populations. Phil. Trans. R. Soc. Lond. B **244**, 331-378.

Chapter 6

Wing measurement variations in the five European horseshoe bat species (Chiroptera: Rhinolophidae)

By C. Dietz, Isabel Dietz and B. M. Siemers

The ms. was published in:

Journal of Mammalogy 87 (6): 1241-1251.

Submitted 09.09.2005

Accepted 30.04.2006

Printed 2006

WING MEASUREMENT VARIATIONS IN THE FIVE EUROPEAN HORSESHOE BAT SPECIES (CHIROPTERA: RHINOLOPHIDAE)

Christian Dietz*, Isabel Dietz and Björn M. Siemers

ABSTRACT

Wing morphology is crucial for flight performance and foraging ecology in bats. We describe variations in 5 wing parameters within the 5 species of European horseshoe bats (genus *Rhinolophus*) based on data taken from 3,081 adult individuals. All 5 species belong to a single ecological guild. Measurements were taken from live bats in the field in southeastern Europe (Bulgaria, Greece, and Turkey), where all 5 species occur in sympatry.

Examination of our data shows that the species and accordingly their wings differ substantially in size. Albeit grossly similar in form, we additionally found several size-independent differences in wing shape. For example, the smallest species, *Rhinolophus hipposideros*, and to a lesser extent also *R. blasii*, have extremely short hand wings, enabling highly maneuverable search flight close to vegetation. The largest species *R. ferrumequinum* and the second largest one, *R. mehelyi*, have rather long hand wings, allowing fast and economic commuting flight over longer distances. We argue that both size and shape are likely to play a role for niche separation between species.

We found both sexual and geographic variation within species. There was sexual dimorphism for most parameters, with females being larger than males. Populations of *R. mehelyi* in southeastern Europe had significant variation in wing measurements. This was not so for *R. ferrumequinum* and *R. euryale*. We give a discriminant function based on only 2 parameters that correctly assigned 98% of the 3081 individuals to species. This function may prove useful for identification of museum specimens.

Key words: guild-structure, *Rhinolophus*, wing measurements, wing morphology

INTRODUCTION

According to the competition exclusion principle, similar species evolve different ecological niches to reduce or avoid competition (Hardin 1960; Schoener 1974; Wiens 1977). Because food acquisition is crucial for survival, foraging ecology plays a major role in this context. When sympatric animal species have similar foraging mechanisms, strategies, and behavior, they face the problem of how to avoid niche overlap, especially when prey are limited. Separation can be achieved by several mechanisms such as character displacement (Brown and Wilson 1956); selection of different habitats, prey types, foraging times and foraging styles (e.g., Aldridge 1986; Jones et al. 1993); morphological variation (Bogdanowicz et al. 1999; Findley et al. 1972; Van Valen 1965); and differences in sensory ecology (Siemers and Swift 2006). An insectivorous bat's ability to use its environment depends largely on its sensory ability to detect and recognize prey (Siemers and Schnitzler 2004), and its ability to maneuver through habitats (Norberg and Rayner 1987) and to retrieve food. Its ability to capture a prey item is determined by its flight capabilities, particularly agility and maneuverability, which in turn are influenced by wing morphology (Fenton 1990; Findley et al. 1972; Vaughan 1959) and body size (Swartz et al. 2003). Changes in morphology result in differences in flight performance (Adams 1996; Aldridge 1986; Findley and Black 1983; Norberg 1981) which directly affect habitat use (Aldridge and Rautenbach 1987; Brigham et al. 1997; Jacobs 1996, 1999; Norberg 1994; Stockwell 2001). Differences in wing morphological features such as wing loading can be significant predictors of habitat use (Kalcounis and Brigham 1995). However, similarity in wing morphology does not necessarily restrict species to similar foraging behaviors or similar habitats (Saunders and Barclay 1992). In closely related and similar species there may be fine modifications of a given suite of features or wing construction rather than dramatic differences (Brigham et al. 1997; Findley and Wilson 1982; Rhodes 2002; Saunders and Barclay 1992; Schum 1984). To evaluate such subtle variations among similar species, a representatively large group is needed to capture variations within populations and to parse out intersexual and other intraspecific variation (Swartz et al. 2003).

The 5 European horseshoe bat species (*R. hipposideros, R. mehelyi, R. blasii, R. euryale* and *R. ferrumequinum*; Chiroptera: Rhinolophidae) offer a suitable model system for investigating possibly minute variations within 1 guild of insectivorous bats, because they are closely-related members of a single genus (Guillén et al. 2003). We collected and analyzed morphological data for all members of this guild in southeastern Europe. The 5 species have extensive overlap in their distribution in southeastern Europe (Mitchell-Jones et al. 1999). All of them produce long duration constant-frequency echolocation calls with a maximum energy concentrated in the 2nd harmonic (Griffin and Simmons 1974; Heller and von Helversen 1989; Jones and Rayner 1989; Möhres 1953; Russo et al. 2001; Siemers et al. 2005). Horseshoe bats use frequency and amplitude shifts modulated onto the echoes of their constant-frequency calls by the wing beats of insects as a means of detecting prey (Schnitzler 1983). All European horseshoe bats are similar in several morphological respects, including short and broad wings with a large wing area giving low wing loading, aspect ratio and tip shape index (Findley et al. 1972; Norberg 1987; Norberg and Rayner 1987). However, the European species differ in size and body mass: The average body mass and forearm length of the lesser horseshoe bat (*R. hipposideros*) are 6-7 g and 37-42 mm respectively, those of the greater horseshoe bat (*R. ferrumequinum*) 20-26 g and 54-61 mm, and those of the 3 medium-sized species (*R. mehelyi*, *R. blasii* and *R. euryale*) are quite similar (9-14 g and 42-54 mm, respectively - Schober and Grimmberger 1998). All 5 species catch prey by “flycatching” from a perch or during patrolling flights close to a cluttered background, and at least some species may also take prey from the ground (Bontadina et al. 2002; Jones and Rayner 1989; Russo et al. 2002, Siemers & Ivanova 2004). With the exception of the lesser horseshoe bat (*R. hipposideros*), these 5 horseshoe bat species prey predominately on nocturnal moths (Beck et al. 1989, 1997; Goiti et al. 2004; Valenciuc 1971). The lesser horseshoe bat (*R.*

hipposideros) is distributed over most of southern and central Europe and has the northernmost limit of distribution of all rhinolophids in Europe, reaching Ireland, the Netherlands and Poland (Mitchell-Jones et al. 1999). The species prefers to roost in buildings, but colonies in the south also are also found in caves (Schober and Grimmberger 1998). The species preys mainly on small Diptera, Lepidoptera and other small insects, predominately in or close to forests (Beck et al. 1989; Bontadina et al. 2002; Jones and Rayner 1989). The greater horseshoe bat (*R. ferrumequinum*) is found in southern and central Europe as far north as southern England and Wales, the Netherlands and Poland (Mitchell-Jones et al. 1999). Breeding colonies in the north are mainly in buildings, in the south predominately in underground roosts (Schober and Grimmberger 1998). These bats forage in a wide variety of habitats from open meadows to parks and woodlands, where they prey mainly on coprophagous beetles and moths (Beck et al. 1997; Bontadina et al. 1995, 1997; Jones and Rayner 1989). The ecology of the 3 medium-sized species are less well known. Their distribution in Europe is confined to the area around the Mediterranean. The Mediterranean horseshoe bat (*R. euryale*) has the widest distribution, extending north to central France, Italy, Slovakia and Romania; Mehelyi's horseshoe bat (*R. mehelyi*) is found in southern and central Iberia, southern France, Sardinia, Sicily, Greece and in the Balkans north to Romania; Blasius' horseshoe bat (*R. blasii*) is restricted to southeastern Europe from the Adriatic coast over the Balkans to Greece and Romania (Mitchell-Jones et al. 1999). All 3 species roost mainly in caves and other underground galleries (Schober and Grimmberger 1998) and prey predominately on moths (Goiti et al. 2004; Valenciuc 1971; Whitaker and Black 1976). *R. euryale* forages mainly in forests, while *R. mehelyi* prefers to forage in less densely vegetated habitats of a savannah-type (Russo et al. 2002, 2005). Habitat preferences of *R. blasii* remain unknown (Siemers and Ivanova 2004).

On the basis of the unique combination of echolocation call design, wing morphology, foraging style and prey consumed, we hypothesized that all 5 European horseshoe bat species can be united in a single guild of ‘aerial insectivore narrow space flutter-detecting foragers’ (Schnitzler and Kalko 1998, 2001; Schnitzler et al. 2003).

We made 5 external wing measurements that can easily be assessed in living bats, on 3,081 adults from the entire guild in their sympatric area of distribution in southeastern Europe.

The wing measurements we took were the lengths of the forearm (as a measurement for the bats’ size), 5th finger (as a measure of wing width), 3rd finger (as a measure of hand wing length) and of the phalanges of the 4th finger (identification character only). Findley et al. (1972) have shown that the first 3 measurements, namely lengths of forearm, 5th and 3rd finger, can be used to produce wing area proxies that correlate very closely with wing area parameters like aspect ratio and tip index. These derived indices, in turn, are strong indicators of aerodynamic performance (Adams 1996; Aldridge 1986; Norberg 1981) and reflect ecological adaptations (Aldridge and Rautenbach 1987; Brigham et al. 1997; Kalcounis and Brigham 1995; Norberg 1994). Building on these previous studies, we used the 3 easily assessable wing measurements and their interrelations as proxies for aerodynamic performance of our study species: A long 3rd finger in relation to forearm size is indicative of rather long hand wings and thereby fast and economic commuting flight. A long 5th finger in relation to forearm size indicates broad wings and thereby high maneuverability and potentially hovering ability. A short 3rd finger in relation to the 5th finger indicates a short, broad hand wing; that is, adaptations for slow flight in narrow spaces.

While one aim was to generate a discriminant function for reliable species identification of museum specimens or bats with an abnormal or deformed nose-leaf, our research focused on the following question: Do the 5 species vary in size only (while remaining structurally the same) or are also other morphological differences present which enable niche separation? As a consequence, we addressed the following related questions: 1) How do absolute wing measurement values differ in the 5 species? 2) Can the species be identified by external wing measurements alone? (This would be useful for identifying museum specimens, since preservation - especially drying - destroys the diagnostic characteristics of the nose leaf.) 3) Is sexual size dimorphism present in the species studied? 4) Are intraspecific differences found between populations in southeastern Europe? 5) Do the 5 congeners differ in wing shape?

MATERIAL AND METHODS

Field sites.– Our study was carried out in southeastern Europe, where all 5 European species of horseshoe bats (*Rhinolophus blasii*, *R. euryale*, *R. ferrumequinum*, *R. hipposideros* and *R. mehelyi*) occur in sympatry. Wing measurements were taken between 1999 and 2004 from individuals captured in roosts in Bulgaria, Greece and Turkey. In northern Bulgaria, bats were captured in the hills and lowlands north of the Balkan range along the rivers Osăm, Vit, Jantra and Lom (caves Nanin Kamăk, Devetaškata Peštera, Mandrata, Uruška Maara, Zorovica Peštera, Orlova Čuka, Emenskata Peštera, Mikrenska Peštera, Sedloarkata and Parnitcite). We refer to bats from these sites as belonging to the northern populations. Recaptures of marked bats suggested that the study area might be inhabited by a single population (Dietz et al. in press). The other study sites were south of the Balkan mountains and are referred to as southern populations: Eastern Rhodope Mountains in Bulgaria (caves Ajna Ini and Samara Peštera) and Greece (caves Maronia, Vouva Lefkimis, Koufovouno and the mines of Kirki), Strandža Mountains in Bulgaria (abandoned building at Primorsko and cave Lejarnicite Peštera) and Turkey (cave Dupnisa Mağarasi) and in the region of Macedonia in north-western Greece (caves of Sidirokastron and surroundings). More bats were captured at various places in Bulgaria, Greece and western Anatolia. Fieldwork was carried out under license of Bulgarian (15-RD-08/15.01.2001, 48-00-56/16.01.2001, 8/02.07.2004 RIOSV Pleven, RIOSV Rousse) and Greek (97371/2554/16-5-2002, 94728/1025/28-2-2003 and 98358/1437/18-3-2004) authorities.

Processing.– Bats were captured with mist-nets or harp-traps when leaving or entering day-roosts in caves, mines and abandoned buildings or with hand-nets inside the roosts. They were kept individually in cloth bags until measured. We followed guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998) in our capture and handling procedures.

Bats were sexed and then identified using nose-leaf and lower lip characteristics only (Schober and Grimmberger 1998; see Identification key to the bats of Europe [Dietz and von Helversen 2004]: www.uni-tuebingen.de/tierphys/Kontakt/mitarbeiter_seiten/dietz.htm., August 2006). Five standard measurements were taken with a mechanical precision caliper (Hommel-Hercules Industries, Viernheim, Germany; precision ± 0.05 mm): length of forearm including wrist (FA+), length of 5th finger excluding wrist (D5-), length of 3rd finger excluding wrist (D3-), length of 1st phalanx of 4th digit (P4.1), and length of 2nd phalanx of 4th digit (P4.2; Fig. 1). These five measurements provided a simple yet comprehensive description of wing characteristics. FA is a standard measurement of bat size; D5 reflects wing width (high values of D5 are characteristic of slow, maneuverable bats with low wing loading; Fenton 1990; Findley et al. 1972; Norberg and Rayner 1987); D3 reflects the length of the hand wing (low values of D3 together with high D5 values are characteristic of slowly foraging bats which can maneuver with sharp turns and hover in flight; Blood and McFarlane 1988; Fenton 1990; Findley et al. 1972; Norberg and Rayner 1987); and P4.1 and P4.2 are important for species identification and can be used in the field to ensure correct identification or to identify dry or alcohol-preserved museum specimens (Miller 1912; Paunovic and Stamenkovic 1998).

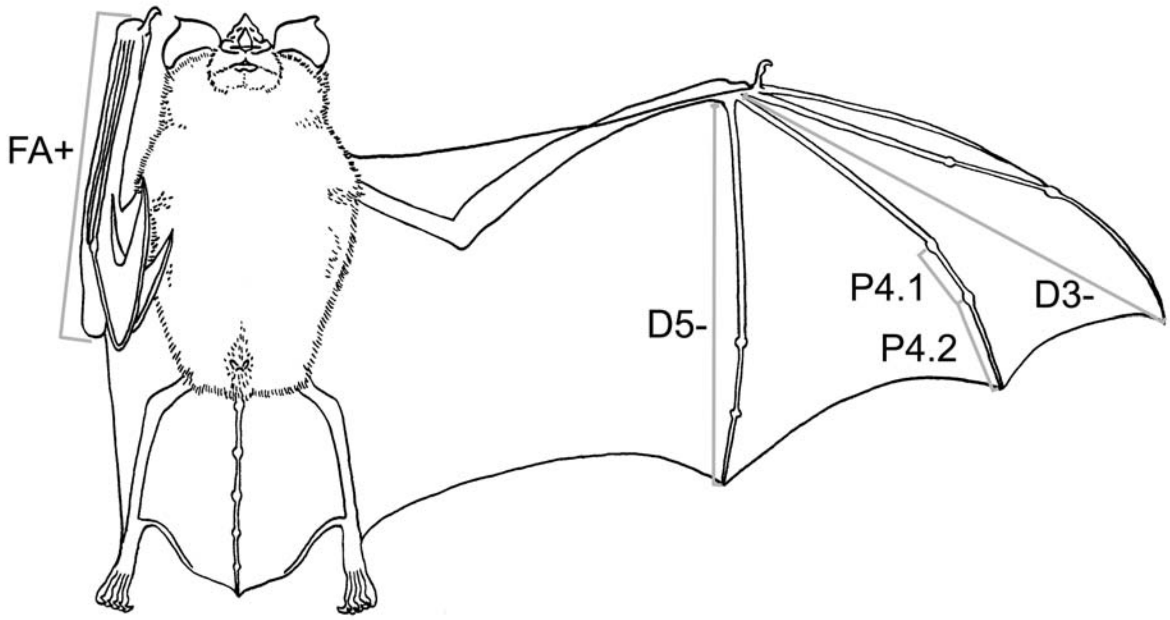


Figure 1: Ventral view of a greater horseshoe bat with outstretched wing; the measurements used in this study are shown. Abbreviations: FA+: forearm length, D5-: length of 5th finger, D3-: length of 3rd finger, P4.1: length of the 1st phalanx of the 4th finger, P4.2: length of the 2nd phalanx of the 4th finger (redrawn from Twisk in Limpens et al. 1997).

Only adult bats were measured. The age class of the bat was determined by the degree of closure of the epiphyseal growth plates of the phalanges and by comparing fur coloration and structure with banded bats of known ages (following the methods of Gaisler 1960, 1965; Gaisler and Titlbach 1964; Matthews 1937; Rollinat and Trouessart 1897; and Young 1975). Pseudoreplication by inadvertently repeating measurements of an individual was minimized by marking a high proportion of the bats captured in Northern Bulgaria individually with durable aluminium bands (bat rings) and by visiting other roosting sites only once or twice. For some analyses we did not use the data for *R. hipposideros* because of small sample size, and in geographical comparisons we ignored *R. blasii* due to the fact that it was captured in the Rhodope Mountains only.

Statistical analysis.– To assess morphological variation, we calculated the mean, standard deviation (SD), minimum and maximum for morphological variables according to sex, species and region. We analysed the data using *t*-tests and analysis of variance (ANOVA) with the Tukey-Kramer-test for post hoc pairwise comparisons.

To assess whether the 5 species differ in wing shape, we calculated general linear models (GLM). Specifically, we regressed D5 on FA (relation of bat size to wing width; FA as continuous factor), D3 on FA (relation of bat size to hand wing length; FA as continuous factor), and D3 on D5 (relation of hand wing length to wing width; D5 as continuous factor). In each model, we used species as nominal factor and the interaction between species and the continuous effect variable as additional factor. A significant interaction term would indicate that the regression slopes differed between species. However, the interaction terms were far from significance in any of the three models (see “Results”). Therefore, we eliminated the interaction from the models and used new general models to compute parallel regressions with a common slope for all species. We then calculated residuals from the average common regression line and compared them using 1-factor ANOVAs. Species pairs were compared post hoc with Tukey-Kramer honestly significant difference tests and a significance level set at 0.05. Analyses were performed using Excel 2002 (Microsoft, Redmond, Washington), Jump 5.1 (SAS Institute Inc., Cary, North Carolina), and Systat 11 (SPSS Inc., Chicago, Illinois).

RESULTS

We obtained external wing measurements from 3,081 adult rhinolophids, including 1,127 *R. ferrumequinum*, 48 *R. hipposideros,* 229 *R. blasii*, 911 *R. euryale* and 766 *R. mehelyi*. External wing measurements overlapped for the most part among the 3 medium-sized species (*R. blasii*, *R. euryale* and *R. mehelyi*) but were clearly distinct for the largest (*R. ferrumequinum*) and the smallest (*R. hipposideros*) species (Table 1). All species were reasonably separable by plotting the length of the 5th finger (D5) against forearm-length (FA; Fig. 2a); however, there was substantial overlap between *R. euryale* and *R. blasii*. FA was significantly longer in females than in males in all 5 species ($t \geq 5.03$, *d.f.* ≥ 46, $P < 0.0001$; Table 1). This dimorphism was also found generally in the measurements of D5, D3, P4.1 and P4.2; $t \geq 3.35$, *d.f.* ≥ 138, $P \leq 0.0020$ except for D5, D3 and P4.1 in *R. hipposideros* ($t \leq 1.20$, *d.f.* ≥ 30, $P \geq 0.2439$) and P4.1 in *R. mehelyi* ($t = 0.33$, *d.f.* $= 763$, $P = 0.7383$).

A general linear model comparing adult measurements found that the factors ‘species’, ‘sex’ and ‘region’ explained most of variability within each of the five wing parameters (all $F \geq 7.65$, *d.f.* = 8, 1581-3072, $R^2 = 0.82$-0.95, all $P < 0.0001$). The factor ‘species’ explained the majority of variability in all 5 measurements (all $F \geq 2291.99$, *d.f.* = 4, 1585-3076).

Table 1: External wing measurements of adult *Rhinolophus* bats of 5 species from southeastern Europe (Bulgaria, Greece, and western Turkey) and *t*-statistics between both sexes. Abbreviations for wing variables are given in Fig. 1.[a]

Species	Sex	FA+ (mm) mean ± SD (n) (min – max)	D5- (mm) mean ± SD (n) (min – max)	D3- (mm) mean ± SD (n) (min – max)	P4.1 (mm) mean ± SD (n) (min – max)	P4.2 (mm) mean ± SD (n) (min – max)
R. hipposideros	m ad.	37.2 ± 0.72 (30) (36.1 – 38.7)	49.7 ± 1.42 (30) (47.3 – 53.0)	53.3 ± 1.29 (21) (51.2 – 56.5)	6.8 ± 0.38 (29) (5.8 – 7.5)	13.4 ± 0.50 (29) (12.3 – 14.2)
	f ad.	38.5 ± 0.60 (18) (37.3 – 39.6)	50.1 ± 1.66 (18) (46.8 – 52.7)	53.9 ± 1.36 (11) (51.8 – 55.5)	6.8 ± 0.46 (18) (5.7 – 7.5)	13.0 ± 0.60 (18) (12.0 – 14.0)
	t-test	t = 6.347, P < 0.0001	t = 0.735, P = 0.4680	t = 1.202, P = 0.2439	t = 0.079, P = 0.9373	t = 2.100, P = 0.0439
R. blasii	m ad.	46.2 ± 1.02 (60) (42.6 – 48.9)	56.5 ± 1.22 (60) (52.7 – 59.0)	67.0 ± 1.75 (25) (63.2 – 70.5)	8.3 ± 0.30 (60) (7.6 – 9.0)	15.4 ± 0.56 (60) (13.3 – 16.4)
	f ad.	47.2 ± 0.88 (169) (44.6 – 50.1)	57.4 ± 1.16 (169) (53.9 – 61.3)	68.3 ± 1.44 (115) (63.1 – 73.8)	8.5 ± 0.31 (169) (7.7 – 9.2)	15.8 ± 0.51 (169) (14.1 – 17.4)
	t-test	t = 6.620, P < 0.0001	t = 5.156, P < 0.0001	t = 3.368, P = 0.0020	t = 3.888, P = 0.0002	t = 3.989, P = 0.0001
R. euryale	m ad.	47.4 ± 0.91 (399) (45.0 – 50.3)	57.8 ± 1.35 (399) (52.9 – 61.0)	70.3 ± 1.76 (208) (62.7 – 74.6)	6.8 ± 0.40 (399) (5.7 – 7.9)	18.0 ± 0.57 (399) (16.6 – 19.8)
	f ad.	47.9 ± 0.98 (512) (45.0 – 51.0)	58.3 ± 1.37 (512) (52.5 – 62.2)	71.4 ± 1.70 (223) (66.7 – 76.0)	6.9 ± 0.39 (510) (6.0 – 8.2)	18.2 ± 0.57 (510) (16.4 – 20.1)
	t-test	t = 8.144, P < 0.0001	t = 6.345, P < 0.0001	t = 6.387, P < 0.0001	t = 4.082, P < 0.0001	t = 3.350, P = 0.0008
R. mehelyi	m ad.	51.1 ± 0.97 (218) (48.2 – 53.8)	61.6 ± 1.43 (218) (57.8 – 65.2)	77.0 ± 1.84 (133) (71.2 – 81.2)	7.8 ± 0.45 (217) (6.6 – 9.2)	19.5 ± 0.72 (217) (17.8 – 21.4)
	f ad.	51.5 ± 1.00 (548) (48.4 – 54.8)	62.4 ± 1.44 (548) (57.1 – 66.6)	77.8 ± 1.83 (340) (71.1 – 83.0)	7.8 ± 0.43 (548) (6.5 – 9.3)	19.7 ± 0.68 (548) (17.4 – 21.5)
	t-test	t = 5.033, P < 0.0001	t = 6.585, P < 0.0001	t = 4.006, P < 0.0001	t = 0.334, P = 0.7383	t = 3.546, P = 0.0004
R. ferrumequinum	m ad.	57.0 ± 1.37 (117) (53.0 – 60.5)	70.3 ± 1.82 (117) (62.9 – 77.2)	84.9 ± 2.32 (89) (77.6 – 91.5)	11.1 ± 0.61 (117) (9.5 – 12.7)	19.8 ± 0.72 (177) (18.3 – 21.7)
	f ad.	58.3 ± 1.28 (1010) (53.7 – 62.4)	71.9 ± 1.88 (1007) (62.9 – 77.2)	86.5 ± 2.34 (425) 78.6 – 93.7)	11.4 ± 0.56 (1004) (9.5 – 13.4)	20.1 ± 0.79 (1005) (16.0 – 22.5)
	t-test	t = 9.690, P < 0.0001	t = 8.775, P < 0.0001	t = 5.728, P < 0.0001	t = 4.831, P < 0.0001	t = 4.334, P < 0.0001

[a] min = minimum; max = maximum.

Discriminant function.– Classical discriminant analysis using the 5 measurements correctly assigned 99% of the individuals to the correct species (jackknifed classification, Wilks' lambda = 0.0041, F = 1114.1, P < 0.0001). The most predictive variables, determined by removing variables from the discriminant analysis in descending order, were FA+ and P4.1; these enabled correct classification of 98% of the individuals (Wilks' lambda = 0.0127, F = 6038.7, P < 0.0001). We used this to generate a canonical discriminant function (Fig. 3); with which all individuals of *R. hipposideros* and *R. ferrumequinum* were correctly classified, followed by 99% *R. blasii*, 97% *R. mehelyi* and 95% *R. euryale*.

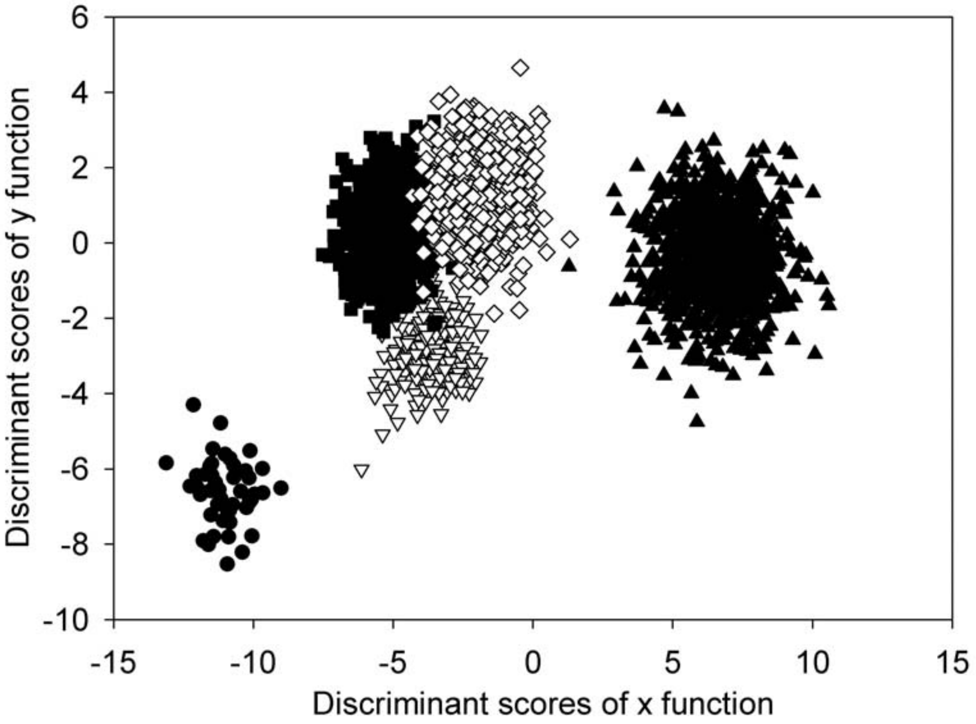


Figure 3: Canonical scores plot for the discriminant function ($X = -41.4137 + 0.5794 * FA+ + 1.2621 * P4.1; Y = -21.0216 + 0.7104 * FA+ - 1.8158 * P4.1$) separating adult individuals of the European horseshoe bats using forearm-length (FA+) and length of the 1st phalanx of the 4th finger (P4.1) in millimeters as predictors. Circles denote *R. hipposideros*, triangles facing downwards *R. blasii*, squares *R. euryale*, diamonds *R. mehelyi*, and triangles facing upwards *R. ferrumequinum*. The graph can be used to interpret the results of the above discriminant function.

Relations between different wing measurements.– We regressed D5 on FA to assess the relation of wing width to bat size (Fig. 2a). A general linear model showed that D5 increased with FA ($F = 402.87$, *d.f.* = 1, 3043, $P < 0.0001$) and differed significantly between species ($F = 94.20$, *d.f.* = 4, 3043, $P < 0.0001$). The regression slope did not differ between species (interaction FA and species; $F = 0.83$, *d.f.* = 4, 3043, $P = 0.5043$). This indicates that the increase in wing width per unit increase in forearm length is about the same for all 5 species. In accordance with the significant species effect in the general linear model, an ANOVA on the D5 residuals revealed that the species differed in the elevation (i.e., vertical position - see Zar 1999) of the regression lines ($F = 1712.63$, *d.f.* = 4, 3048, $P < 0.0001$). Taken together, the species' regression lines were parallel, but had different elevations, that is, they were not coincidental (Fig. 2a). *R. ferrumequinum* had the widest wings relative to forearm size, *R. hipposideros* and *R. mehelyi* were intermediate, while *R. blasii* and *R. euryale* did not differ from each other and had the smallest wings (Tukey-Kramer, $P < 0.05$).

Similarly, we regressed D3 on FA to assess the relation of hand wing length to bat size (Fig. 2b). D3 increased with FA ($F = 183.50$, *d.f.* = 1, 1555, $P < 0.0001$) and differed between species ($F = 41.80$, *d.f.* = 4, 1555, $P < 0.0001$). The regression slope did not differ between species (interaction FA and species; $F = 0.38$, *d.f.* = 4, 1555, $P = 0.8422$); that is, they have the same pattern of increase for hand wing lengths per unit forearm length within each species. The D3 residuals on FA, which mirror the elevations of the regression lines in Fig. 2b, differed between species (ANOVA, $F = 1076.11$, *d.f.* = 4, 1560, $P < 0.0001$). All species differed significantly from each other in post hoc pairwise comparisons (Tukey-Kramer, $P < 0.05$). *R. ferrumequinum* had the longest and *R. hipposideros* the shortest hand wing relative to forearm size; the other species were intermediate (cf. Fig. 2b).

Finally, we regressed D3 on D5 to assess the relation of hand wing length to wing width (Fig. 2c). D3 increased with D5 ($F = 413.39$, *d.f.* = 1, 1555, $P < 0.0001$) and differed between species ($F = 73.12$, *d.f.* = 4, 1555, $P < 0.0001$). Again, the regression slope did not differ between species (interaction D5 and species; $F = 1.25$, *d.f.* = 4, 1555, $P = 0.2866$); that is, they have the same pattern of increase for hand wing lengths per unit wing width within each species. The D3 residuals on D5, which mirror the elevations of the regression lines in Fig. 2c, differed between species (ANOVA, $F = 1418.95$, *d.f.* = 4, 1560, $P < 0.0001$). Although all species differed significantly from each other in pairwise comparisons (Tukey-Kramer, $P < 0.05$), the most prominent effect was that *R. hipposideros* had a considerably shorter hand wing relative to wing width than its congeners (cf. Fig. 2c).

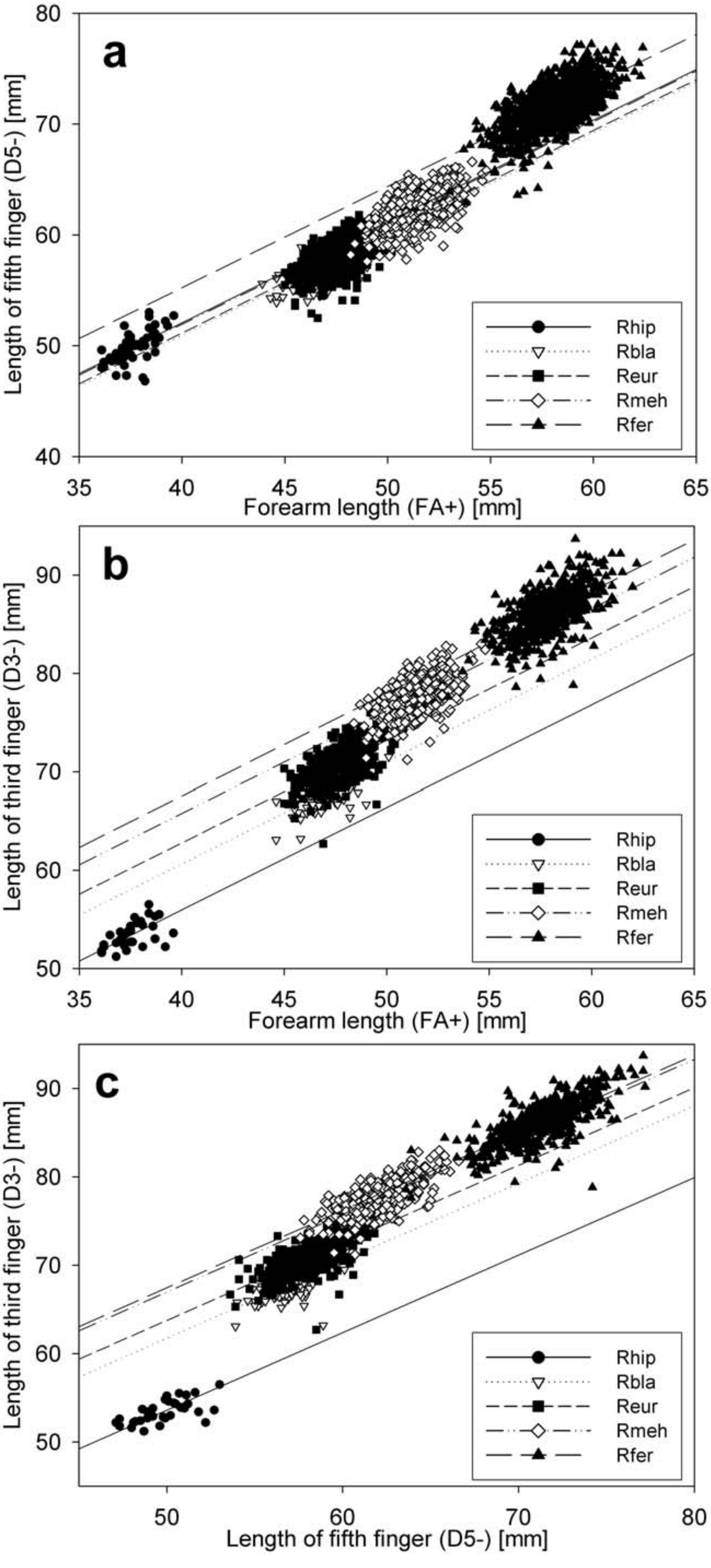


Figure 2: Bivariate plots and species-wise regression lines of external wing measurements of the 5 European horseshoe bat species. a) Regression of D5- on FA+, assessing the relation of wing width to bat size (as indicated by forearmlength). b) Regression of D3- on FA+, exploring the relation of hand wing length to bat size. c) Regression of D3- on D5-, showing the relation of hand wing length to wing width. Statistics and further details are given in the text. Abbreviations for wing variables are given in Fig. 1. Abbreviations for species: Rhip = *Rhinolophus hipposideros*, Rbla = *R. blasii*, Reur = *R. euryale*, Rmeh = *R. mehelyi*, Rfer = *R. ferrumequinum*.

Geographical comparison.– *R. euryale* and *R. ferrumequinum* exhibited no regional differences (all 5 measurements compared between populations from 4 regions in south-eastern Europe separately within males and females; F = 0.01-4.45, *d.f.* = 3, 426-1121, P = 0.0352-0.9297; only some comparisons were significant but not consistent in both sexes or within the same region). However, for *R. mehelyi*, both males and females from the southern population (from the Greek and Bulgarian part of the Eastern Rhodope Mountains) were significantly smaller ($F \geq 36.13$, *d.f.* = 3, 470-763, $P < 0.0001$) than the northern population (Table 2). These subtle but significant size differences corresponded to slight morphological differences between the 2 populations. Adult *R. mehelyi* in Northern Bulgaria has a lighter ventral pelage and a bluntly rounded connecting process of the nose-leaf. *R. mehelyi* from the Rhodope Mountains is more yellowish-white ventrally, sometimes with a reddish tinge and often a more pointed connecting process.

Table 2: Comparison of the measurements of the northern population (North Bulgarian Plain) and the southern population from the Eastern Rhodopes (Greece and Bulgaria) of adult *Rhinolophus mehelyi*. Abbreviations for wing variables are given in Fig. 1.[a]

	FA+ (mm) mean ± SD (n) (min – max)	D5- (mm) mean ± SD (n) (min – max)	D3- (mm) mean ± SD (n) (min – max)	P4.1 (mm) mean ± SD (n) (min – max)	P4.2 (mm) mean ± SD (n) (min – max)
Males North	51.2 ± 0.98 (189) (48.2 - 53.8)	61.9 ± 1.30 (189) (58.2 - 65.2	77.3 ± 1.75 (106) (71.4 - 81.2	7.8 ± 0.44 (188) (6.6 - 9.2)	19.6 ± 0.69 (188) (17.8 - 21.4)
South	50.5 ± 0.69 (27) (49.4 – 52.2)	59.8 ± 0.89 (27) (57.8 – 61.4)	75.9 ± 1.76 (25) (72.1 – 78.3)	7.5 ± 0.37 (27) (6.8 – 8.2)	18.9 ± 0.61 (27) (17.8 – 19.9)
Females North	51.5 ± 0.99 (521) (48.4 – 54.8)	62.5 ± 1.37 (521) (58.1 – 66.6)	77.9 ± 1.79 (317) (73.4 – 83.0)	7.8 ± 0.42 (521) (6.5 – 9.3)	19.8 ± 0.64 (521) (17.4 – 21.5)
South	50.7 ± 0.69 (27) (49.0 – 52.1)	60.4 ± 1.39 (27) (57.1 – 63.3)	76.4 ± 1.93 (23) (71.1 – 80.6)	7.3 ± 0.39 (27) (6.6 – 8.3)	18.8 ± 0.76 (27) (17.4 – 20.3)

[a] min = minimum; max = maximum.

DISCUSSION

Examination of our data identified size variation within and among 5 species of European horseshoe bats in southeastern Europe and made it possible to test for inter- and intraspecific differences. Similar to Krystufek (1993) and de Paz (1995), we found that individual *R. ferrumequinum* from these southeastern populations are among the largest in Europe. Based on measurements of forearm length, *R. ferrumequinum* are on average about 1 mm larger in Bulgaria than in France (Caubère et al. 1968). Forearm lengths of *R. euryale* and *R. mehelyi* from Bulgaria are also slightly larger than those from Corsica and Sardinia, but of similar size to those from Portugal and smaller than those from Iran (Almaça 1967; DeBlase 1980; Dinale 1972; Russo et al. 2001; Sharifi 2004).

Interspecific size comparisons.– The results of wing measurements (forearm, 5th finger, 3rd finger and 1st and 2nd phalanges of 4th digit) overlapped considerably among the species. However, on the basis of forearm length and the length of the 5th and 3rd fingers, it is possible to group the 5 horseshoe bats into 3 groups: a large (*R. ferrumequinum*), a small (*R. hipposideros*), and 3 quite similar medium-sized species (*R. blasii, R. euryale, R. mehelyi*). Variations within the data are best explained in multivariate comparisons by the factor 'species', followed by 'sex' and 'region', indicating the presence of species-specific ranges within the wing measurements (question 1 in "Introduction").

We generated a discriminant function to determine whether our data might be useful for identifying museum specimens, whose nose-leaves are usually not well preserved. The most important predictors of species were the lengths of the forearm and 1st phalanx of the 4th finger. Although the phalanges have been used by other studies to discriminate between medium-sized horseshoe bat species (Andersen and Matschie 1904; Miller 1912; Paunovic and Stamenkovic 1998), the sample population sizes in those studies were either small or were not representative of all European species. Our discriminant function made it possible to sort the 5 species reliably and with more than 95% confidence even in the case of the 3 medium-sized horseshoe bat species. The relatively low percentage of correctly assigned individuals in *R. euryale* (95%) can be explained by the overlap in the FA measurement with *R. mehelyi* and *R. blasii*, as well as by the overlap in the P4.1 measurement between *R. euryale* and *R. mehelyi*.

Sexual dimorphism.– We found evidence of sexual size dimorphism. Females were larger than males in all 5 species. This confirmed earlier observations for single species studies (Caubère et al. 1968; Dinale 1972; Grulich 1949; Ransome 1998; Saint-Girons and Caubère 1966). However, we found no sexual dimorphism in the size-independent relationships between several measurements (see wing-shape differences).

Geographical size differences.– Although no notable size differences occurred in the wing measurements of populations of *R. euryale* and *R. ferrumequinum* from different parts of southeastern Europe, differences did occur for *R. mehelyi*. Bats from the south were smaller than those from the north (question 4 in “Introduction”). Without detailed studies based on genetic and comparative ecological data, any explanation must remain speculative. The differences between northern and southern populations in *R. mehelyi* might be explained either by intrinsic (evolutionary) or extrinsic (climatic) causes. Both populations might be completely isolated from each other by the east-west running range of the Balkans and probably even belong to different subspecies.

According to Bergmann’s (1847) rule endotherms should increase in size with increasing latitude (see McNab 1971). This rule seems to apply to *R. mehelyi* (larger individuals in the north, smaller in the south). However, the distance between both populations is only 300 km and the climate (especially the temperature) is much more continental and therefore more stable in the north than in the south of Bulgaria (Dimitrov 1966; Galabov 1953), leading to the expectation of an inverse size cline instead of the observed one.

On the other hand, the size of rhinolophids can be highly variable even over short geographic distances (e.g., Dinale 1972). Climatic differences between both Bulgarian distributional areas in combination with different prey and habitat availability could explain the smaller size of the southern population. One of us (ID) observed that tagged Mehely's horseshoe bats forage predominately above meadows and cultivated fields in northern Bulgaria, a habitat naturally available in steppes. If *R. mehelyi* is indeed a native steppe bat as indicated by its distribution as far as Iran and Arabia (DeBlase 1980), it is possible that the Eastern Rhodopes with their extended scrubland provide either suboptimal foraging habitats leading to stunted growth (cf. Ransome 1989, 1998; Jones et al. 1995) or lead to a size reduction for the sake of increased maneuverability.

Wing-shape differences.– Despite a similar general wing construction within the guild studied (broad, short wings), our regression analysis showed that the species differ significantly in size-independent relationships of wing measurements. The minute variations between species, presumably reflect adaptations to different foraging modes and habitats (see Aldridge and Rautenbach 1987; Kalcounis and Brigham 1995). These differences are interesting in the context of functional ecology, because they may indicate differences in flight capabilities. For example, the wings of *R. hipposideros* differ from those of the other guild members in having extremely short hand wings. In comparison with other bats with similar wings such as the brown long-eared bat (Norberg 1976) or *Nyctophilus* species (Brigham et al. 1997), *R. hipposideros* should be able to fly more slowly than its congeners, use edge and gap situations, and be more maneuverable than the other guild members. The ecology of the species (Bontadina et al. 2002; Gaisler 1963; Jones and Rayner 1989; McAney and Fairley 1988) matches this hypothesis well.

In contrast, the largest species, *R. ferrumequinum*, had in the regression analysis the broadest wing and longest hand wing in relation to its size. The foraging behavior of *R. ferrumequinum* is well known. It exploits various habitats, but avoids dense vegetation (Bontadina et al. 1995; 1997; Jones and Rayner 1989; Pir 1994; Ransome and Hutson 2000). The reluctance of *R. ferrumequinum* to forage in dense vegetation might be mainly a result of its larger size (see Bogdanowicz et al. 1999, Swartz et al. 2003).

The 3 little-known, medium-sized horseshoe bats were arranged by the regression analysis in between the 2 well known species *R. ferrumequinum* and *R. hipposideros*. All 3 analyses placed *R. blasii* closest to *R. hipposideros*, so that this species should exhibit a flight- and presumably also foraging behavior like that of *R. hipposideros* and can be expected to forage close to and within the dense vegetation of scrubland and forest edges. Very little is known about the foraging behavior of *R. blasii*, but the species has been shown to take prey from vegetation and the ground in an experimental flight tent and to be maneuverable (Siemers & Ivanova 2004), a characteristic also observed by us (CD & ID) in the wild.

The regression analyses highlighted a relatively longer hand wing of *R. meheyli* than in the other 2 medium-sized species and accordingly placed it close to *R. ferrumequinum*. From this finding we would predict habitat use of predominately open, less densely vegetated areas and the avoidance of foraging within the dense vegetation. This is because flight speed in bats is positively correlated with the length of the hand wing (expressed by the length of the 3rd finger) in combination with a negative correlation of wing width (D5 length - Findley et al. 1972; Vaughan 1959). Fast-flying bats, like most molossids, have a very long 3rd finger and a short 5th finger (Vaughan 1966). Thus a higher flight speed than that of the congeners can be predicted for *R. mehelyi*. Not much is known about the foraging ecology of *R. meheyli*, but Russo et al. (2005) have shown the species' preference for foraging in open, savannah-type habitats. However, our own studies (ID) suggest that *R. mehelyi* forages erratically and maneuverably, mainly away from bushes and trees but nevertheless in a highly structured habitat close to and within meadows and fields. Our field observations also indicated high flight speeds, especially when the bats are commuting.

The outcome of the regression analysis place *R. euryale* in an intermediate position between the other 4 species, possibly indicating a variable foraging mode and habitat use. Examination of telemetry data suggests that *R. euryale* uses richly structured habitats and forages close to trees and hedges (Aihartza et al. 2003; Goiti et al. 2003; Russo et al. 2002).

Overall, the ecological data on the well-known species *R. hipposideros* and *R. ferrumequinum* and the limited data available for the 3 medium-sized species fit well with predictions made from our regression analysis. Both body size (represented by FA) and wing shape (relation of wing width and hand wing length with each other and with forearm length) are likely to affect flight performance and habitat use. Hence, we argue that habitat use and habitat structure can be predicted to some degree by analysis of easily assessable wing measurements. Namely, a species' ability to forage within and close to dense vegetation like bushes and scrubland will be linked to small body size and a short hand wing in relation to forearm and 5th finger, whereas open habitats will be preferred by larger species, those with longer hand wings, or both.

Ecological adaptations.– In conclusion, the 5 guild members in this study exhibited morphological differences that might be regarded as adaptations to different foraging tactics or habitats. The species vary in size, with the largest and smallest species differing widely from the 3 medium-sized species. Size differences are important for structuring animal communities or guilds (Schoener 1974), and morphological differences between bat species have been shown to reflect adaptations to flight and foraging strategies (e.g., Aldridge 1986; Norberg 1981). Because the 5 horseshoe bats can be reliably separated by a canonical scores plot of a discriminant function using morphological measurements, these morphometric differences are consistent at the level of individuals. Therefore, one might assume that the differences are big enough to have ecological significance for niche separation.

However, European horseshoe bats are not only size-graduated; size-independent relations between measurements also differ in regression analysis. Intraspecifically, females are bigger than males in all measurements.

We argue that morphological differences between the species are large enough to permit predictions about differences in maneuverability, foraging style, and habitat use. Such differences have been found in studies investigating the morphology and echolocation behavior of horseshoe bats (Kingston et al. 2000), in experiments combining morphological data and obstacle-avoidance ability, and in ecological studies (Aldridge 1986; Aldridge and Rautenbach 1987; Kalcounis and Brigham 1995; Saunders and Barclay 1992). The ability of all guild members to coexist in certain areas even when food is limited may be explained by subtle differences in wing-ratios, along with differences in echolocation (Heller and von Helversen 1989; Russo et al. 2001; Siemers et al. 2005), habitat use (Aihartza et al. 2003; Bontadina et al. 1995, 1997, 2002; Goiti et al. 2003; Jones and Rayner 1989; Russo et al. 2002, 2005), body size parameters such as jaw length (Popov and Ivanova 2002). The species' geographical distribution may therefore be limited by ecological factors acting on single species rather than by competition, exclusion, or both within the guild.

ACKNOWLEDGEMENTS

Our work in Bulgaria was made possible by the cooperation and support of the Bulgarian Bat Research and Protection group, especially of T. Ivanova. We are grateful for their help with many aspects of the project, including helpful comments and discussions on the data, assistance in obtaining permits, and sharing of knowledge on the Bulgarian roost sites. We are indebted to S. Merdschanov, D. Merdschanova, K. Christov, I. Borrisov, B. Petrov, T. Pröhl and S. Staneva for their help in catching bats and to O. von Helversen and E. Papadatou for showing us the capture sites and for their help in catching bats in Greece. We are particularly grateful to E. Papadatou for her support and help in getting permits in Greece and for her valuable comments. P. Pilz is gratefully acknowledged for statistical advice. We are especially grateful to P. Bates, M. Brigham, T. Rice and 2 anonymous reviewers for helpful comments, constructive criticism and many linguistic improvements on earlier versions of this manuscript.

This research was funded by grants of the Graduiertenförderung des Landes Baden-Württemberg to CD and of the Deutsche Bundesstiftung Umwelt to ID. Further support was given by the Reinhold-und-Maria-Teufel-Stiftung to CD and ID and the German Science Foundation (DFG, Si 816/2-1) and the Schuler Foundation to BMS.

REFERENCES

ADAMS, R.A. 1996. Size-specific resource use in juvenile little brown bats, *Myotis lucifugus* (Chiroptera: Vespertilionidae): Is there an ontogenetic shift? Canadian Journal of Zoology 74: 1204-1210.

AIHARTZA, J.R., I. GARIN, U. GOITI, J. ZABALA AND I. ZUBEROGOITA. 2003. Spring habitat selection by the Mediterranean horseshoe bat (*Rhinolophus euryale*) in the Urdaibai Biosphere Reserve (Basque Country). Mammalia 67: 25-32.

ALDRIDGE, H. 1986. Manoeuvrability and ecological segregation in the little brown (*Myotis lucifugus*) and Yuma (*M. yumanensis*) bats (Chiroptera: Vespertilionidae). Canadian Journal of Zoology 64: 1878-1882.

ALDRIDGE, H.D.J.N. AND I.L. RAUTENBACH. 1987. Morphology, echolocation and resource partitioning in insectivorous bats. Journal of Animal Ecology 56: 763-778.

ALMAÇA, C. 1967. Nouvelles observations sur *Rhinolophus mehelyi* au Portugal. Arquivos do Museu Bocage 1: 35-38.

ANDERSEN, K. AND P. MATSCHIE. 1904. Uebersicht ueber einige geographische Formen der Untergattung *Euryalus.* Sitzungs-Bericht der Gesellschaft naturforschender Freunde zu Berlin 5: 71-83.

Animal Care and Use Committee. 1998. Guidelines for the capture, handling, and care of mammals approved by the American Society of Mammalogists. Journal of Mammalogy 79: 1416-1431.

BECK, A., S. GLOOR, M. ZAHNER, F. BONTADINA, T. HOTZ, M. LUTZ AND E. MÜHLETHALER. 1997. Zur Ernährungsbiologie der Großen Hufeisennase in einem Alpental der Schweiz. Tagungsband: „Zur Situation der Hufeisennasen in Europa" Nebra, den 26.-28. Mai 1995, Arbeitskreis Fledermäuse Sachsen-Anhalt e.V. 1997: 15-18. IFA-Verlag, Berlin, Germany.

BECK, A., H.-P.B. STUTZ AND V. ZISWILER. 1989. Das Beutespektrum der Kleinen Hufeisennase *Rhinolophus hipposideros.* Revue suisse de zoologie 96: 643-650.

BERGMANN, C. 1847. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. Göttinger Studien 3: 595-708.

BLOOD, B.R. AND D.A. MCFARLANE. 1988. A new method for calculating the wing area of bats. Mammalia 52: 600-603.

BOGDANOWICZ, W., M.B. FENTON AND K. DALESZCZYK. 1999. The relationship between echolocation calls, morphology and diet in insectivorous bats. Journal of Zoology (London) 247: 381-393.

BONTADINA, F., A. BECK, S. GLOOR, T. HOTZ, M. LUTZ AND E. MÜHLETHALER. 1995. Jagt die Grosse Hufeisennase *Rhinolophus ferrumequinum* im Wald? Grundlagen zum Schutz von Jagdgebieten der letzten grösseren Kolonie in der Schweiz. Der Ornithologische Beobachter 92: 325-327.

BONTADINA, F., T. HOTZ, S. GLOOR, A. BECK, M. LUTZ AND E. MÜHLETHALER. 1997. Schutz von Jagdgebieten der Großen Hufeisennase. Umsetzung der Ergebnisse einer Telemetrie-Studie in einem Alpental der Schweiz. Tagungsband: „Zur Situation der Hufeisennasen in Europa" Nebra, den 26.-28. Mai 1995, Arbeitskreis Fledermäuse Sachsen-Anhalt e.V. 1997: 33-40. IFA-Verlag, Berlin, Germany.

BONTADINA, F., H. SCHOFIELD AND B. NAEF-DAENZER. 2002. Radio-tracking reveals that lesser horseshoe bats (*Rhinolophus hipposideros*) forage in woodland. Journal of Zoology (London) 258: 281-290.

BRIGHAM, R.M., R.L. FRANCIS AND S. HAMDORF. 1997. Microhabitat use by two species of *Nyctophilus* bats: a test of ecomorphology theory. Australian Journal of Zoology 45: 553-560.

BROWN, W.L. AND E.O. WILSON. 1956. Character displacement. Systematic Zoology 5: 49-64.

CAUBÈRE, B., H. MENU AND M.-C. SAINT-GIRONS. 1968. Notes sur les Mammifères de France VII. Dimensions de l´avant-bras de *Rhinolophus ferrumequinum*. Mammalia 32: 95-103.

DEBLASE, A.F. 1980. The bats of Iran: systematics, distribution, ecology. Fieldiana Zoology (New Series) 4: 424 pp.

DE PAZ, O. 1995. Geographic variation of the greater horseshoe bat (*Rhinolophus ferrumequinum*) in the west-half of the Palearctic region. Myotis 32/33: 33-44.

DIETZ, C., I. DIETZ, T. IVANOVA, AND B. M. SIEMERS. in press. Movements of horseshoe bats (*Rhinolophus*, Chiroptera: Rhinolophidae) in Northern Bulgaria. Myotis 43.

DIMITROV, D. 1966. Klimatična podjalba v Bălgarija, Geografija na Bălgarija 1, Fizičeska geografija; Bulgarian Academy of Sciences, Sofia, Bulgaria.

DINALE, G. 1972. Biometrical notes on a collection of *Rhinolophus euryale* from Corse (France). Mammalia 36: 536-538.

FENTON, M.B. 1990. The foraging behaviour and ecology of animal-eating bats. Canadian Journal of Zoology 68: 411-422.

FINDLEY, J.S. AND H. BLACK. 1983. Morphological and dietary structuring of a Zambian insectivorous bat community. Ecology 64: 625-630.

FINDLEY, J.S., E.H. STUDIER AND D.E. WILSON. 1972. Morphological properties of bat wings. Journal of Mammalogy 53: 429-444.

FINDLEY, J.S. AND D.E. WILSON. 1982. Ecological significance of chiropteran morphology. Pp. 243-260 in Ecology of bats (T.H. Kunz, ed.). Plenum Publishing Corporation, New York.

GAISLER, J. 1960. Postnatale Entwicklung der Kleinen Hufeisennase (*Rhinolophus hipposideros*) unter natürlichen Bedingungen. Symposium Theriologicum 1960: 118-125.

GAISLER, J. 1963. Nocturnal activity in the lesser horseshoe bat, *Rhinolophus hipposideros*. Zoologicke Listy, Folia Zoologica 12: 223-230.

GAISLER, J. 1965. The female sexual cycle and reproduction in the lesser horseshoe bat (*Rhinolophus hipposideros hipposideros*). Vestnik Ceskoslovenske Spolecnosti Zoologicke 29: 336-352.

GAISLER, J. AND M. TITLBACH. 1964. The male sexual cycle in the lesser horseshoe bat (*Rhinolophus hipposideros hipposideros*). Vestnik Ceskoslovenske Spolecnosti Zoologicke 28: 268-277.

GALABOV, S. 1953. Mjastoto na geomorphologiijata v krăga na geologo-geografskite nauki. Proceedings of the Bulgarian Geographical Society 1: 273 pp.

GOITI, U., J.R. AIHARTZA AND I. GARIN. 2004. Diet and prey selection in the Mediterranean horseshoe bat *Rhinolophus euryale* (Chiroptera, Rhinolophidae) during the pre-breeding season. Mammalia 68: 397-402.

GOITI, U., J.R. AIHARTZA, I. GARIN AND J. ZABALA. 2003. Influence of habitat on the foraging behaviour of the Mediterranean horseshoe bat, *Rhinolophus euryale*. Acta Chiropterologica 5: 75-84.

GRIFFIN, D.R. AND J.A. SIMMONS. 1974. Echolocation of insects by horseshoe bats. Nature 250: 731-732.

GRULICH, I. 1949. Contribution to the knowledge of the variability of *Rhinolophus hipposideros*. Acta Academiae Scientiarum Naturalium Moravo-Silesiacae 21: 1-60.

GUILLÉN, A., C.M. FRANCIS AND R.E. RICKLEFS. 2003. Phylogeny and biogeography of the horseshoe bats. Pp. XII-XXIV in Horseshoe bats of the world (Chiroptera: Rhinolophidae) (G. Csorba, P. Ujhelyi and N. Thomas, eds.). Alana Books Shropshire, United Kingdom.

HARDIN, G. 1960. The competitive exclusion principle. Science 131: 1292-1297.

HELLER, K.-G. AND O. VON HELVERSEN. 1989. Resource partitioning of sonar frequency bands in rhinolophid bats. Oecologia 80: 178-186.

JACOBS, D.S. 1996. Morphological divergence in an insular bat, *Lasiurus cinereus semotus*. Functional Ecology 10: 622-630.

JACOBS, D.S. 1999. Intraspecific variation in wingspan and echolocation call flexibility might explain the use of different habitats by the insectivorous bat, *Miniopterus schreibersii*. Acta Chiropterologica 1: 93-103.

JONES, G., P.L. DUVERGÉ AND R.D. RANSOME. 1995. Conservation biology of an endangered species: field studies of greater horseshoe bats. Symposia of the Zoological Society of London 67: 309-324.

JONES, G., M. MORTON, P.M. HUGHES AND R.M. BUDDEN. 1993. Echolocation, flight morphology and foraging strategies of some West African hipposiderid bats. Journal of Zoology (London) 230: 385-400.

JONES, G. AND J.M.V. RAYNER. 1989. Foraging behavior and echolocation of wild horseshoe bats *Rhinolophus ferrumequinum* and *R. hipposideros*. Behavioral Ecology and Sociobiology 25: 183-191.

KALCOUNIS, M.C. AND R.M. BRIGHAM. 1995. Intraspecific variation in wing loading affects habitat use by little brown bats (*Myotis lucifugus*). Canadian Journal of Zoology 73: 89-95.

KINGSTON, T., G. JONES, A. ZUBAID AND T.H. KUNZ. 2000. Resource partitioning in rhinolophoid bats revisited. Oecologia 124: 332-342.

KRYSTUFEK, B. 1993. Geographic variation in the greater horseshoe bat *Rhinolophus ferrumequinum* in south-eastern Europe. Acta Theriologica 38: 67-79.

LIMPENS, H., K. MOSTERT AND W. BONGERS. 1997. Atlas van de Nederlandse vleermuizen. 260 pp. Koninklije Nederlandse Naturrhistorische Vereniging, Utrecht, The Netherlands.

McAney, C.M. and J.S. Fairley. 1988. Habitat preference and overnight and seasonal variation in the foraging activity of lesser horseshoe bats. Acta Theriologica 28: 393-402.

MACNAB, B.K. 1971. On the ecological significance of Bergmann's rule. Ecology 52: 845-854.

MATHEWS, L.H. 1937. The female sexual cycle in the British horse-shoe bats, *Rhinolophus ferrum-equinum insulanus* and *R. hipposideros minutes.* Transactions of the Zoological Society of London 32: 224-266.

MILLER, G.S. 1912. Catalogue of the mammals of Western Europe in the collections of the British Museum. 1019 pp. William Clowes, London, United Kingdom.

MITCHELL-JONES, A.J., G. AMORI, W. BOGDANOWICZ, B. KRYSTUFEK, P.J.H. REIJNDERS, F. SPITZENBERGER, M. STUBBE, J.B.M. THISSEN, V. VOHRALIK AND J. ZIMA. 1999. The atlas of European mammals. 484 pp. Poyser Natural History, London, United Kingdom.

MÖHRES, F.P. 1953. Über die Ultraschallorientierung der Hufeisennasen. Zeitschrift für Vergleichende Physiologie 34: 547-588.

NORBERG, U.M. 1976. Aerodynamics, kinematics, and energetics of horizontal flapping flight in the long-eared bat *Plecotus auritus*. Journal of Experimental Biology 65: 179-212.

NORBERG, U.M. 1981. Flight, morphology and the ecological niche in some birds and bats. Symposia of the Zoological Society of London 48: 173-197.

NORBERG, U.M. 1987. Wing form and flight mode in bats. Pp. 43-56 in Recent advances in the study of bats (M.B. Fenton, P. Racey and J.M.V. Rayner, eds.). Cambridge University Press, Cambridge, United Kingdom.

NORBERG, U.M. 1994. Wing design, flight performance, and habitat use in bats. Pp. 205-239 in Ecological morphology (P.C. Wainwright and S.M. Reilly, eds.). University of Chicago Press, Chicago, Illinois.

NORBERG, U.M. AND J.M.V. RAYNER. 1987. Ecological morphology and flight in bats: wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society of London B. Biological Sciences 316: 335-427.

PAUNOVIC, M. AND S. STAMENKOVIC. 1998. A revision of the distribution and status of *Rhinolophus euryale* and *Rhinolophus blasii* in Yugoslavia, based on the discrimination properties of distinctive morphological characters. Myotis 36: 7-23.

PIR, J.B. 1994. Etho-Ökologische Untersuchung einer Wochenstubenkolonie der Grossen Hufeisennase (*Rhinolophus ferrumequinum*) in Luxemburg. Diplomarbeit an der Universität Giessen.

POPOV, V.V. AND T.I. IVANOVA. 2002. Comparative craniometrical analysis and distributional patterns of medium-sized horseshoe bats (Chiroptera: Rhinolophidae) in Bulgaria. Folia Zoologica 51: 187-200.

RANSOME, R.D. 1989. Population changes of greater horseshoe bats studied near Bristol over the past twenty-six years. Biological Journal of the Linnean Society 38: 71-82.

RANSOME, R.D. 1998. The impact of maternity roost conditions on populations of greater horseshoe bats. English Nature, Peterborough, Great Britain, Research Reports No. 292: 1-80.

RANSOME, R.D. AND A.M. HUTSON. 2000. Action plan for the conservation of the greater horseshoe bat in Europe (*Rhinolophus ferrumequinum*). Nature and Environment 109: 56 pp.

RHODES, M.P. 2002. Assessment of sources of variance and patterns of overlap in microchiropteran wing morphology in southeast Queensland, Australia. Canadian Journal of Zoology 80: 450-460.

ROLLINAT, R. AND E. TROUESSART. 1897. Sur la reproduction des chauves-souris. II. Les Rhinolophes (1). Mémoires de la Societé Zoologique de France 10: 114-138.

RUSSO, D., D. ALMENAR, J. AIHARTZA, U. GOITI, E. SALSAMENDI AND I. GARIN. 2005. Habitat selection in sympatric *Rhinolophus mehelyi* and *R. euryale* (Mammalia: Chiroptera). Journal of Zoology (London) 266: 327-332.

RUSSO, D., G. JONES AND A. MIGLIOZZI. 2002. Habitat selection by the Mediterranean horseshoe bat, *Rhinolophus euryale* (Chiroptera: Rhinolophidae) in a rural area of southern Italy and implications for conservation. Biological Conservation 107: 71-81.

RUSSO, D., G. JONES AND M. MUCEDDA. 2001. Influence of age, sex and body size on echolocation calls of Mediterranean and Mehely's horseshoe bats, *Rhinolophus euryale* and *R. mehelyi* (Chiroptera: Rhinolophidae). Mammalia 65: 429-436.

SAINT-GIRONS, M.-C. AND B. CAUBÈRE. 1966. Notes sur les mammifères de France III. Sur la répartition de *Rhinolophus hipposideros hipposideros* et *Rhinolophus hipposideros minimus*. Mammalia 30: 308-326.

SAUNDERS, M.B. AND R.M.R. BARCLAY. 1992. Ecomorphology of insectivorous bats: a test of predictions using two morphologically similar species. Ecology 73: 1335-1345.

SCHNITZLER, H.-U. 1983. Fluttering target detection in horseshoe bats. Journal of the Acoustical Society of America 74: 31.

SCHNITZLER, H.-U. AND E.K.V. KALKO. 1998. How echolocating bats search and find food. Pp. 183-196 in Bat biology and conservation (T.H. Kunz and P.A. Racey, eds.). Smithsonian Institution Press, Washington, D.C.

SCHNITZLER, H.-U. AND E.K.V. KALKO. 2001. Echolocation by insect-eating bats. Bioscience 51: 557-569.

SCHNITZLER, H.-U., C.F. MOSS AND A. DENZINGER. 2003. From spatial orientation to food acquisition in echolocating bats. Trends in Ecology and Evolution 18: 386-394.

SCHOBER, W. AND E. GRIMMBERGER. 1998. Die Fledermäuse Europas. Kosmos-Naturführer, Stuttgart, Germany.

SCHOENER, T.W. 1974. Resource partitioning in ecological communities. Science 185: 27-39.

SCHUM, M. 1984. Phenetic structure and species richness in North and Central American bat faunas. Ecology 65: 1315-1324.

SHARIFI, M. 2004. Postnatal growth and age estimation in the Mehely's horseshoe bat (*Rhinolophus mehelyi*). Acta Chiropterologica 6: 155-161.

SIEMERS, B.M., K. BEEDHOLM, C. DIETZ, I. DIETZ AND T. IVANOVA. 2005. Is species identity, sex, age or individual quality conveyed by echolocation call frequency in European horseshoe bats? Acta Chiropterologica 7: 259-274.

SIEMERS, B.M. AND T. IVANOVA. 2004. Ground gleaning in horseshoe bats: comparative evidence from *Rhinolophus blasii*, *R. euryale* and *R. mehelyi*. Behavioral Ecology and Sociobiology 56: 464-471.

SIEMERS, B.M. AND H.-U. SCHNITZLER. 2004. Echolocation signals reflect niche differentiation in five sympatric congeneric bat species. Nature 429: 657-661.

SIEMERS, B.M. AND S.M. SWIFT. 2006. Differences in sensory ecology contribute to resource partitioning in the bats *Myotis bechsteinii* and *Myotis nattereri* (Chiroptera: Vespertilionidae). Behavioral Ecology and Sociobiology 59: 373 - 380.

STOCKWELL, E.F. 2001. Morphology and flight manoeuvrability in New World leaf-nosed bats. Journal of Zoology (London) 254: 505-514.

SWARTZ, S.M., P.W. FREEMAN AND E.F. STOCKWELL. 2003. Ecomorphology of bats: comparative and experimental approaches relating structural design to ecology. Pp. 257-300 in Bat ecology (T.H. Kunz and M.B. Fenton, eds.). The University of Chicago Press, Chicago, Illinois.

VALENCIUC, N. 1971. Donées concernant la nourriture et la manière de se la procurer chez quelques espèces de la faune de Roumanie. Studii si Comunicari 1971: 353-357.

VAN VALEN, L. 1965. Morphological variation and width of ecological niche. American Naturalist 99: 377-390.

VAUGHAN, T.A. 1959. Functional morphology of three bats: *Eumops, Myotis*, and *Macrotus.* University of Kansas, Museum of Natural History 12: 1-153.

VAUGHAN, T.A. 1966. Morphology and flight characteristics of molossid bats. Journal of Mammalogy 47: 249-260.

WHITAKER, J.O. JR. AND H. BLACK. 1976. Food habits of cave bats from Zambia, Africa. Journal of Mammalogy 57: 199-204.

WIENS, J.A. 1977. On competition and variable environments. American Scientist 65: 590-597.

YOUNG, R.A. 1975. Aging criteria, pelage colour polymorphism and moulting in *Rhinolophus megaphyllus* (Chiroptera) from south-eastern Queensland, Australia. Mammalia 39: 75-111.

ZAR, J.H. 1999. Biostatistical analysis. 4th edition. Prentice Hall, Inc., Upper Saddle River, New Jersey.

Chapter 7

Comparative wing morphology of five sympatric horseshoe bat species (Chiroptera: Rhinolophidae)

By C. Dietz, I. Dietz, T. Ivanova, H.-U. Schnitzler & B.M. Siemers

The ms. is not published yet.

Comparative wing morphology of five sympatric horseshoe bat species (Chiroptera: Rhinolophidae)

Christian Dietz[1), Isabel Dietz[1), Teodora Ivanova[2), H.-U. Schnitzler[1), & Björn M. Siemers[1)3)

1) Animal Physiology, Zoological Institute, Tübingen University, Auf der Morgenstelle 28, 72076 Tübingen; Germany. Email: Christian.Dietz@uni-tuebingen.de

2) Nature Park Roussenski Lom, Skobelev blvd. 7, 7000 Rousse; Bulgaria.

3) Sensory Ecology Group, Max-Planck-Institute for Ornithology, 82319 Seewiesen, Germany.

ABSTRACT

Wing morphology was studied in five sympatric horseshoe bat species (genus *Rhinolophus*) in southeastern Europe. Wing area measurements were obtained by wing photogrammetry of 479 adult horseshoe bats. With the exception of one species, we obtained samples from at least 50 males and females per species. We used wing loading, aspect ratio and tip shape index to compare the five congeners. In each species the measurement error was assessed by repeatedly processing the same individual 20 times; in the derived wing parameters like wing loading or aspect ratio the measurement errors summed up to 2-3% of the values. To standardize the wing loading of bats captured in different seasons we calculated a standard body mass for males, nonreproductive, and lactating females in each species. Examination of the data showed that the species and their wings differed substantially in size, while a sexual dimorphism was present only in the handwing area of all species with females being larger than males. The derived wing parameters also differed significantly but the factors species and sex explained only parts of this variation. Predictions on flight capabilities and flight behaviour drawn from the derived wing parameters are compared to field data of foraging behaviour, habitat use, and commuting flight speeds obtained from a telemetry study. However, the correlations revealed little significant relationships. Only the individual body mass and wing loading correlated significantly to the percentage of perch hunting, similarly wingspan and hand wing lengths correlated negatively to the use of dense vegetation. In three out of the five species theoretically predicted economical flight speeds did not differ from those measured in the field while bats were commuting. The difficulties in relating field data to wing morphology are discussed and may mainly be due to high intraspecific variability and flexibility of foraging behaviour. We conclude that mainly the size differences between the five species rather than adaptations in wing shape help to reduce niche overlap and interspecific competition within the five species.

Key-words: *Rhinolophus*, wing morphology, wing photogrammetry, guild structure, niche separation.

INTRODUCTION

Guilds are groups of animals showing strong similarities in their ecology mainly due to a similar way of exploiting the same class of environmental resources, e.g. the members may use similar feeding or prey capture strategies (Root 1967). Under the assumtion that resources are limited, mechanisms should have evolved within each guild that structure the communities to avoid or reduce niche overlap. A reduced competition in syntopic species enables the stable coexistence of them at least as long as the environment remains stable (Hardin 1960; Simberloff and Dayan 1991; Wiens 1977). Often size differences are important for structuring such animal communities (Schoener 1974; Swartz et al. 2003). Bats offer suitable model systems to study guilds as they evolved many different species having many characteristics in common such as a volant and nocturnal lifestyle and echolocation, but also show specialized adaptations in echolocation, prey selection and habitat use. Bats are physically and behaviorally adapted to exploit their environment in different ways by using different kinds of foraging areas, habitats, prey acquisition modes or prey types (Swartz et al. 2003). As each strategy requires particular adaptations, syntopic bats have been shown to utilize foraging habitats depending on flight morphology and echolocation characteristics (e.g. Aldridge and Rautenbach 1987; Findley 1993; Heller and Helversen 1989), thus the relationship between form and function can be used to predict ecological differences from morphological ones (Swartz et al. 2003). Among the many adaptations especially wing morphology is crucial for flight performance and foraging ecology in bats (Norberg 1990; Stockwell 2001). Accordingly morphological differences between bat species have been shown to reflect adaptations to flight and foraging strategies (e.g., Aldridge 1986a; Norberg 1981). Thereby ecomorphology offers a strong tool to use morphological differences between species to predict a possible species’ niche. Differences in the species’ ecology lead to the use of different niches and might act as mechanisms to avoid interspecific competition within gilds.

The European horseshoe bats belong to a single well defined group of closely related species (Guillén et al. 2003). They produce long duration constant-frequency echolocation calls with maximum energy in the 2nd harmonic (Griffin and Simmons 1974; Heller and Helversen 1989; Jones and Rayner 1989; Siemers et al. 2005). Horseshoe bats use frequency and amplitude shifts modulated onto the echoes of their constant-frequency calls by the wing beats of insects as a means of detecting prey (Schnitzler 1983). All European species are similar in several morphological respects, including short and broad wings with low wing loading and aspect ratio (Findley et al. 1972; Norberg 1987; Norberg and Rayner 1987). All European species prey mainly on Lepidoptera, Diptera and some other insect orders (Beck et al. 1989, 1997; Bontadina et al. 1995, 1997, 2002; Dietz et al. 2007b; Goiti et al. 2004; Jones and Rayner 1989; Valenciuc 1971; Whitaker and Black 1976). Based on these morphological and behavioral similarities we hypothesized that all five European horseshoe bat species can be united in a single guild of 'aerial insectivore narrow space flutter-detecting foragers' (Schnitzler and Kalko 1998, 2001; Schnitzler et al. 2003). The five species occur in Europe in sympatry on the Balkan Peninsula only (Dietz et al. 2007b; Mitchell-Jones et al. 1999).

In a study on external wing measurements (forearm, 5th finger, 3rd finger and phalanges of 4th digit) we found that the measurements overlapped considerably among the species (Dietz et al. 2006a). However despite a similar general wing construction, we detected differences in size-independent relationships of wing measurements that might be regarded as adaptations to different foraging tactics or habitats (see Aldridge and Rautenbach 1987; Kalcounis and Brigham 1995) and we assumed that the differences are big enough to have ecological significance for niche separation (Dietz et al. 2006a). The species vary in size, with the largest and smallest species differing widely from the three medium-sized species. Intraspecifically, females are bigger than males in all measurements. We argued that morphological differences between the species are large enough to permit predictions about differences in maneuverability, foraging style, and habitat use (Aldridge 1986a; Aldridge and Rautenbach

1987; Kalcounis and Brigham 1995; Kingston et al. 2000; Saunders and Barclay 1992). For example, the smallest species, *Rhinolophus hipposideros*, and to a lesser extent also *R. blasii*, have extremely short hand wings, enabling highly maneuverable search flight close to vegetation. The largest species *R. ferrumequinum* and the second largest one, *R. mehelyi*, have rather long hand wings, allowing fast and economic commuting flight over longer distances (Dietz et al. 2006a).

In the present study we aim to compare the wing morphology of the European horseshoe bats based on wing area data and derived wing indices obtained from wing photogrammetry. We intended to test whether the conclusions reached on the basis of standard wing measurements (Dietz et al. 2006a) are supported by the present photogrammetric area measurements. We further test predictions on habitat use or foraging mode derived from the wing morphology data. In order to verify the predictions we compare the wing indices with behavioral and ecological data that we obtained through radio-telemetry.

Several new studies have shown how complex the aerodynamics of bat flight are (Hedenström 2007; Norberg and Winter 2006; Rayner et al. 1986; Swartz et al. 2003) and how far we still are from an understanding of many of the underlying principles in aerodynamics of flight. One might therefore assume that not much insight into the underlying ecological principles can be gained when using simple models based on two-dimensional measurements. However, as many studies have shown the merits of the classical wing morphology to match flight probabilities in bat flight quite closely (Aldridge 1986a; Aldridge and Rautenbach 1987; Baagøe 1987; Crome and Richard 1988; Findley 1993; Kalcounis and Brigham 1995; O'Shea and Vaughan 1980; Swartz et al. 2003), as no better models for comparing live bats in the field are available at the moment and as we compare closely related species with a quite similar wing design, we still believe in the potential of ecomorphology based on wing area measurements.

Our hypothesis to be tested in this study are:

- flying within vegetation requires slow flight and short wings. Such wings must be broad to compensate for their shortness with enough wing area to permit slow flight leading to low wing loading and low aspect ratios. *Accordingly we expect the European horseshoe bats to exhibit low wing loadings, low aspect ratios and large tip shape index values compared to the majority of other European bat species.*

- As flight for bats of this type of wing morphology is correspondingly expensive (Norberg and Rayner 1987) the bats should use perch hunting in a flycatcher style to save energy by reducing the time spent flying. This should apply especially for the heavier species with higher wing loading within a guild. *We therefore expect the time spend perching to be positively correlated with body mass / wing loading and negatively correlated with aspect ratio.*

- For predictions about habitat use we expect *long wings* (high wing span, long hand-wing lengths) *to be characteristic for bats foraging in more open habitats while short wings* (low wing span, short hand-wing lengths) *increase maneuverability amidst foliage and dense vegetation and can be expected to be characteristically for bats foraging in forests and scrubland.*

- flight is an expensive mode of locomotion (Norberg 1990) as a consequence there should be a strong selection to minimize costs, *thus when commuting the species should fly closely to their maximum range speed as predicted from wing morphology.*

- interspecific competition among the guild members should be reduced by *clear differences in wing morphology and parameters describing flight performance* enabling the species to occupy different niches, e.g. exploiting different habitats or by using different prey acquisition modes.

MATERIALS AND METHODS

Our study was carried out in southeastern Europe, where all five European species of horseshoe bats (*Rhinolophus blasii*, *R. euryale*, *R. ferrumequinum*, *R. hipposideros* and *R. mehelyi*) occur in sympatry. Wing photographs were taken between 1999 and 2004 from bats captured in Bulgaria and northern Greece. The vast majority of bats (with exception of *R. blasii*) were caught in northern Bulgaria in caves along the rivers Osăm, Vit, Jantra and Lom. The main other study sites were the Eastern Rhodope Mountains in Bulgaria and Greece and the Strandža Mountains in Bulgaria. Fieldwork was carried out under license of Bulgarian (15-RD-08/15.01.2001, 48-00-56/16.01.2001, 8/02.07.2004 RIOSV Pleven, RIOSV Rousse) and Greek (97371/2554/16-5-2002, 94728/1025/28-2-2003 and 98358/1437/18-3-2004) authorities. The bats were mainly captured with mist-nets or harp-traps when leaving or entering day-roosts in caves, mines and abandoned buildings. They were kept individually in cloth bags until measured. Bats were identified using characteristics of the nose-leaf and lower lip (Schober and Grimmberger 1998; Dietz et al. 2007b; see Dietz and von Helversen 2004: Identification key to the bats of Europe [www.uni-tuebingen.de/tierphys/Kontakt/mitarbeiter_seiten/dietz.htm.]). From each bat five standard measurements were taken with a Hommel mechanical precision caliper (precision ± 0.01 mm; see Dietz et al. 2006a) and the bats weighted with a Soehnle precision balance (precision ± 0.05 g).

Wing photographs

To take wing photographs, we used a custom made collapsible tripod with a fixed pocket camera Olympus mju-II (35 mm f/2.8 lens and internal flash) mounted in a distance of 32 cm above a table. The film plane was thereby kept parallel to the table to avoid any distortion. We used ISO 400 black and white negative films. For later calibration with the analysis software, we fixed graph paper ruled in millimetres on the table. Date, locality, species, sex and ID-number were written down and photographed with each bat. The bats were placed on the table in a standardized way with the ventral side down and the right wing opened according the following criteria: head and body in one line; wing opened and outstretched in a way that the wrist was at the same height as the head and the fifth finger parallel to the body axis (Fig. 3-4). The tail membrane was photographed separately with the tail straight and the legs spread in 90-100° from each other.

Only adult bats were measured. The age class of the bat was determined by the degree of closure of the epiphyseal growth plates of the phalanges (Rybář 1972) and by comparing fur coloration and structure with banded bats of known ages (following the methods of Gaisler 1960, 1965; Gaisler and Titlbach 1964; Matthews 1937; Rollinat and Trouessart 1897; and Young 1975). Pseudoreplication by inadvertently measuring the same individual twice was minimized by marking a high proportion of the bats captured in Northern Bulgaria individually with bat rings (but see Dietz et al. 2006b for a cautionary note on ringing horseshoe bats) and by visiting other roosting sites only once or twice. As we caught bats throughout summer season (April–October), body mass varied strongly according to reproductive condition or activity level. To compensate for this effect, we calculated a standard body mass for each species and sex to obtain comparable data for wing loading from weights of bats leaving the roost in the evening prior to foraging.

To analyse the wing photographs they were scanned with a slide scanner (Minolta Dimage Scan Dual III). We use photos of the graph paper to calibrate the scans in the horizontal and vertical axes in the Software Optimas (Optimas 5.1a, Optimas Corporation, Bothell, Washington, USA). After setting the scale and the grey shade of the background most of the measurements could be taken automatically by the software, exploiting differences in the grey shades of the wing membranes, wing bones and the background. However, all automatically delimited areas were counterchecked by eye. The area and width of the body and the lengths of arm- and handwing were measured on the computer screen manually with the mouse.

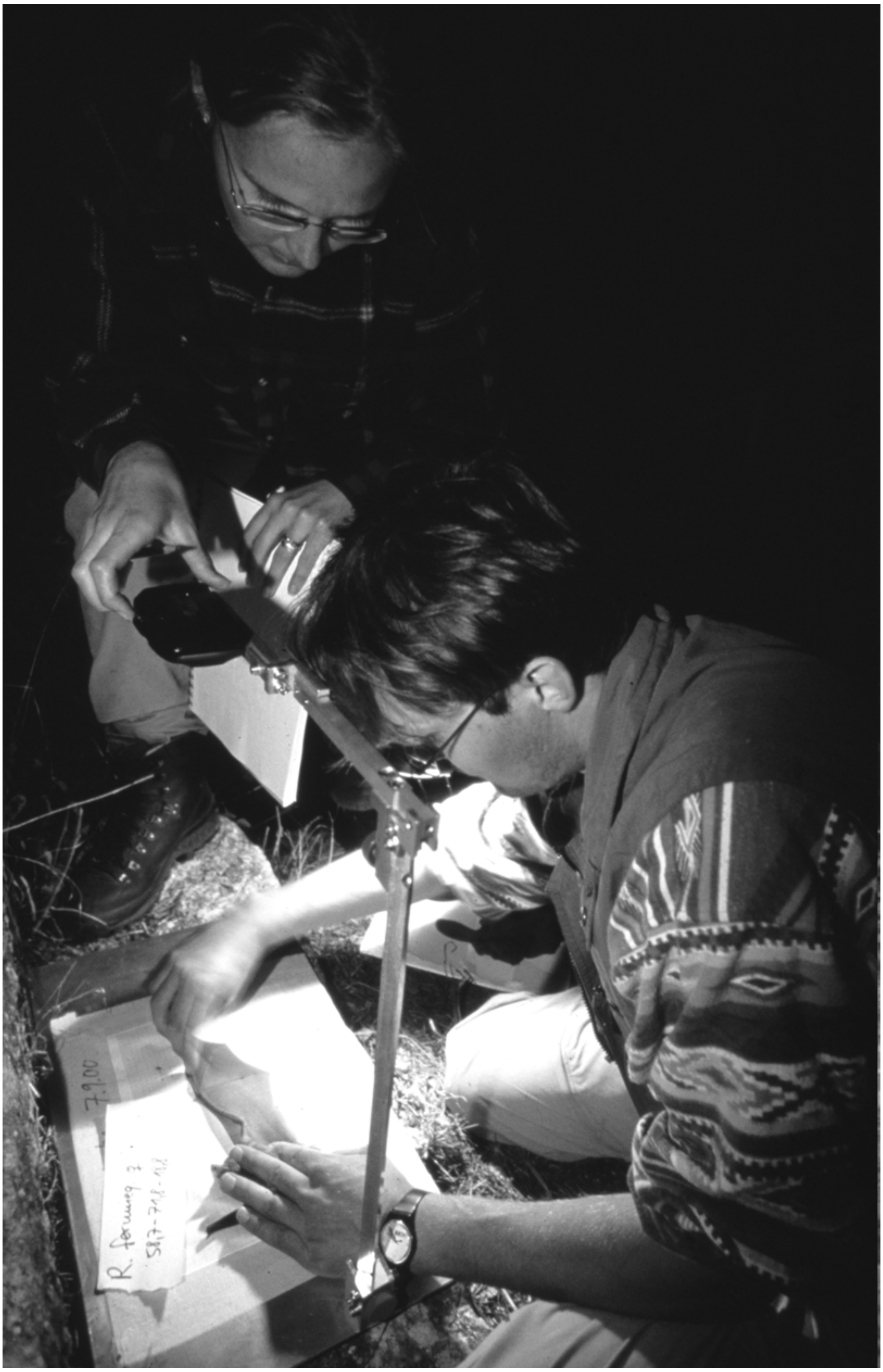


Figure 1: Taking wing photographs in the field requires two people to fix the bats wing membranes in a standardized position and to take the pictures. © K. Echle.

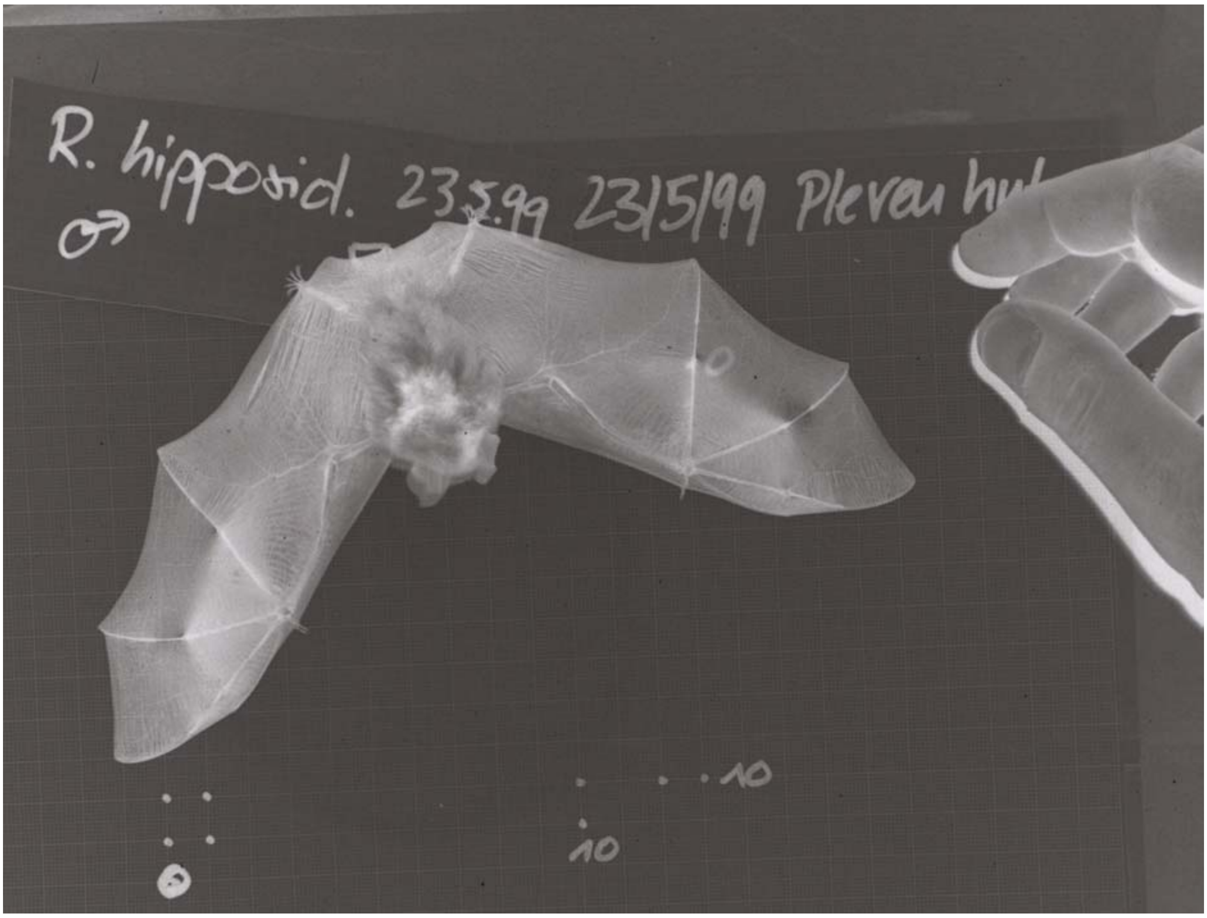


Figure 2: Wing photograph of a lesser horseshoe bat (*R. hipposideros*) with outstretched wings on the table of the photogrammetry equipment. As this was the only bat staying on the table without being fixed and to obtain pictures in a standardized way we placed the bats as given in figures 3 and 4.

Figure 3: Wing photograph of a Mehely’s horseshoe bat (*R. mehelyi*). The tail membrane was photographed separately.

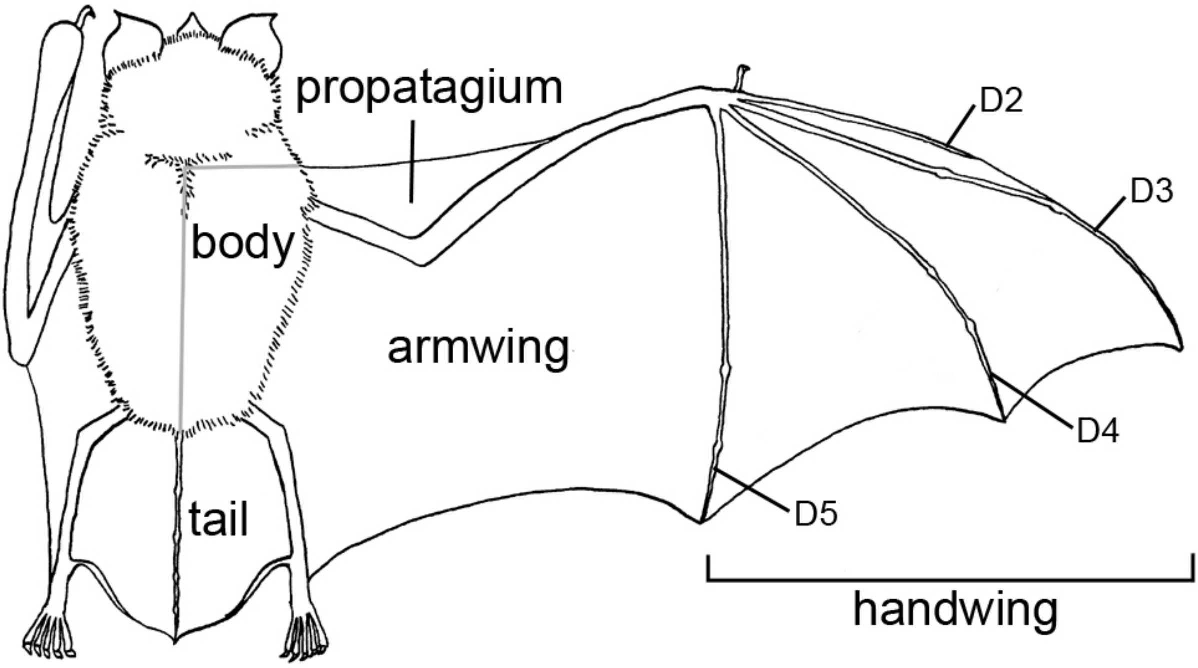


Figure 4: Dorsal view of a greater horseshoe bat (*R. ferrumequinum*) with outstretched wing: the wing areas used in this study are shown. Abbreviations: D2 = second finger; D3 = third finger; D4 = fourth finger; D5 = fifth finger. The body area was measured from the insertion of the propatagium to the midline between the shoulder blades to the insertion of the tail (bordered by the grey line).

Wing measurements

We took four lengths and seven area measurements from the wing photographs. Lengths measurements: 1) body width, measured as the doubled distance between the midline between the shoulder blades and the insertion of the upper arm to the body; 2) length of the armwing, from the insertion of the upper arm to the wrist; 3) length of the handwing, from the wrist to the tip of the third finger; 4) wingspan, measured as the doubled length from the midline of the body to the tip of the third finger. Area measurements: 1) body area, the doubled area between the midline of the body to the insertion of the wing membranes excluding the head (see Figure 4); 2) tail area; 3) propatagium; 4) armwing and, 5-7), the three handwing segments between the metacarpal and finger bones (Figure 4).

Accuracy of wing photogrammetry

To assess the measurement error associated with different ways of placing the bat, opening the wings and digitally extracting the measurements, we repeated the procedure 20 times for one adult female per species (table 1 for data on *R. ferrumequinum*, data on other species not shown). Variations were highest in measurements of body width, body area, tail area and hand wing area between 2nd and 3rd digit. For the body measurements, it proved to be somewhat problematic to place the bat it in a standardized way without providing it much discomfort. For the same reasons it was difficult to get standardized measurements of the tail area. The measurements of the hand wing area between the digits 2 and 3 varied a lot depending on how strong the digit 2 was extended. However, this had little effect on the total wing area measurements as this part of the wing area is quite small. All together the measurement errors summed up to 2-3% of the values in the derived wing parameters in all five species (e.g. wing loading and aspect ratio - Table 1).

Table 1: Measurements of the wing areas and two derived wing parameters from repeatedly taken wing photographs in an adult female *Rhinolophus ferrumequinum*. *N* = 20. Results for the other four species are very similar (data not shown). Abbreviations: BW = body width; LAW = length of armwing; LHW = length of handwing; Body = half area of the body without head; Tail = half area of the tail; Propat = area of the propatagium; ArmW = area of the armwing; HandW 4-5 = area of the handwing between digit 4 and 5; HandW 3-4 = area of the handwing between digit 3 and 4; HandW 2-3 = area of the handwing between digit 2 and 3; L = wing loading; AR = aspect ratio.

	BW (cm)	LAW (cm)	LHW (cm)	Body (cm²)	Tail (cm²)	Propat (cm²)	ArmW (cm²)	HandW 4-5 (cm²)	HandW 3-4 (cm²)	HandW 2-3 (cm²)	L (g/cm²)	AR
Mean	3.84	7.04	8.64	15.70	9.82	5.15	47.94	17.86	14.97	1.87	9.41	6.38
Min	2.95	6.71	8.48	12.84	6.22	4.53	44.65	17.29	14.56	1.52	9.08	6.06
Max	4.26	7.30	8.96	17.88	12.56	5.69	50.54	18.38	15.48	2.17	9.86	6.64
SD	0.36	0.19	0.10	1.36	1.64	0.32	1.71	0.30	0.28	0.17	0.23	0.20
% SD of the Mean	9.4	2.7	1.2	8.7	16.6	6.2	3.6	1.7	1.8	9.1	2.4	3.1

Derived data from wing morphology

We used the following established wing size and wing shape parameters that ecomorphologists employ to compare species: wing loading, aspect ratio and tip shape index. Wing loading (L) relates body mass to wing size and is calculated as the body mass (g) divided by the wing area (cm^2). Slow flight is possible with a low wing loading and relates to large wings, while bats with small wings have to fly faster for their body size. As wing loading is strongly influenced by daily and seasonal body mass changes (e.g. Webb et al. 1992), data comparison is somewhat problematic. To achieve comparable data for the summer season we calculated a standardized wing loading by using a standard body mass for males, nonreproducing females and lactating females. This standard body mass (Table 2) is the mean of all bats captured per species, sex and reproductive class in the evening when emerging from the roost (prior to foraging) from May to beginning of September (males and non reproducing females) or during lactation period (usually Mid of June till latest End of July in reproducing females; Dietz et al. 2007a).

Table 2: Body mass of adult horseshoe bats (Rhinolophidae) of both sexes and different reproductive classes in females during summer (Mai-September). Data are given by their mean ± SD (*n*).

species	males (g)	non reproductive females (g)	lactating females (g)
R. hipposideros	4.9 ± 0.5 (27)	4.9 ± 0.6 (6)	5.0 ± 0.6 (9)
R. blasii	11.0 ± 0.7 (62)	11.2 ± 0.7 (45)	11.8 ± 0.8 (31)
R. euryale	11.6 ± 1.0 (403)	11.4 ± 0.8 (183)	12.1 ± 0.8 (139)
R. mehelyi	14.5 ± 1.1 (211)	14.2 ± 0.9 (111)	15.8 ± 1.2 (304)
R. ferrumequinum	20.2 ± 1.6 (111)	20.6 ± 1.4 (324)	21.7 ± 1.5 (584)

Aspect ratio (AR) is a non dimensional parameter reflecting the shape of the wing. It is defined as the ratio of the wing span to the mean chord of the wing. Slow flying highly manoeuvrable bats exhibit low aspect rations due to broad wings with low total flight power. On the other hand fast flying bats with very narrow wings have high aspect ratios and have either to fly very fast or to beat the wings very fast to obtain sufficient weight support (Norberg 1994). Tip shape index (I) is independent of the overall size of the arm- and hand-wing but is determined by their relative size. It is defined as the ratio of the hand-wing area to the arm-wing area divided by the ratio of the length of the hand-wing to the length of the arm-wing minus the ratio of the hand-wing area to the arm-wing area (Norberg and Rayner 1987). High tip shape index values indicate rounded or nearly square wing tips while low values are related to pointed triangular wing tips.

High agility is positively correlated with large tips shape index values, low aspect ratio and long wing span in slow flying bats. In fast flying species high agility is positively correlated with high wing loading, small tip shape index values, high aspect ratio and short wings. High manoeuvrability is achieved by low wing loading in both, slow and fast flying bats (Norberg 1994).

In order to compare theoretically predicted flight speeds with those measured in the field we calculated the minimum power speed and maximum range speed (Pennycuick 1975) following the equations given by Norberg and Rayner (1987).

Telemetry

To obtain measurements of flight speed during commuting flights, on the foraging mode and on habitat use, we conducted radio-telemetry of free ranging bats. In *R. ferrumequinum* and some *R. mehelyi* position sensitive transmitters with mercury switches (BD-2AP: Holohil Systems, Carp, Canada) and in the other species normal transmitters (LB-2: Holohil Systems, Carp, Canada or Pip: Biotrack, Wareham, UK) were used with a frequency range of 144-152 MHz. The signals were received with modified Yaesu FT-290 RII (Andreas Wagener Telemetrieanlagen, Köln, Germany) and Regal 2000 (Titley Electronics, Ballina, Australia) telemetry receivers with collapsible three-element and five-element Yagi-antennas or omni-directional dipole antennas. To follow the bats in dense vegetation H-Adcock antennas were used in some instances. At fixed positions we used up to six meter high poles for the five-element Yagi antennas to increase gain, while a mobile car mounted five-element Yagi antenna was at 2.2 m above ground. The transmitters were attached between the shoulder blades with a custom-made modification of medical skin adhesive (U-Bond: Manfred Sauer GmbH, Lobbach, Germany). Bats were released within two hours of capture. Only a single bat was tracked during each session and followed continuously by a team of four observers until the transmitter fell off or stopped working. Two people took bearings from fixed positions on the top of hills, one person followed in a car and one person tried to be as close as possible to the bat by walking. Fixes were obtained by a combination of triangulation and homing in on the animal (Kenward 2001). Walkie-talkies (Standard Minix C836L, Richter & Co. Funkgeräte, Hannover, Germany) were used to coordinate the work of the four operators. When radio contact was broken with a moving bat, we tried to reestablish contact within the next 1-2 hours, otherwise tracking continued the next evening.

The flight speed of a bat was measured on known commuting routes by several persons. The exact passing time of the bat at the starting and end point of the commuting route was determined by the highest signal strength at fully attenuated receiver gain. Tests had shown that the transmitter had to be in a 10 m radius around the receiver under these conditions. The foraging mode was investigated by noting permanently whether the bat was flying or hanging. In *R. ferrumequinum* and some *R. mehelyi*, the changing intervals between signal pulses of the position-sensitive transmitters allowed to discriminate between the two stages quite easily. In the other bats we used the modulations of the signal strength to discriminate between hanging and flying. Frequent alterations in signal strength, caused by the whipping motions of the trailing transmitter antenna in flight and / or by quick changes in obstacle density between bat and receiver indicated a flying bat. Rapid directional movements between distant sites were classified as commuting while signals of the flying bat in a defined area of variable size was taken as indicative of foraging on the wing. Hanging for less than five minutes combined with short flying phases less than three minutes were counted as foraging in a flycatcher mode. Hanging longer than five minutes without flying was equated with night roosting. Usually during night roosting the signal became very constant and stable while it remained unsteady during perching due to the permanent head and body movements of the bats. Activity times with unclear behavior were attributed to an category “undetermined” and not considered for analysis. The individual tracking results on the foraging mode were very heterogeneous due to big differences in radio contact time between individual bats (20%-95% of the time spend outside the roost). The individual habitat use was calculated from 50 m buffers around high-quality fixes of foraging bats (commuting, roosting and night-roosting excluded; accuracy of the used fixes better than ± 50 m) in ArcView GIS 3.3 (Environmental Systems Research Institute, Valparaiso) by overlaying the buffers with detailed habitat maps (own mapping; details will be published separately: I.Dietz in prep.).

Statistical analysis

To assess morphological variation, we calculated the mean, standard deviation (SD), minimum and maximum for morphological variables according to sex and species. We analyzed the data using *t*-tests and analysis of variance (ANOVA). Analyses were performed in Excel 2002 (Microsoft, Redmond, Washington) and Jump 5.1 (SAS Institute Inc., Cary, North Carolina).

RESULTS

We obtained wing area measurements from 479 adult rhinolophids, including 115 *R. ferrumequinum*, 37 *R. hipposideros,* 102 *R. blasii*, 110 *R. euryale* and 115 *R. mehelyi*. With the exception of *R. hipposideros*, these included at least 50 adult males and 50 adult females per species. The wing area measurements overlapped for the most part among the species. However, when plotting the wing area (as an indicator for the total surface of the flight membranes and the body) against the forearm length (as an indicator for the bat's size), the five species were reasonably separated (Fig. 5). Especially the smallest species (*R. hipposideros*) and the largest one (*R. ferrumequinum*) get well separated from the quite similar three medium-sized species (*R. blasii*, *R. euryale* and *R. mehelyi*).

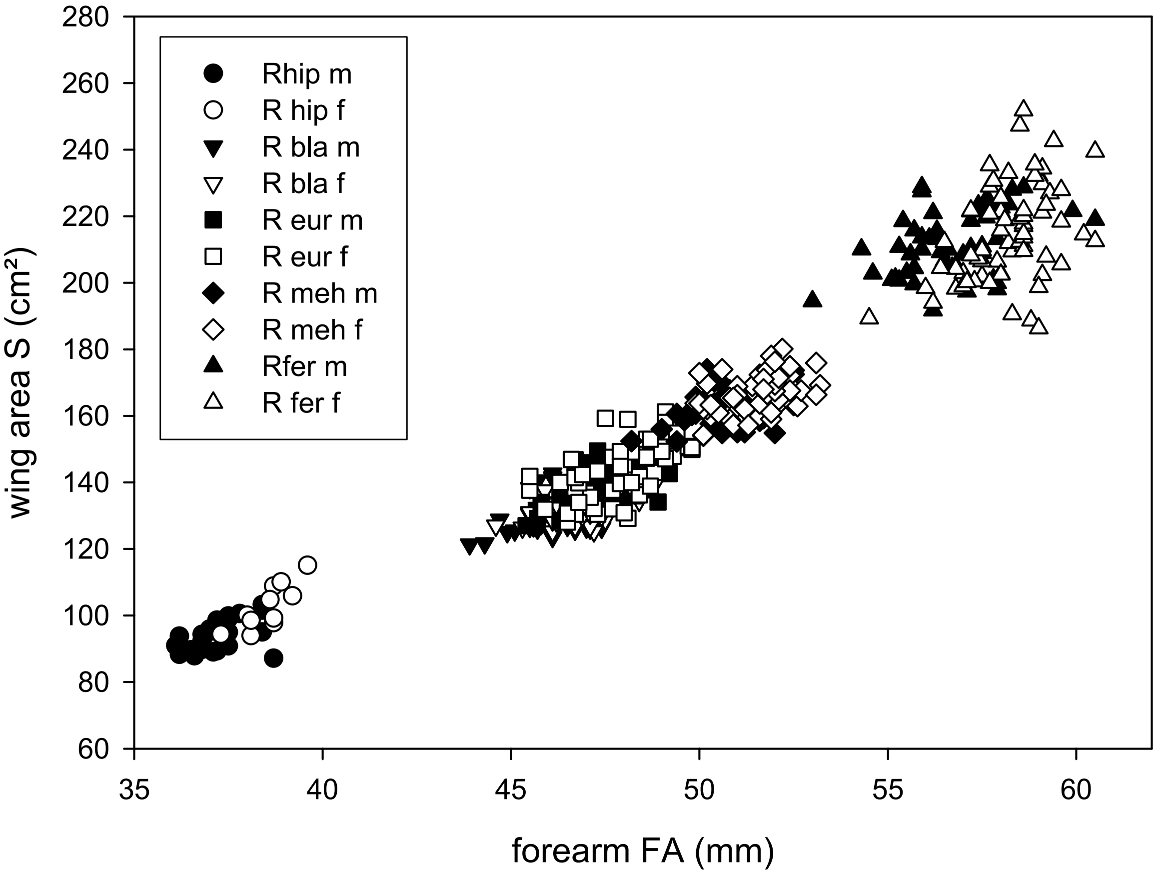


Figure 5: Scatterplot of the total wing area against the forearm length of the five European horseshoe bat species. Abbreviations: m = males; f = females; Rhip = *R. hipposideros*; Rbla = *R. blasii*; Reur = *R. euryale*, Rmeh = *R. mehelyi*; Rfer = *R. ferrumequinum*.

Although the means of most measurements were bigger in females, a significant sexual dimorphism could only be found in some of them (Table 3). Handwing area was the only measurement being significantly larger in females of all species than in males ($t \geq 2.466$, *d.f.* ≥ 2,35-113, $P \leq 0.0152$). Armwing area and total wing area of females were significant bigger in four out of the five species ($t \geq 2.119$, *d.f.* ≥ 2,35-113, $P \leq 0.0366$) with exception of *R. ferrumequinum* ($t = 0.193$-0.734, *d.f.* = 2,113, $P = 0.4643$-0.8470). Standardized wing loading was bigger in females than in males in three species ($t \geq 2.825$, *d.f.* ≥ 2,100-113, $P \leq 0.0056$), but smaller in female than in male *R. hipposideros* ($t = 3.216$, *d.f.* = 2,36, $P = 0.0028$) and did not differ between both sexes in *R. euryale* ($t = 1.604$, *d.f.* = 2,108, $P = 0.1116$).

A general linear model comparing adult measurements found that the factors 'species' and 'sex' explained most of the variability within each of the 7 measured wing areas (all $F \geq 110.08$, *d.f.* = 9,469, $R^2 = 0.68$-0.94, all $P < 0.0001$). The model explained the variability best in the measurements with the lowest measurement errors (armwing area, handwing areas between digit three and four and four and five; all $F \geq 616.09$, *d.f.* = 9,469, $R^2 \geq 0.92$, all $P < 0.0001$), while the least fit was achieved in the measurements with high measurement errors (body area, propatagium area and handwing area between digit two and three; all $F \leq 156.68$, *d.f.* = 9,469, $R^2 \leq 0.75$, all $P < 0.0001$). In the overall GLM the factor 'species' explained the majority of variability in all 7 measurements (all $F \geq 234.97$, *d.f.* = 9,469), while 'sex' had a minor effect (all $F \leq 19.433$, *d.f.* = 9,469).

Similarly we explored the three derived wing parameters wing loading, aspect ratio and tip-shape-index with a general linear model: this time the factors 'species' and 'sex' explained only a smaller part of the variability within the three parameters ($F = 13.16$-58.79, *d.f.* = 9,469, $R^2 = 0.20$-0.53, all $P < 0.0001$), but again the factor 'species' was the most important factor of the applied model ($F = 24.78$-111.33, *d.f.* = 4,474).

Due to a high proportion of pregnant or prehibernating bats, the body masses of the individuals measured in the study presented here differed significantly from the normal body mass of the species in summer in both sexes in *R. ferrumequinum* and *R. mehelyi* and in female *R. blasii* ($t \geq 2.160$, *d.f.* ≥ 2,80-646, $P \leq 0.0160$), while it did not differ in *R. hipposideros*, *R. euryale* and male *R. blasii* ($t \leq 2.451$, *d.f.* ≥ 2,51-451, $P \geq 0.1899$). To obtain comparable data for the summer season we determined the standard body mass per species and sex (Table 2) and used it to calculate a standardized wing loading. Within the standardized wing loading a GLM using the factors 'species' and 'sex' explained a much higher proportion of the variability than in the wing loading with the original body mass data ($F = 71.34$, *d.f.* = 9,469, $R^2 = 0.85$, all $P < 0.0001$), again the factor 'species' explained the majority of the variability ($F = 566.56$, *d.f.* = 4,474).

Nevertheless, the five species are very similar, especially in the size independent parameters like aspect ratio or in the standardized wing loading (Fig. 6). Within the guild the smallest species, *R. hipposideros*, can be regarded as the most specialized one as the derived wing parameters differ from the others in a pronounced way (Fig. 6).

Table 3: Wing area measurements of adult *Rhinolophus* bats of 5 species from southeastern Europe (Bulgaria and Greece) and *t*-statistics between both sexes. Abbreviations: M = male; F = female; ad. = adult; ArmW = area of the armwing; HandW = area of the handwing; S = total wing area of one wing, half of the tail and half of the body; B = wingspan; L = wing loading; L stand = standardized wing loading calculated with a standard body mass for males and lactating females (see table 3); AR = aspect ratio; I = tip-shape-index.

species and sex	ArmW (cm^2) mean ± SD (min – max)	HandW (cm^2) mean ± SD (min – max)	½ S (cm^2) mean ± SD (min – max)	B (cm) mean ± SD (min – max)	L (g/cm^2) mean ± SD (min–max)	L stand (g/cm^2) mean ± SD (min–max)	AR mean ± SD (min–max)	I mean ± SD (min–max)
R. hipposideros								
M ad. (n = 26)	24.0 ± 1.6 (20.9 – 26.5)	15.6 ± 0.8 (13.9 – 17.0)	47.2 ± 2.4 (43.6 – 51.6)	23.8 ± 0.5 (22.7 – 24.6)	5.2 ± 0.5 (4.2 – 6.0)	5.1 ± 0.2 (4.7 – 5.5)	6.1 ± 0.3 (5.7 – 6.8)	2.1 ± 0.3 (1.6 – 2.7)
F ad. (n = 11)	26.6 ± 2.0 (24.3 – 29.9)	16.5 ± 1.0 (14.7 – 18.2)	51.3 ± 3.4 (47.0 – 57.6)	25.1 ± 0.7 (24.0 – 26.5)	5.6 ± 1.3 (3.9 –8.7)	4.8 ± 0.3 (4.3 – 5.2)	6.2 ± 0.2 (5.9 – 6.5)	2.4 ± 0.4 (1.7 – 3.0)
t-test	t = 4.264, P = 0.0001	t = 2.681, P = 0.0111	t = 4.342, P = 0.0001	t = 6.566, P < 0.0001	t = 1.465, P = 0.1420	t = 3.216, P = 0.0028	t = 0.899, P = 0.3747	t = 2.447, P = 0.0196
R. blasii								
M ad. (n = 51)	34.2 ± 2.0 (31.0 – 38.6)	21.4 ± 0.9 (19.3 – 23.4)	65.9 ± 2.9 (60.7 – 73.1)	29.1 ± 0.6 (27.8 – 30.5)	8.2 ± 0.5 (7.3 – 9.5)	8.2 ± 0.4 (7.1 – 8.9)	6.5 ± 0.3 (5.6 – 6.9)	2.2 ± 0.3 (1.8 – 2.9)
F ad. (n = 51)	35.0 ± 1.8 (31.5 – 37.7)	22.0 ± 1.2 (19.5 – 24.0)	67.4 ± 2.9 (62.6 – 72.0)	29.6 ± 0.6 (27.9 – 31.1)	9.0 ± 0.5 (7.9 – 10.6)	8.6 ± 0.4 (8.0 – 9.2)	6.6 ± 0.2 (6.2 – 7.2)	2.2 ± 0.2 (1.8 – 2.8)
t-test	t = 2.119, P = 0.0366	t = 2.970, P = 0.0037	t = 2.716, P = 0.0078	t = 3,735, P = 0.0003	t = 7.204, P < 0.0001	t = 5.383, P < 0.0001	t = 2.219, P = 0.0288	t = 1.444, P = 0.1517
R. euryale								
M ad. (n = 50)	36.0 ± 1.9 (32.3 – 40.0)	23.5 ± 1.0 (21.1 – 25.4)	69.7 ± 2.7 (63.5 – 75.2)	30.3 ± 0.7 (29.0 – 31.8)	8.0 ± 0.6 (6.9 – 9.6)	8.2 ± 0.3 (7.6 – 9.0)	6.8 ± 0.3 (6.0 – 7.4)	2.0 ± 0.3 (1.4 – 2.6)
F ad. (n = 60)	37.3 ± 2.7 (31.7 – 42.6)	24.2 ± 1.5 (21.3 – 28.0)	71.7 ± 4.3 (64.1 – 80.9)	30.8 ± 0.9 (28.5 – 33.3)	8.2 ± 0.6 (6.9 – 9.6)	8.3 ± 0.5 (7.3 – 9.3)	6.8 ± 0.4 (5.9 – 7.5)	2.1 ± 0.3 (1.6 – 2.7)
t-test	t = 2.997, P = 0.0034	t = 2.705, P = 0.0079	t = 2.849, P = 0.0052	t = 2.956, P = 0.0038	t = 1.298, P = 0.1970	t =1.604, P = 0.1116	t = 0.544, P = 0.5878	t = 1.215, P = 0.2269
R. mehelyi								
M ad. (n = 52)	41.7 ± 1.9 (38.1 – 46.0)	26.9 ± 1.2 (24.0 – 29.7)	81.4 ± 2.7 (76.1 – 87.0)	32.8 ± 0.8 (31.0 – 34.2)	9.6 ± 1.8 (7.5 – 14.4)	8.7 ± 0.3 (7.9 – 9.3)	6.7 ± 0.3 (5.4 – 7.2)	2.0 ± 0.2 (1.6 – 2.9)
F ad. (n = 63)	42.8 ± 1.8 (39.3 – 46.8)	27.2 ± 1.1 (25.5 – 30.1)	83.2 ± 2.7 (77.1 – 90.1)	33.0 ± 0.7 (31.7 – 34.4)	9.7 ± 1.9 (7.4 – 14.9)	9.3 ± 0.3 (8.6 – 10.0)	6.7 ± 0.3 (6.0 – 7.3)	2.0 ± 0.2 (1.6 – 2.3)
t-test	t = 3.027, P = 0.0031	t = 3.463, P = 0.0008	t = 3.726, P = 0.0003	t = 1.879, P = 0.0628	t = 0.083, P = 0.9342	t = 10.128, P < 0.0001	t = 0.484, P = 0.6295	t = 0.050, P = 0.9606
R. ferrumequinum								
M ad. (n = 51)	56.0 ± 3.2 (49.5 – 61.2)	34.0 ± 2.0 (29.0 – 38.4)	106.3 ± 5.1 (95.9 – 116.1)	36.9 ± 1.0 (34.5 – 39.3)	9.7 ± 1.5 (7.6 – 14.9)	9.3 ± 0.4 (8.5 – 10.3)	6.5 ± 0.2 (5.9 – 7.0)	2.3 ± 0.2 (1.8 – 3.0)
F ad. (n = 64)	56.2 ± 5.1 (44.2 – 66.8)	35.0 ± 2.0 (31.3 – 40.7)	107.2 ± 7.3 (93.2 – 125.9)	37.1 ± 1.3 (34.5 – 39.6)	10.0 ± 1.0 (7.6 – 11.9)	9.7 ± 0.9 (7.8 – 11.4)	6.5 ± 0.6 (5.5 – 7.7)	2.2 ± 0.3 (1.4 – 2.8)
t-test	t = 0.193, P = 0.8470	t = 2.466, P = 0.0152	t = 0.734, P = 0.4643	t = 0.980, P = 0.3290	t = 1.185, P = 0.2385	t = 2.825, P = 0.0056	t = 0.914, P = 0.1082	t = 2.013, P = 0.0465

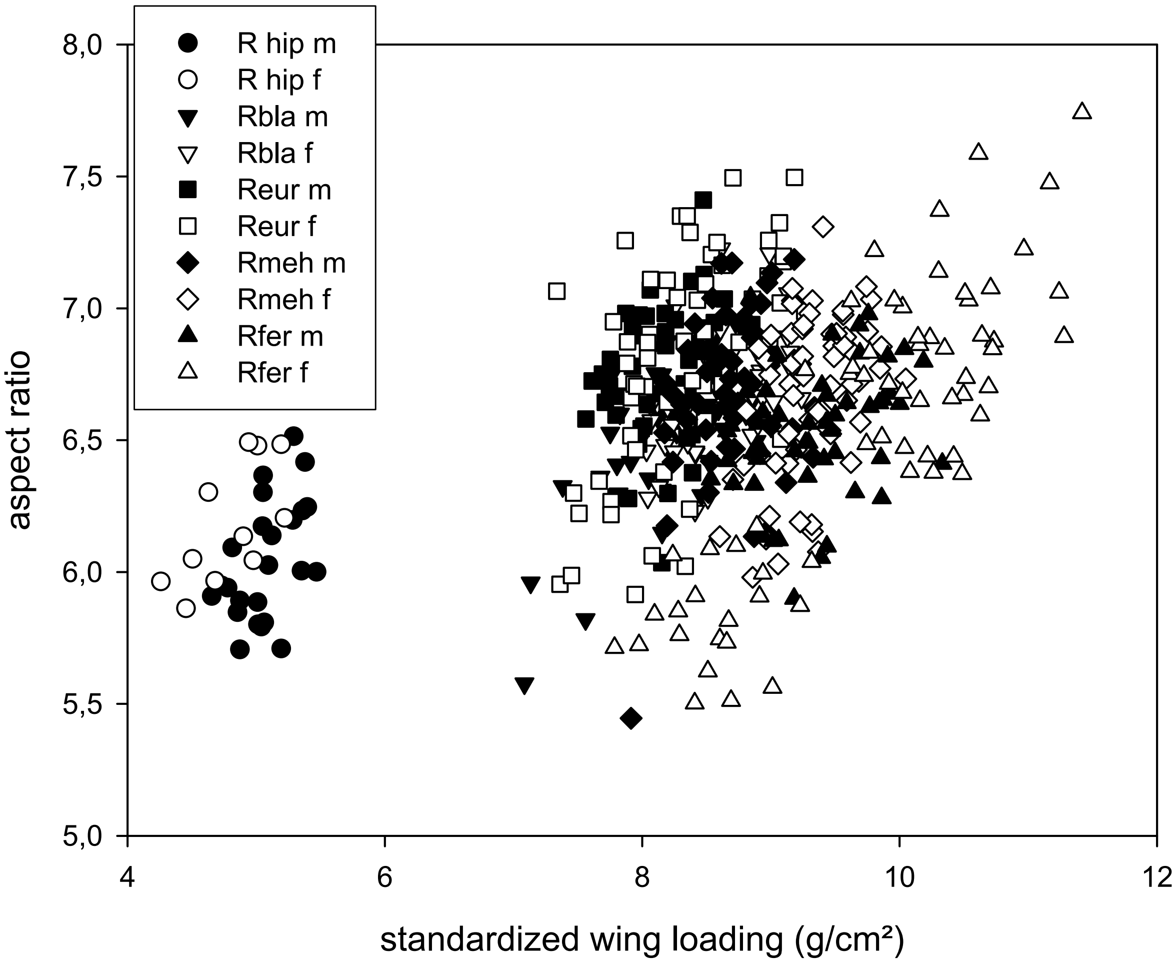


Figure 6: Scatterplot of the aspect ratio against the standardized wing loading of the five European horseshoe bat species. The four larger species are very similar to each other. Abbreviations: m = males; f = females; Rhip = *R. hipposideros*; Rbla = *R. blasii*; Reur = *R. euryale*, Rmeh = *R. mehelyi*; Rfer = *R. ferrumequinum*.

According to Norberg and Rayner (1987) perch hunting should be mainly found in relatively heavy bats with large wingspan but an in general low aspect ratio with large wingtips (enabling good acceleration). From these findings we predicted the main foraging mode per species and compared the results with our telemetry data (Table 4).

Table 4: Predicted foraging modes from our wing morphology data (following Norberg and Rayner (1987)) and foraging behavior assessed by telemetry of adult horseshoe bats (Rhinolophidae). Columns 3 and 4 give the percentage of "foraging on the wing" and "flycatcher mode" during telemetry: summarised foraging times from continuous data recording (tracked time given in minutes) and the number (*n*) of tracked adult bats per species.

species	predicted foraging mode	observed foraging before midnight: "on the wing" vs. "flycatcher"	observed foraging after midnight: "on the wing" vs. "flycatcher"	main observed foraging mode
R. hipposideros	On the wing	100 % / 0 % (2274 min; n = 7)	100 % / 0 % (1066 min; n = 7)	On the wing
R. blasii	On the wing	100 % / 0 % (64 min; n = 2)	-	On the wing
R. euryale	On the wing / (Flycatcher)	92.0 % / 8.0 % (1205 min; n = 7)	92.6 % / 7.4 % (1412 min; n = 7)	On the wing (Flycatcher)
R. mehelyi	On the wing / Flycatcher	81.8 % / 18.2 % (1182 min; n = 7)	19.4 % / 81.6 % (893 min; n = 7)	On the wing / Flycatcher
R. ferrumequinum	Flycatcher / On the wing	89.6 % / 10.4 % (1475 min; n = 6)	74.3 % / 26.7 % (1482 min; n = 6)	On the wing / Flycatcher

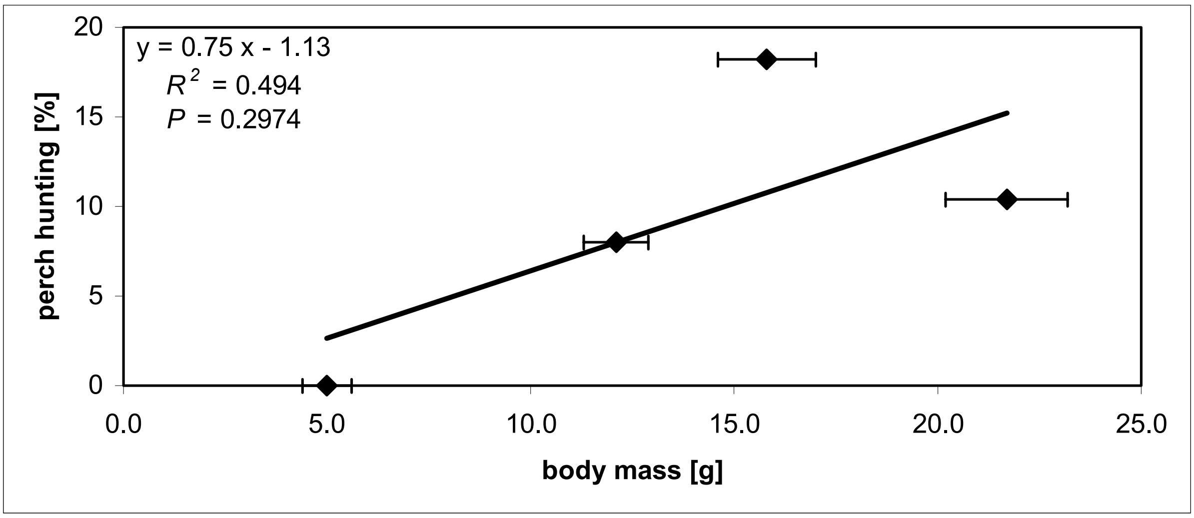


Figure 7: Regression of the mean percentage of perch hunting before midnight (Table 4) on the mean body mass in females of four species of European horseshoe bats (from left to right: *R. hipposideros*, *R. euryale*, *R. mehelyi* and *R. ferrumequinum*; *R. blasii* was excluded due to low sample size in telemetry data).

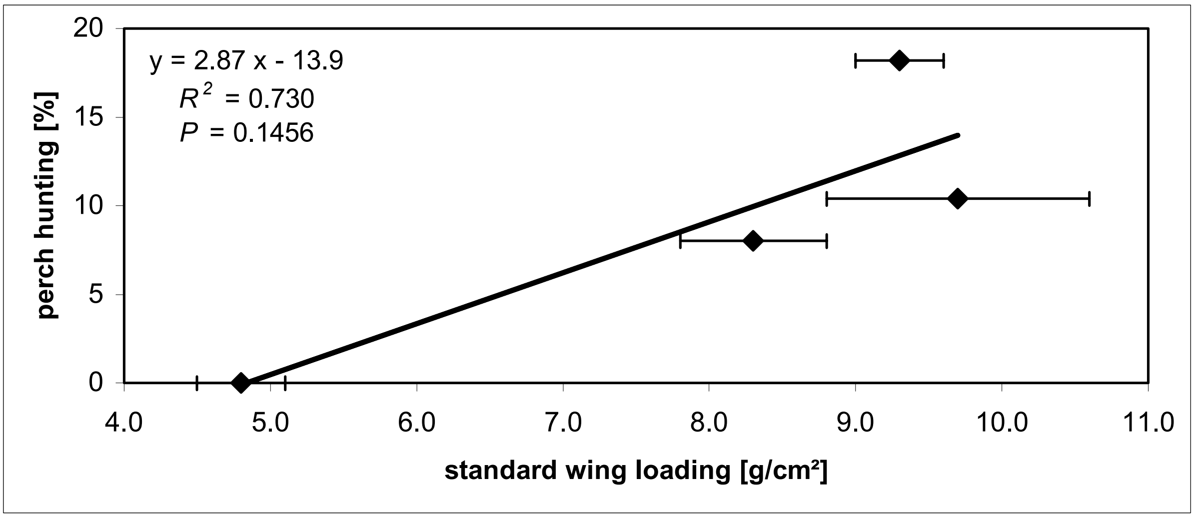


Figure 8: Regression of the mean percentage of perch hunting before midnight (Table 4) on the mean standard wing loading in females of four species of European horseshoe bats (for details see Fig. 7).

To assess whether body mass or wing loading have an influence on the foraging behaviour we regressed the time spend perch hunting on them. As the telemetry data were obtained from females, we used the standard body mass for lactating females and the corresponding standard aspect ratios. As the telemetry data of *R. blasii* were gathered on two individuals only, we excluded this species from analysis. There is no significant correlation between mean body mass or mean standard wing loading with the mean percentage of perch hunting before midnight ($R^2 = 0.494$; *d.f.* = 2,2; $P = 0.2974$; Fig. 7 and $R^2 = 0.730$; *d.f.* = 2,2; $P = 0.1456$; Fig. 8). Similarly the regression of the mean percentage of perch hunting after midnight and throughout the night on the mean body mass and the mean standard wing loading showed no significant correlation (data not shown).

As the individual body mass and individual wing loading have been recorded from the tracked bats as well we also regressed the individual percentage of perch hunting on the individual body mass and wing loading (Figs. 9 and 10). Here significant effects could be detected that explain at least parts of the variation within the data ($R^2 = 0.257$; *d.f.* = 2,27; $P = 0.0070$; Fig. 9 and $R^2 = 0.369$; *d.f.* = 2,27; $P = 0.0008$; Fig. 10).

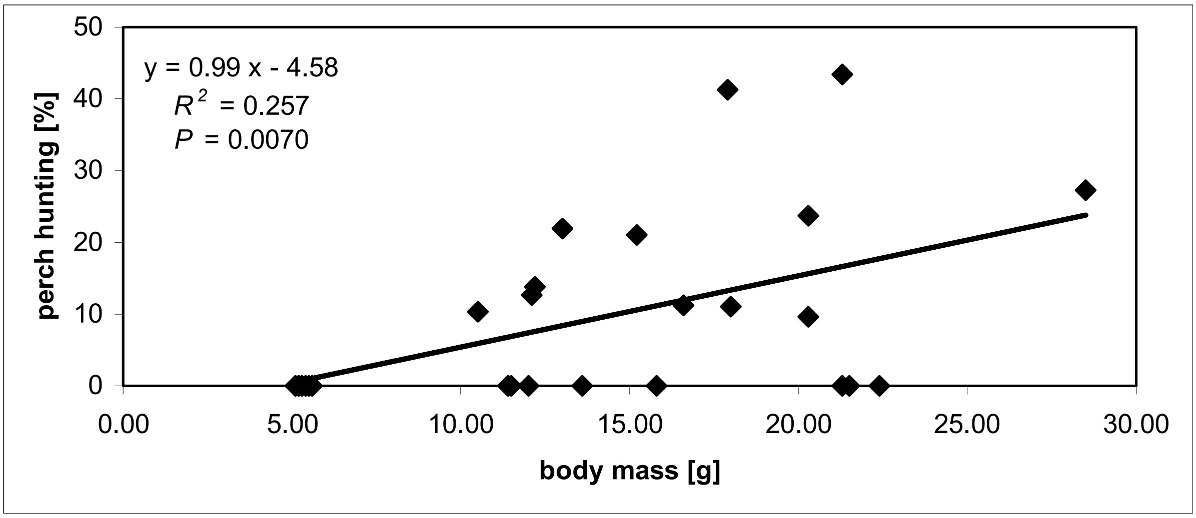


Figure 9: Regression of the individual percentage of perch hunting before midnight on the individual body mass of the tracked females of four species of European horseshoe bats.

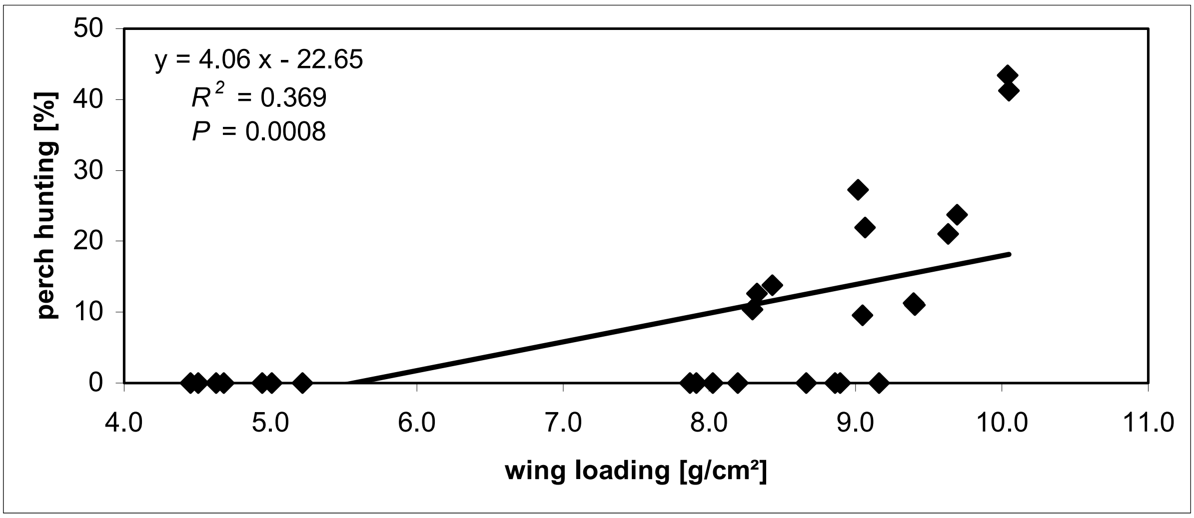


Figure 10: Regression of the individual percentage of perch hunting before midnight on the individual wing loading of the tracked females of four species of European horseshoe bats.

Neither the mean percentage of perch hunting before midnight showed a significant correlation with the mean aspect ratio of the species ($R^2 = 0.501$; *d.f.* = 2,2; $P = 0.2923$; Fig. 11) nor the individual percentage of perch hunting before midnight when regressed on the individual aspect ratios of the tracked individuals ($R^2 = 0.002$; *d.f.* = 2,27; $P = 0.8289$; Fig. 12).

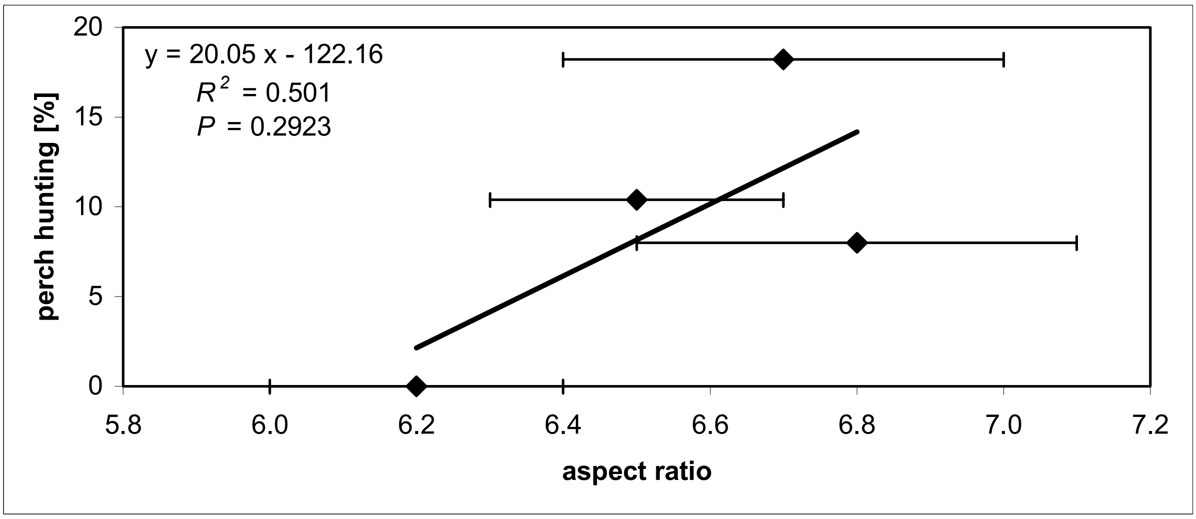


Figure 11: Regression of the mean percentage of perch hunting before midnight (Table 4) on the mean aspect ratio in females of four species of European horseshoe bats (for details see Fig. 7).

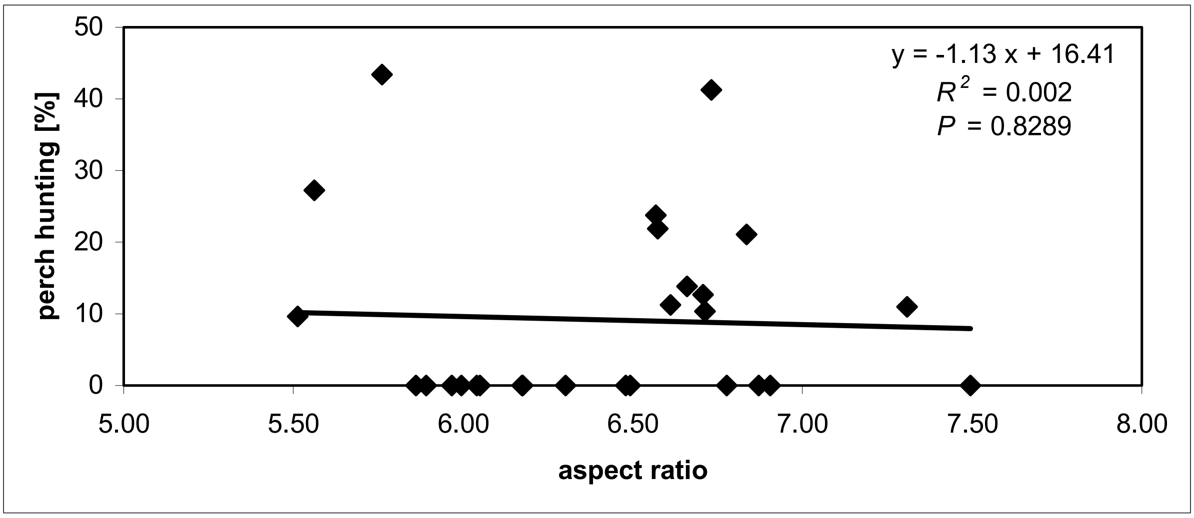


Figure 12: Regression of the individual percentage of perch hunting before midnight (on the individual aspect ratio of the tracked females of four species of European horseshoe bats.

To explore the effects of wing span and hand wing length on the habitat use (mainly on the preference of open vs. densely vegetated habitat types) we regressed the percentage of telemetry fixes within densely vegetated habitats (scrubland, forest, hedges) observed during radio-tracking (Table 5) on these two variables obtained from the wing photographs.

Table 5: Habitat use while foraging in the five European horseshoe bat species. All high quality telemetry fixes per species of foraging bats (excluding roosting, night roosting or commuting) were buffered by a 50 m radius and the habitat content within this buffer determined in a GIS application. The habitats were classified as open (e.g. meadows, fields, pastures) or densely vegetated (forests, scrubland, hedges) according to the main foraging behavior (two-dimensional vs. three-dimensional).

species	percentage of fixes in open habitats	percentage of fixes in densely vegetated habitats	n fixes while foraging – n tracked bats
R. hipposideros	35.2 % ± 12.0 %	64.8 % ± 11.1 %	793 – 7
R. blasii	6.0 % ± 13.0 %	94.0 % ± 12.2 %	67 – 2
R. euryale	48.0 % ± 9.6 %	52.0 % ± 10.0 %	648 – 7
R. mehelyi	79.0 % ± 8.9 %	21.0 % ± 6.6 %	1173 – 8
R. ferrumequinum	44.5 % ± 11.7 %	55.5 % ± 15.5 %	777 – 6

The regression of the mean percentage of used densely vegetated habitats neither showed significant correlations with the mean wingspan of the species ($R^2 = 0.167$; *d.f.* = 2,2; $P = 0.5907$; Fig. 13) nor with the handwing length ($R^2 = 0.223$; *d.f.* = 2,2; $P = 0.5283$; Fig. 14). However, when regressing the individual habitat use (measured by the percentage of used densely vegetated habitats) on the individual wingspan and handwing lengths a weak but significant negative correlation could be found ($R^2 = 0.334$; *d.f.* = 2,27; $P = 0.0016$; Fig. 15 and $R^2 = 0.389$; *d.f.* = 2,27; $P = 0.0005$; Fig. 16).

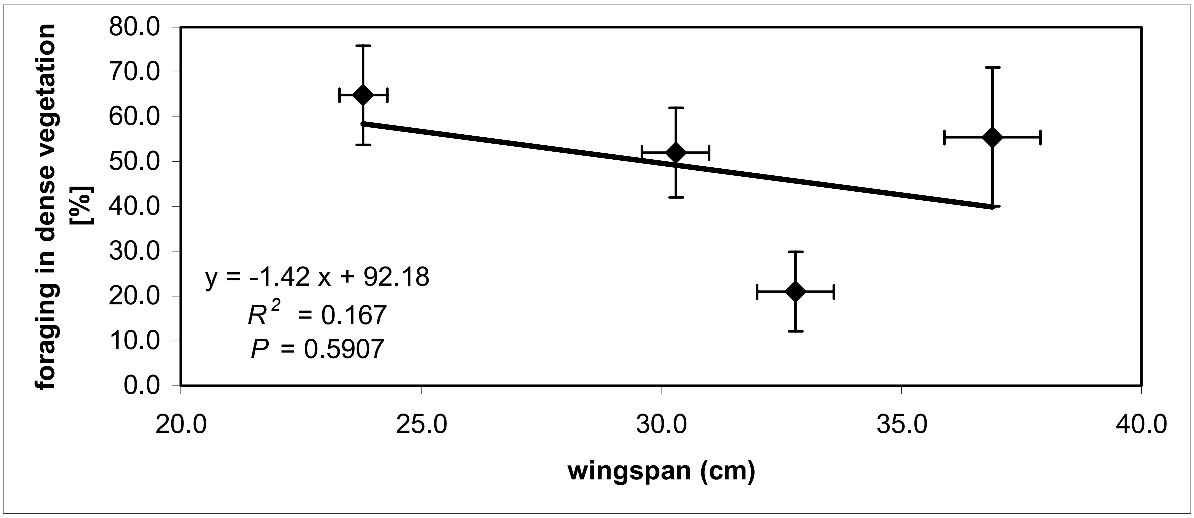


Figure 13: Regression of the mean percentage of telemetry fixes while foraging in densely vegetated habitats (Table 5) on the mean wingspan in females of four species of European horseshoe bats (for details see Fig. 7).

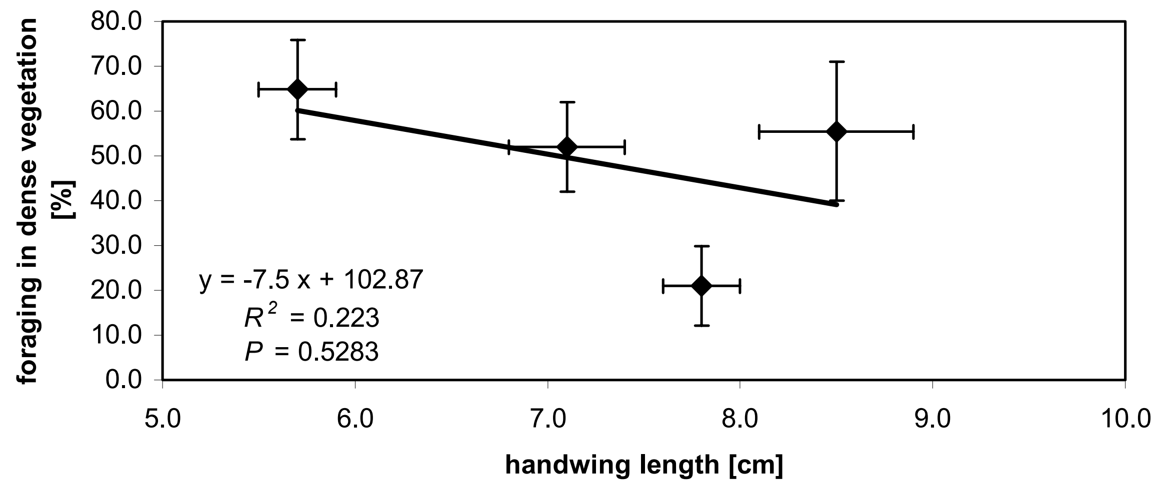


Figure 14: Regression of the mean percentage of telemetry fixes while foraging in densely vegetated habitats (Table 5) on the mean handwing length in females of four species of European horseshoe bats (for details see Fig. 7).

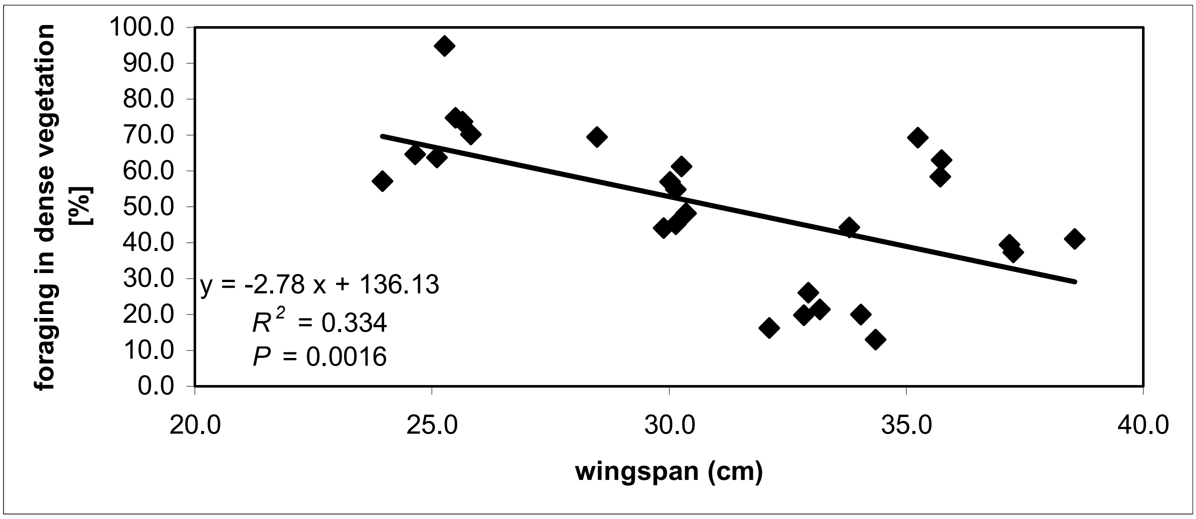


Figure 15: Regression of the individual percentage of telemetry fixes while foraging in densely vegetated habitats on the individual wingspan of the tracked females of four species of European horseshoe bats.

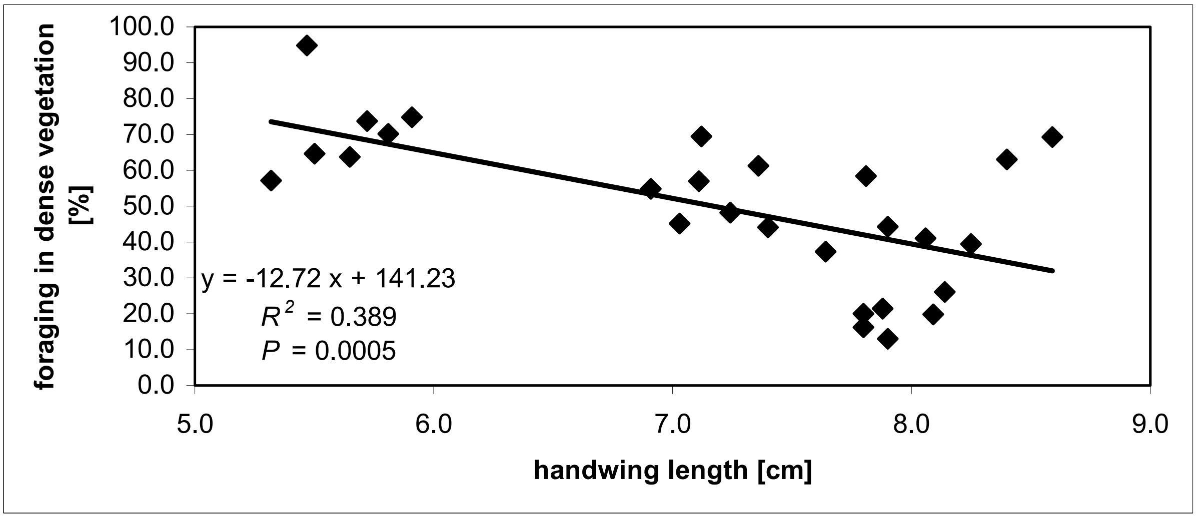


Figure 16: Regression of the individual percentage of telemetry fixes while foraging in densely vegetated habitats on the individual handwing length of the tracked females of four species of European horseshoe bats.

To test for possible differences between the flight speeds while commuting (measured in the field by telemetry) and the flight speeds predicted from wing morphology (Table 6), we conducted t-tests.

Table 6: Predicted flight speeds from wing morphology and flight speeds measured in the field during long-distance flights. Abbreviations: Vmp = minimum power speed: speed at which the bat can fly the longest time on a given amount of fuel; Vmr = maximum range speed: speed where the power to speed ratio reaches its minimum; Vobs = observed flight speeds during commuting flights over the distances given in the last column.

species	Vmp (m/s) mean ± SD (n) (min – max)	Vmr (m/s) mean ± SD (n) (min – max)	Vobs (m/s) mean ± SD (n) (min – max)	distances (m)
R. hipposideros	2.8 ± 0.18 (37) (2.44 – 3.43)	3.71 ± 0.24 (37) (3.24 – 4.56)	2.86 ± 1.29 (4) (1.03 – 4.06)	1,800 – 3,700
R. blasii	3.41 ± 0.10 (102) (3.17 – 3.73)	4.51 ± 0.14 (102) (4.21 – 4.95)	1.9 (1) -	1,250
R. euryale	3.32 ± 0.10 (110) (3.09 – 3.69)	4.39 ± 0.14 (110) (4.09 – 4.81)	5.53 ± 0.65 (6) (4.66 – 6.18)	7,500 – 19,000
R. mehelyi	3.59 ± 0.27 (115) (3.23 – 4.35)	4.75 ± 0.36 (115) (4.27 – 5.76)	5.04 ± 1.76 (8) (2.78 – 8.29)	3,470 – 9,950
R. ferrumequinum	3.69 ± 0.2 (115) (3.29 – 4.35)	4.88 ± 0.26 (115) (4.35 – 5.76)	4.88 ± 1.02 (5) (2.22 – 5.85)	6,800 – 12,780

While commuting *R. euryale*, *R. mehelyi* and *R. ferrumequinum* flew significantly faster than the predicted minimum-power-speed (Vmp – two-sample *t-test*, $t \geq 3.483$; *d.f.* = 2,64-69; $P \leq 0.0017$ – *Bonferroni*-adaptation $P*2$), the single commuting flight speed measured in *R. blasii* was significant lower than the predicted Vmp ($t = 17.313$; *d.f.* = 2,50; $P < 0.0001$ – *Bonferroni*-adaptation $P*2$) and commuting *R. hipposideros* did not differ from Vmp ($t = 0.0018$; *d.f.* = 2,13; $P = 0.9986$ – *Bonferroni*-adaptation $P*2$). In comparison to the maximum-range speed (Vmr) the only measured commuting flight of *R. blasii* was significantly slower ($t = 22.252$; *d.f.* = 2,50; $P < 0.0001$ – *Bonferroni*-adaptation $P*2$) and *R. euryale* flew faster (*t*

= 11.593; *d.f.* = 2,64; $P < 0.0001$ – *Bonferroni*-adaptation *P**2), while flight speeds of *R. hipposideros*, *R. mehelyi* and *R. ferrumequinum* did not differ significantly from Vmr ($t < 2.269$; *d.f.* = 2,13-69; $P = 0.0818$-0.8075 – *Bonferroni*-adaptation *P**2).

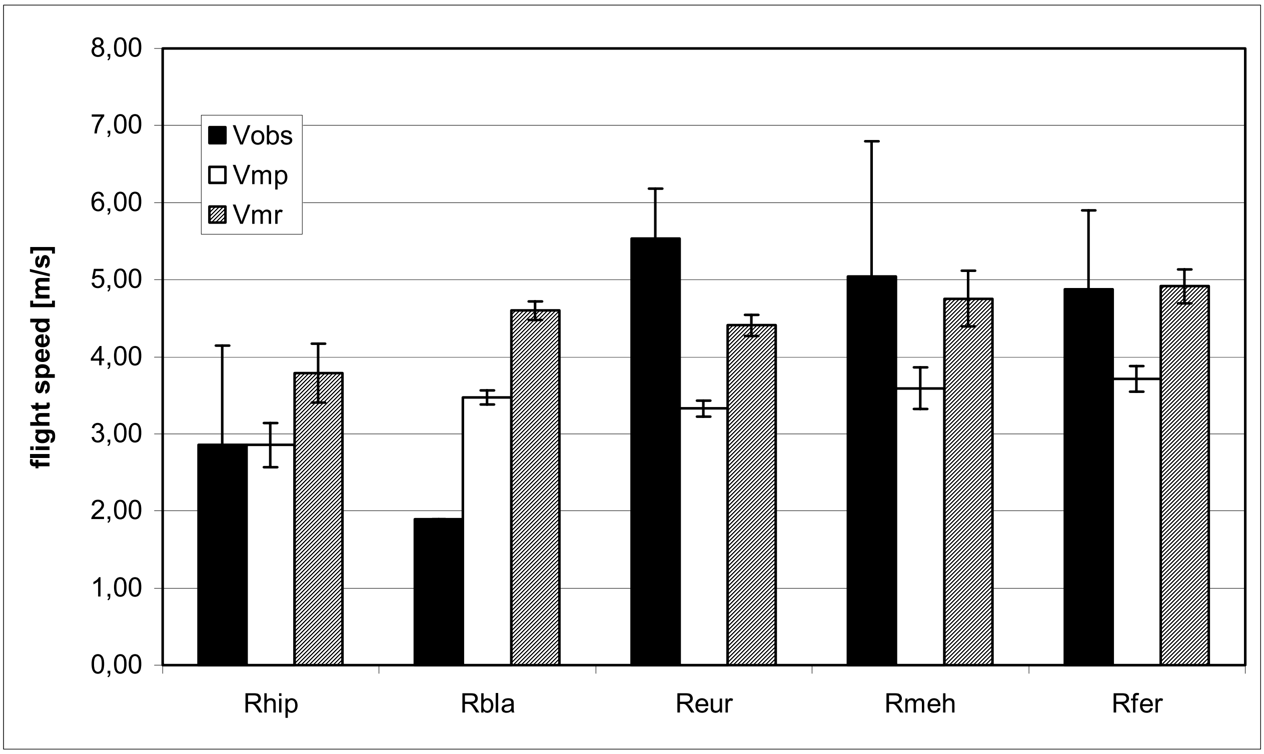


Figure 17: Comparison of flight speeds measured in the field during long-distance flights and predicted flight speeds from wing morphology. Abbreviations: Vobs = observed flight speeds during commuting flights over the distances; Vmp = minimum power speed: speed at which the bat can fly the longest time on a given amount of fuel; Vmr = maximum range speed: speed where the power to speed ratio reaches its minimum; Rhip = *Rhinolophus hipposideros*; Rbla = *R. blasii*, Reur = *R. euryale*; Rmeh = *R. mehelyi*; Rfer = *R. ferrumequinum*. In *R. blasii* only a singe commuting flight was measured in the field.

DISCUSSION

The optimal wing shape adapted for different modes of flight is probably dictated by a combination of different factors such as flight performance, habitat and food choice (Norberg 1994). Following ecomorphological studies describing patterns in bat community structures (Aldridge and Rautenbach 1987; Baagøe 1987; Crome and Richards 1988; Findley 1993; Kalcounis and Brigham 1995; McKenzie and Rolfe 1986; McKenzie et al. 1995; O'Shea and Vaughan 1980; Swartz et al. 2003) we aimed to compare five sympatric congeners with regard to their ecomorphology and to test some of the predictions derived from morphology with ecological data collected in the field. Guild members, by definition, exploit the same resources in a similar way (Root 1967; Simberloff and Dayan 1991), a precondition that fits well to the European horseshoe bats. They belong to a guild whose members are characterized by many specialisations in general wing morphology, echolocation and prey selection.

Our measurements obtained from 479 living bats of five *Rhinolophus* species give for the first time detailed data on the wing morphology of all the European horseshoe bat species and for both sexes. They increase the knowledge on these species, that hitherto was based on a few specimen per species or on single- or two-species studies only (Norberg and Rayner 1987; Aldridge 1986; Heller and Helversen 1989; Ransome 1990; Salsamendi et al. 2005). The method applied here to obtain wing area measurements from wing photographs lead to comparable results with data from wing tracings in *R. euryale* and *R. mehelyi* (Salsamendi et al. 2005). However, the tail membrane was measured less accurately in the latter method and no method-induced measurement errors are given (Salsamendi et al. 2005). Further, the variance between repeated measurements form an individual was much lower than for wing tracings (Rhodes 2002), indicating that wing photogrammetry might be superior to the wing tracing method, which is currently still widely applied in ecomorphological studies on bats. Finally, our data differ in parts significantly from data taken from museum specimen (cited in

Norberg and Rayner 1987) and certainly will reflect the morphology of live animals more accurately.

The European *Rhinolophus*-species exhibit wing loadings and aspect ratios with low or medium values that are within the range typical for the genus (Norberg and Rayner 1987; Kingston et al. 2000). They are, in accordance with our hypothesis 1 (see introduction), within the range of the gleaning or edge and gap foraging *Myotis* and *Plecotus* species and much lower than in most of the bats foraging in open space (e.g. *Pipistrellus* and *Nyctalus* species). Tip-shape-index values of the European horseshoe bats were found to be larger than in most other European bat species (data on the other species mainly taken from Norberg and Rayner 1987). The low wing loading in horseshoe bats can be regarded together with low aspect ratio and high tip-shape-index as an adaptation for close-to-the-roost foraging with high manoeuvrability enabling rapid changes in flight directions within highly cluttered environments (e.g., within dense vegetation). Furthermore the low wing loading enables horseshoe bats to carry heavy additional loads, e.g. when transporting the young from one roost to an other or when accumulating large quantities of fat prior to hibernation. This ability to add weight to the body mass makes it difficult to compare different individuals or species that were sampled at different times of the year, because the reproductive or physiological status has a big influence on body mass. We found the fluctuations of body mass and in wing loading to differ significantly throughout the summer season, a phenomenon well known in temperate bats (Hughes and Rayner 1991; Ransome 1990; Stern et al. 1997; Webb et al. 1992): Our approach to use a standardized body mass to calculate a standardized wing loading helped to overcome this problem and increased the explanatory power of the variability within the data by the main factor “species”.

Sexual dimorphism was found in the area measurements of the wing and in wing loading with females being larger than males, but the differences were less distinctive than in length measurements of wing elements in the same species (Dietz et al. 2006a). Sexual dimorphism is commonly found in bats with in general females being larger, most probably due to the necessity to carry foetuses and young during the reproduction period. Interestingly the standardized wing loading was found to be smaller in female *R. hipposideros* than in males. A possible explanation could be that the body mass is limited by the necessity to carry a foetus or to accumulate stores of fat for hibernation especially in females. As *R. hipposideros* is the smallest of the European species (and close to the lowest size possible for a mammal) this limitation might be especially pronounced, so the species has a relatively lower body mass at other times of the year than during reproduction or in autumn.

Despite an in general very similar wing morphology the five species differ significantly in the wing area measurements and in the derived wing parameters, indicating that morphological differences might be large enough to reflect niche separating mechanisms. Within the area measurements mainly the body size related data differ strongly between species, readily separating the largest (*R. ferrumequinum*) and the smallest (*R. hipposideros*) species from the three medium-sized species (*R. blasii*, *R. euryale* and *R. mehelyi*). Within the three medium-sized species *R. mehelyi* is clearly the largest one. A bat's size and its body mass were found to be important criteria for manoeuvrability in flight performance experiments (Stockwell 2001); accordingly bats foraging in the most cluttered habitats should be small in size. The derived wing parameters wing loading and aspect ratio also differ significantly between species again mainly due to body size related differences, while tip-shape-index values were very similar. In wing loading (especially in the standardized wing loading) the species again become well separated by size with the largest (*R. ferrumequinum*) and the smallest (*R. hipposideros*) species differentiated from the three medium-sized species (*R. blasii*, *R. euryale* and *R. mehelyi*). Kalcounis and Brigham (1995) found that wing loading was a significant predictor of habitat use; individuals with higher wing loading foraged in less cluttered habitat. Short an broad wings facilitate manoeuvrability in restricted spaces and are typical for bats foraging within dense vegetation like forest while bats with large and narrow wings typically fly in open space or at least in less densely vegetated habitats. Accordingly, aspect ratio (the square of the wingspan divided by the wing area) correlates well with flight manoeuvrability, with lower values endowing greater manoeuvrability. In this respect *R. hipposideros* differs from the other species indicating an exceptional high manoeuvrability. Wing tip-shape-index is determined by the relative size of arm- and handwings. High index values correspond to rounded wing tips and indicate high manoeuvrability (Norberg and Rayner 1987), as the five species were very similar in these values they can be expected to express similar flight capabilities in this respect.

Our attempts to correlate ecological and behavioural data colleted by telemetry with the data from wing morphology revealed little significant relationships. Only the individual body mass and wing loading of the tracked bats correlated significantly to the percentage of perch hunting but explained only a small part of the variability. This was mainly due to the high intraspecific variability and possibly also due to methodological problems in assessing the foraging mode in the field and the heterogeneous radio-contact times between individuals. E.g., *R. euryale* used perch hunting as alternative foraging mode mainly under unfavourable weather conditions (relatively low temperatures, rain) and in the second half of the night. Little radio-contact time in the second half of the night and/or during unfavourable weather conditions presumably lead to the absence of perch hunting in some individuals' data sets, which made the regression quite bad. The same applies for the correlations of individual use of densely vegetated habitats (forest, scrubland) with wingspan and handwing length, again only weak, albeit significant, relationships were found. Here, possible correlations were most likely obscured by problems in assigning the positions of the tracked bats to a certain habitat type (several habitats may occur within the buffer zone). E.g., a *R. ferrumequinum* was tracked *in* a forested area but in reality might not have been foraging *within* the forest but along edges and gaps e.g. along a path.

From aerodynamic theory, the maximum range speed should be chosen whenever the longest distances is to be covered. However, during commuting flights between foraging areas the optimal flight speed may be probably higher than the maximum range speed in order to maximise the energy gain by having longer foraging times in the foraging areas. Most studies in the field comparing measured flight speeds with their theoretical optimal speeds indeed found that bats usually commute at higher than maximum range speeds (e.g. Jones and Rayner 1987; Norberg 1987). This seems to apply especially for *R. euryale* that in our study indeed flew significantly faster than predicted. This was also the species covering the longest distances of up to 19 kilometres and more between foraging sites and roost. Most probably the bats had to hurry up not to miss the insect peak of the early night in the evening (Jones and Rayner 1987) and in the morning to come back to the roost before it gets too light. Three of the species, namely *R. hipposideros*, *R. mehelyi* and *R. ferrumequinum* flew at speeds indistinguishable from the theoretically predicted economical flight speeds. Interestingly, in *R. ferrumequinum* the measured flight speeds in the field over moderate distances of 7-12 kilometres did not only match the calculated maximum range speed but also the minimum power speed calculated from kinematic studies by Aldridge (1986b). The highest flight speed recorded in a tracked *R. hipposideros* was a female carrying its young when transporting to an alternative roosting site over a distance of two kilometers. The bat had to carry an additional weight of 80% (weights of the female: 5.2 g, of the juvenile male: 3.7 g and of the transmitter: 0.45 g), clearly supporting the rule that flight speed increases with additional wing loading (Hughes and Rayner 1991; Norberg and Rayner 1987; Pennycuick 1975). In our field data only *R. blasii* was slower than maximum range and minimum power speed; this finding is dubious, because the few data on the species were gathered from foraging instead of commuting bats. In summary, our data fit well the predictions drawn from aerodynamic theories (Norberg 1976, 1987, 1990; Norberg and Rayner 1987). They further are in accordance to results of a study on flight speeds in captivity, demonstrating clearly the bats' ability to regulate flight speed in response to body mass and by this the attempt of the bats to fly closely to Vmp and Vmr (Winter 1999).

While many adaptive trends in the wing morphology of bats are obvious on the gross scale of entire bat communities (e.g. Norberg and Rayner 1987; Findley 1993; Swartz et al. 2003) it was quite difficult to obtain clear patterns within the single guild containing five species in the study presented here. This is surprising as competition interaction should be most intense within guilds and thus most likely to produce morphological divergence within the guilds reflecting differences in resource use (Brown and Bowers 1985; Findley and Black 1983; Ricklefs and Miles 1994; Willig and Moulton 1989). The measurements and derived wing parameters used here showed little correlation with ecology and thus on the first view offered only limited insights in the underlying within-guild ecomorphological specialisations. There are several reasons that may help to explain these weak or even missing correlations between morphology and ecology: When comparing the total diversity of a bat community, morphological and ecological extremes show the relationships between form and function very clearly and can be readily described and interpreted, while within the guild studied here extremes are missing and an in general similar morphology and ecology with high overlap makes it difficult to find general principles (see also Brigham et al. 1997; Rhodes 2001). An other important reason might be that the three-dimensional wing conformation offer much more possibilities for fine scale modifications in flight (Hedenström 2007; Norberg and Winter 2006; Rayner et al. 1986; Swartz et al. 2003) than covered by the characters used here. On the other hand bats may be quite flexible with a given suite of wing characteristics to adapt their behaviour or to adjust their flight kinematics to different habitats and foraging behaviour (e.g. Aldridge 1987). Other factors like prey availability or food choice (Aldridge 1986a; Saunders and Barclay 1992) may reduce the necessity to have a perfectly adapted wing. Factors like body mass increase prior to hibernation or during pregnancy may have a strong influence as well (e.g. Hughes and Rayner 1991; Webb et al. 1992).

Constraints of foraging ecology that were investigated in our study are of course not the only adaptive pressure in the evolution of wing morphology, a fact that might explain the quite low correlations between the ecological data and the wing area measurements compared here (Swartz et al. 2003). In this context Saunders and Barclay (1992) stated that bats choose their foraging habitats much more according to prey availability than through morphological limitations or constrains in echolocation.

Following competition theory (Schoener 1974) a species community requires several niche dimensions to effectively minimize resource overlap between species, especially when the community is specious. Thus the five European horseshoe bat species may be separated along several resource dimensions (prey type, prey size, roosts, habitats) leading to multifactorial and complicated interactions with their environment - and wing morphology is only one of them. This becomes clear when structuring the five species not only according to wing morphology but also taking into account several ecological and behavioural characteristics (that do not or only weakly correlate with the wing morphology). In doing so the species become well differentiated and the results are in accordance with single-species ecological studies (Aihartza et al. 2003; Beck et al. 1989, 1997; Bontadina et al. 1995, 1997, 2002; Goiti et al. 2003, 2004; Jones et al. 1995; Jones and Rayner 1989; Russo et al. 2002, 2005, Siemers and Ivanova 2004; Valenciuc 1971; Whitaker and Black 1976):

The five species are clearly separated when taken several morphological, behavioural and ecological factors into account:

R. hipposideros: smallest of the five bats, exclusively foraging on the wing within dense vegetation or in other highly cluttered situations and preying for tiny insects. Foraging very manoeuvrable due to extraordinarily low wing loading and aspect ratio and by this exploiting resources possibly being not accessible for the other species.

R. blasii: medium sized horseshoe bat, the limited telemetry data suggest exclusively foraging on the wing mainly in dense cluttered habitats like scrubland. Wing morphology suggests similar flight capabilities like *R. euryale*. The absence of differences in flight capabilities may not be sufficient for maintaining niche segregation between the two species basing on wing morphology alone, while the echolocation call frequencies differ significantly with *R. blasii* using lower frequencies (Heller and Helversen 1989; Siemers et al. 2005).

R. euryale: a medium sized horseshoe bat mostly foraging on the wing. Perch hunting occurs mainly in cold and wet weather conditions and mainly in the second half of the night. Foraging habitats are mainly densely vegetated, cluttered situations or edge and gap situations bordering open habitats that are exploited in a manoeuvrable flight close to or within the vegetation.

R. mehelyi: in the largest of the three medium-sized species a high wing loading and high aspect ratios clearly point toward some use of perch hunting and the use of more open habitats, a prediction being exceeded by the telemetry data: the bats foraged considerable times of the night from perches even in favourable weather conditions and used mainly meadows, pastures and fields for foraging.

R. ferrumequinum: the largest of the five species has the largest wing loading and is known to use perch hunting. However, during our study they were foraging mainly on the wing; perch hunting occurred in some individuals only but at all times of the night and also under favourable weather conditions. Densely vegetated habitats were slightly preferred but more detailed observations point to the use of edge and gap situations along forest tracks or the forest edges rather than foraging within the vegetation.

In this comparison body size is the major aspect structuring the guild. This is in accordance with many studies investigating niche separation principles, ecology and physiology (Schmidt-Nielsen 1984; Schoener 1974; Stockwell 2001; Swartz et al. 2003). Habitat use is the other important characteristic separating the species. It appears that niche segregation within the guild is maintained by size differences and possibly by the differences in the efficiency to manoeuvre in dense vegetation. These different flight efficiencies are reinforced by wing morphological differences. From these results niche partition scenarios for the entire guild can be built basing on multiple ecomorphological, ecological and behavioural characteristics. Nevertheless, we are still far from a complete understanding of competition avoidance and niche separation strategy. Thus further studies will be required to assess how differences in agility, turning abilities and on other morphological or ecological characters may contribute to competition avoidance and niche separation within the guild of the horseshoe bats in Europe.

ACKNOWLEDGEMENTS

Our work in Bulgaria was made possible by the cooperation and support of the Bulgarian Bat Research and Protection group; we are very grateful to S. Merdschanov, D. Merdschanova, K. Christov, I. Borrisov, S. Staneva, B. Petrov and E. Dimanova for their help with many aspects of the project. We are particularly grateful to E. Papadatou for her support and help in getting permits in Greece. This research was funded by grants of the Graduiertenförderung des Landes Baden-Württemberg to CD and of the Deutsche Bundesstiftung Umwelt to ID. Further support was given by the Reinhold-und-Maria-Teufel-Stiftung to CD and ID and the German Science Foundation (DFG, Si 816/2-1) and the Schuler Foundation to BMS.

LITERATURE CITED

AIHARTZA, J.R., I. GARIN, U. GOITI, J. ZABALA AND I. ZUBEROGOITA. 2003. Spring habitat selection by the Mediterranean horseshoe bat (*Rhinolophus euryale*) in the Urdaibai Biosphere Reserve (Basque Country). Mammalia 67: 25-32.

ALDRIDGE, H. 1986a. Manoeuvrability and ecological segregation in the little brown (*Myotis lucifugus*) and Yuma (*M. yumanensis*) bats (Chiroptera: Vespertilionidae). Canadian Journal of Zoology 64: 1878-1882.

ALDRIDGE, H.D.J.N. 1986b. Kinematics and aerodynamics of the greater horseshoe bat, *Rhinolophus ferrumequinum*, in horizontal flight at various flight speeds. Journal of Experimental Biology 126: 479-497.

ALDRIDGE, H.D.J.N. 1987. Turning flight of bats. Journal of Experimental Biology 128: 419-425.

ALDRIDGE, H.D.J.N. AND I.L. RAUTENBACH. 1987. Morphology, echolocation and resource partitioning in insectivorous bats. Journal of Animal Ecology 56: 763-778.

BAAGØE, H.P. 1987. The Scandinavian bat fauna: adaptive wing morphology and free flight in the field. Pp. 57-74 in Recent advances in the study of bats (M.B. FENTON, P. RACEY AND J.M.V. RAYNER, eds.); Cambridge University Press, Cambridge, United Kingdom.

BECK, A., S. GLOOR, M. ZAHNER, F. BONTADINA, T. HOTZ, M. LUTZ AND E. MÜHLETHALER. 1997. Zur Ernährungsbiologie der Großen Hufeisennase in einem Alpental der Schweiz. Tagungsband: „Zur Situation der Hufeisennasen in Europa“ Nebra, den 26.-28. Mai 1995, Arbeitskreis Fledermäuse Sachsen-Anhalt e.V. 1997: 15-18. IFA-Verlag, Berlin, Germany.

BECK, A., H.-P.B. STUTZ AND V. ZISWILER. 1989. Das Beutespektrum der Kleinen Hufeisennase *Rhinolophus hipposideros.* Revue suisse de zoologie 96: 643-650.

BONTADINA, F., A. BECK, S. GLOOR, T. HOTZ, M. LUTZ AND E. MÜHLETHALER. 1995. Jagt die Grosse Hufeisennase *Rhinolophus ferrumequinum* im Wald? Grundlagen zum Schutz von Jagdgebieten der letzten grösseren Kolonie in der Schweiz. Der Ornithologische Beobachter 92: 325-327.

BONTADINA, F., T. HOTZ, S. GLOOR, A. BECK, M. LUTZ AND E. MÜHLETHALER. 1997. Schutz von Jagdgebieten der Großen Hufeisennase. Umsetzung der Ergebnisse einer Telemetrie-Studie in einem Alpental der Schweiz. Tagungsband: „Zur Situation der Hufeisennasen in Europa“ Nebra, den 26.-28. Mai 1995, Arbeitskreis Fledermäuse Sachsen-Anhalt e.V. 1997: 33-40. IFA-Verlag, Berlin, Germany.

BONTADINA, F., H. SCHOFIELD AND B. NAEF-DAENZER. 2002. Radio-tracking reveals that lesser horseshoe bats (*Rhinolophus hipposideros*) forage in woodland. Journal of Zoology (London) 258: 281-290.

BRIGHAM, R.M., R.L. FRANCIS AND S. HAMDORF. 1997. Microhabitat use by two species of *Nyctophilus* bats: a test of ecomorphology theory. Australian Journal of Zoology 45: 553-560.

BROWN, J.H. AND M.A. BOWERS. 1985. Community organization in hummingbirds: relationships between morphology and ecology. Auk 102: 251–269.

CROME, F.H.J. AND G.C. RICHARDS. 1988. Bats and gaps: microchiropteran community structure in a Queensland rain forest. Ecology 69: 1960–1969.

DIETZ, C., I. DIETZ AND B. M. SIEMERS. 2006a. Wing measurement variations in the five European horseshoe bat species (Chiroptera: Rhinolophidae). Journal of Mammalogy 87: 1241-1251.

DIETZ, C., I. DIETZ, T. IVANOVA AND B.M. SIEMERS. 2006b. Effects of forearm bands on horseshoe bats (Chiroptera: Rhinolophidae). Acta Chiropterologica 8: 523-535.

DIETZ, C., I. DIETZ AND B. M. SIEMERS. 2007a. Growth of horseshoe bats (Chiroptera: Rhinolophidae) in temperate continental conditions and the influence of climate. Mammalian Biology 72: 129-144.

DIETZ, C., O. VON HELVERSEN AND D. NILL. 2007b. Handbuch der Fledermäuse Europas und Nordwestafrikas, 399 pp.; Kosmos, Stuttgart, Germany.

FINDLEY, J.S. 1993. Bats, a community perspective; 167 pp.; Cambridge University Press.

FINDLEY, J.S. AND H. BLACK. 1983. Morphological and dietary structuring of a Zambian insectivorous bat community. Ecology 64: 625-630.

FINDLEY, J.S., E.H. STUDIER AND D.E. WILSON. 1972. Morphological properties of bat wings. Journal of Mammalogy 53: 429-444.

GAISLER, J. 1960. Postnatale Entwicklung der Kleinen Hufeisennase (*Rhinolophus hipposideros*) unter natürlichen Bedingungen. Symposium Theriologicum 1960: 118-125.

GAISLER, J. 1965. The female sexual cycle and reproduction in the lesser horseshoe bat (*Rhinolophus hipposideros hipposideros*). Vestnik Ceskoslovenske Spolecnosti Zoologicke 29: 336-352.

GAISLER, J. AND M. TITLBACH. 1964. The male sexual cycle in the lesser horseshoe bat (*Rhinolophus hipposideros hipposideros*). Vestnik Ceskoslovenske Spolecnosti Zoologicke 28: 268-277.

GOITI, U., J.R. AIHARTZA AND I. GARIN. 2004. Diet and prey selection in the Mediterranean horseshoe bat *Rhinolophus euryale* (Chiroptera, Rhinolophidae) during the pre-breeding season. Mammalia 68: 397-402.

GOITI, U., J.R. AIHARTZA, I. GARIN AND J. ZABALA. 2003. Influence of habitat on the foraging behaviour of the Mediterranean horseshoe bat, *Rhinolophus euryale*. Acta Chiropterologica 5: 75-84.

GRIFFIN, D.R. AND J.A. SIMMONS. 1974. Echolocation of insects by horseshoe bats. Nature 250: 731-732.

GUILLÉN, A., C.M. FRANCIS AND R.E. RICKLEFS. 2003. Phylogeny and biogeography of the horseshoe bats. Pp. XII-XXIV in Horseshoe bats of the world (Chiroptera: Rhinolophidae) (G. CSORBA, P. UJHELYI AND N. THOMAS, eds.). Alana Books Shropshire, United Kingdom.

HARDIN, G. 1960. The competitive exclusion principle. Science 131: 1292-1297.

HEDENSTRÖM, A., L.C. JOHANSSON, M. WOLF, R. VON BUSSE, Y. WINTER AND G.R. SPEDDING. 2007. Bat flight generates complex aerodynamic tracks. – Science 316: 894-897.

HELLER, K.-G. AND O. VON HELVERSEN. 1989. Resource partitioning of sonar frequency bands in rhinolophid bats. Oecologia 80: 178-186.

HUGHES, P. AND J.M.V. RAYNER. 1991. Addition of artificial loads to long-eared bats *Plecotus auritus*: handicapping flight performance. Journal of Experimental Biology 161: 285-298.

JONES, G., P.L. DUVERGÉ AND R.D. RANSOME. 1995. Conservation biology of an endangered species: field studies of greater horseshoe bats. Symposia of the Zoological Society of London 67: 309-324.

JONES, G. AND J.M.V. RAYNER. 1987. Optimal flight speed in pipistrelle bats, *Pipistrellus pipistrellus*. Pp. 247-253 in European bat research (V. HANÁK, I. HORÁČEK AND J. GAISLER, eds.); Charles University Press, Praha, Czech Republic.

JONES, G. AND J.M.V. RAYNER. 1989. Foraging behavior and echolocation of wild horseshoe bats *Rhinolophus ferrumequinum* and *R. hipposideros.* Behavioral Ecology and Sociobiology 25: 183-191.

KALCOUNIS, M.C. AND R.M. BRIGHAM. 1995. Intraspecific variation in wing loading affects habitat use by little brown bats (*Myotis lucifugus*). Canadian Journal of Zoology 73: 89-95.

KENWARD, R.E. 2001. A manual for wildlife radio tracking, 311 pp.; Academic Press, San Diego, United States.

KINGSTON, T., G. JONES, A. ZUBAID AND T.H. KUNZ. 2000. Resource partitioning in rhinolophoid bats revisited. Oecologia 124: 332-342.

MCKENZIE, N.L. AND J.K. ROLFE. 1986. Structure of bat guilds in the Kimberley mangroves, Australia. Journal of Animal Ecology 55: 401–420.

MCKENZIE, N.L., A.C. GUNNELL, M. YANI AND M.R. WILLIAMS. 1995. Correspondence between flight morphology and foraging ecology in some palaeotropical bats. Australian Journal of Zoology 43: 241–257.

MATHEWS, L.H. 1937. The female sexual cycle in the British horse-shoe bats, *Rhinolophus ferrum-equinum insulanus* and *R. hipposideros minutes.* Transactions of the Zoological Society of London 32: 224-266.

MITCHELL-JONES, A.J., G. AMORI, W. BOGDANOWICZ, B. KRYSTUFEK, P.J.H. REIJNDERS, F. SPITZENBERGER, M. STUBBE, J.B.M. THISSEN, V. VOHRALIK AND J. ZIMA. 1999. The atlas of European mammals. 484 pp. Poyser Natural History, London, United Kingdom.

NORBERG, U.M. 1976. Aerodynamics, kinematics, and energetics of horizontal flapping flight in the long-eared bat *Plecotus auritus*. Journal of Experimental Biology 65: 179-212.

NORBERG, U.M. 1981. Flight, morphology and the ecological niche in some birds and bats. Symposia of the Zoological Society of London 48: 173-197.

NORBERG, U.M. 1987. Wing form and flight mode in bats. Pp. 43-56 in Recent advances in the study of bats (M.B. FENTON, P. RACEY AND J.M.V. RAYNER, eds.). Cambridge University Press, Cambridge, United Kingdom.

NORBERG, U.M. 1990. Vertebrate Flight. Springer, Berlin, Germany.

NORBERG, U.M. 1994. Wing design, flight performance, and habitat use in bats. Pp. 205-239 in Ecological morphology (P.C. WAINWRIGHT AND S.M. REILLY, eds.). University of Chicago Press, Chicago, United States.

NORBERG, U.M. AND J.M.V. RAYNER. 1987. Ecological morphology and flight in bats: wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society of London B. Biological Sciences 316: 335-427.

NORBERG, U.M.L. AND Y. WINTER. 2006. Wing beat kinematics of a nectar-feeding bat, *Glossophaga soricina*, flying at different flight speeds and Strouhal numbers. – Journal of Experimental Biology 209: 3887-3897.

O'SHEA, T.J. AND T.A. VAUGHAN. 1980. Ecological observations on an East African bat community. Mammalia 44: 485–496.

PENNYCUICK, C.J. 1975. Mechanics of flight. Pp. 1-75 in Avian Biology vol. 5 (D.S. FARNER AND J.R. KING, eds.); Academic Press, London, United Kingdom.

RANSOME, R. 1990. The natural history of hibernating bats, 235 pp.; Christopher Helm, London, United Kingdom.

RAYNER, J.M.V., G. JONES AND A. THOMAS. 1986. Vortex flow visualizations reveal change in upstroke function with flight speed in bats. Nature 321: 162-164.

RHODES, M.P. 2002. Assessment of sources of variance and patterns of overlap in microchiropteran wing morphology in southeast Queensland, Australia. Canadian Journal of Zoology 80: 450-460.

RICKLEFS, R.E. AND D.B. MILES. 1994. Ecological and evolutionary inferences from morphology: an ecological perspective. Pp. 13-41 in Ecological morphology: integrative organismal biology (P.C. WAINWRIGHT AND S.M. REILLY, eds); University of Chicago Press, Chicago, United States.

ROLLINAT, R. AND E. TROUESSART. 1897. Sur la reproduction des chauves-souris. II. Les Rhinolophes (1). Mémoires de la Societé Zoologique de France 10: 114-138.

ROOT, R.B. 1967. The niche exploitation pattern of the blue-grey gnat-catcher. Ecological Monographs 37: 317–50.

RUSSO, D., D. ALMENAR, J. AIHARTZA, U. GOITI, E. SALSAMENDI AND I. GARIN. 2005. Habitat selection in sympatric *Rhinolophus mehelyi* and *R. euryale* (Mammalia: Chiroptera). Journal of Zoology (London) 266: 327-332.

RUSSO, D., G. JONES AND A. MIGLIOZZI. 2002. Habitat selection by the Mediterranean horseshoe bat, *Rhinolophus euryale* (Chiroptera: Rhinolophidae) in a rural area of southern Italy and implications for conservation. Biological Conservation 107: 71-81.

RYBÁŘ, P. 1972. Eine Möglichkeit der Altersbestimmung von Fledermäusen nach der Ossifikation der Flügelknochen. – Nyctalus 4: 27-34.

SALSAMENDI, E., J. AIHARTZA, U. GOITI, D. ALMENAR AND I. GARIN. 2005. Echolocation calls and morphology in the Mehely's (*Rhinolophus mehelyi*) and Mediterranean (*R. euryale*) horseshoe bats: implications for resource partitioning. Hystrix Italian Journal of Mammalogy (n.s.) 16: 149-158.

SAUNDERS, M.B. AND R.M.R. BARCLAY. 1992. Ecomorphology of insectivorous bats: a test of predictions using two morphologically similar species. Ecology 73: 1335-1345.

SCHMIDT-NIELSEN, K. 1984. Scaling: Why is animal size so important? Cambridge University Press, Cambridge.

SCHNITZLER, H.-U. 1983. Fluttering target detection in horseshoe bats. Journal of the Acoustical Society of America 74: 31.

SCHNITZLER, H.-U. AND E.K.V. KALKO. 1998. How echolocating bats search and find food. Pp. 183-196 in Bat biology and conservation (T.H. Kunz and P.A. Racey, eds.). Smithsonian Institution Press, Washington, D.C., United States.

SCHNITZLER, H.-U. AND E.K.V. KALKO. 2001. Echolocation by insect-eating bats. Bioscience 51: 557-569.

SCHNITZLER, H.-U., C.F. MOSS AND A. DENZINGER. 2003. From spatial orientation to food acquisition in echolocating bats. Trends in Ecology and Evolution 18: 386-394.

SCHOBER, W. AND E. GRIMMBERGER. 1998. Die Fledermäuse Europas. Kosmos-Naturführer, Stuttgart, Germany.

SCHOENER, T.W. 1974. Resource partitioning in ecological communities. Science 185: 27-39.

SIEMERS, B.M., K. BEEDHOLM, C. DIETZ, I. DIETZ AND T. IVANOVA. 2005. Is species identity, sex, age or individual quality conveyed by echolocation call frequency in European horseshoe bats? Acta Chiropterologica 7: 259-274.

SIEMERS, B.M. AND T. IVANOVA. 2004. Ground gleaning in horseshoe bats: comparative evidence from *Rhinolophus blasii*, *R. euryale* and *R. mehelyi*. Behavioral Ecology and Sociobiology 56: 464-471.

SIMBERLOFF, D. AND T. DAYAN. 1991. The guild concept and the structure of ecological communities. Annual Reviews of Ecology and Systematics 22: 115–143.

STERN, A.A., T.H. KUNZ AND S.S. BHATT. 1997. Seasonal wing loading and the ontogeny of flight in *Phyllostomus hastatus* (Chiroptera: Phyllostomidae). Journal of Mammalogy 78: 1199-1209.

STOCKWELL, E.F. 2001. Morphology and flight manoeuvrability in New World leaf-nosed bats. Journal of Zoology (London) 254: 505-514.

SWARTZ, S.M., P.W. FREEMAN AND E.F. STOCKWELL. 2003. Ecomorphology of bats: comparative and experimental approaches relating structural design to ecology. Pp. 257-300 in Bat ecology (T.H. Kunz and M.B. Fenton, eds.). The University of Chicago Press, Chicago, United States.

VALENCIUC, N. 1971. Données concernant la nourriture et la manière de se la procurer chez quelques espèces de la faune de Roumanie. Studii si Comunicari 1971: 353-357.

WEBB, P.I., J.R. SPEAKMAN AND P.A. RACEY. 1992. Inter- and intra-individual variation in wing loading and body mass in female pipistrelle bats: theoretical implications for flight performance. Journal of Zoology (London) 228: 669-673.

WHITAKER, J.O. JR. AND H. BLACK. 1976. Food habits of cave bats from Zambia, Africa. Journal of Mammalogy 57: 199-204.

WIENS, J.A. 1977. On competition and variable environments. American Scientist 65: 590-597.

WILLIG, M.R. AND M.P. MOULTON. 1989. The role of stochastic and deterministic processes in structuring neotropical bat communities. Journal of Mammalogy 70: 323–329.

WINTER,Y. 1999. Flight speed and body mass of nectar-feeding bats (Glossophaginae) during foraging. Journal of Experimental Biology 202: 1917-1930.

YOUNG, R.A. 1975. Aging criteria, pelage colour polymorphism and moulting in *Rhinolophus megaphyllus* (Chiroptera) from south-eastern Queensland, Australia. Mammalia 39: 75-111.

Zusammenfassung

Promotionsthema

Das Thema der Promotion lautet: „apects of ecomorphology in the five European horseshoe bats (Chiroptera: Rhinolophidae) in the area of sympatry“ und umfasst damit die vergleichende Untersuchung ökomorphologischer Anpassungen der fünf europäischen Hufeisennasen-Fledermäuse an ihren Lebensraum in ihrem sympatrischen Vorkommen in Bulgarien. Dabei steht die Frage im Mittelpunkt, ob Unterschiede in der Flügelmorphologie vorhanden sind und dazu beitragen, die Nahrungskonkurrenz zwischen den Arten zu verringern beziehungsweise zu vermeiden.

Einleitung

Im Mittelmeergebiet kommen fünf Arten der Hufeisennasen-Fledermäuse vor: die Große Hufeisennase (*Rhinolophus ferrumequinum*), die Kleine Hufeisennase (*R. hipposideros*), die Mittelmeer-Hufeisennase (*R. euryale*), die Mehely-Hufeisennase (*R. mehelyi*) und die Blasius-Hufeisennase (*R. blasii*). Auf der Balkan-Halbinsel und im östlichen Mittelmeergebiet überlappen sich die Verbreitungsgebiete dieser fünf Fledermausarten, sie kommen hier sympatrisch vor. Die Arten gleichen sich in ihrem Bauplan weitgehend und sind eng verwandte Mitglieder einer Gattung. Aufgrund ihrer Echoortung mit langen frequenzkonstanten Lauten, ihres Jagdverhaltens und der bevorzugten Beute können sie zudem zu einer einheitlichen Gilde, den ‘aerial insectivore narrow space flutter-detecting foragers’ zusammengefasst werden, die von anderen Fledermäusen und darüber hinaus auch von anderen insektenfressenden Tieren deutlich abgegrenzt werden kann. Die morphologische und ökologische Ähnlichkeit der Arten legt nahe, dass eine hohe Konkurrenz, vor allem um Nahrung, bestehen und sich die Arten zumindest teilweise ausschließen könnten. Allerdings sind zahlreiche syntope Vorkommen belegt, die die Vermutung zulassen, dass es Mechanismen zur Konkurrenzvermeidung gibt. Bislang ist allerdings weitestgehend unbekannt, wie die fünf Arten koexistieren können. Dies prädestiniert sie für Studien zur Nischenaufteilung bzw. Konkurrenzvermeidung. Da zwei der im Mittelmeergebiet häufige Arten, die Große und die Kleine Hufeisennase auch in Mitteleuropa vorkommen und dort gut untersucht sind, sollten zudem aufschlussreiche Vergleiche zwischen Populationen im Bereich der sympatrischen Vorkommen im Mittelmeergebiet und den allopatrischen Vorkommen im nördlichen Verbreitungsgebiet möglich sein.

Aus dem Promotionsthema ergaben sich etliche Fragestellungen, die wie folgt skizziert in den sieben Kapiteln der Dissertation bearbeitet wurden:

1) Für Feldstudien ist eine eindeutige Artzuordnung unabdingbar, da nur so zuverlässige Daten an lebenden Tieren im Freiland erbracht werden können: → *Wie lassen sich die fünf Arten zuverlässig bestimmen und wie sicher ist diese Artbestimmung?*
2) Da es zwischen verschiedenen Alters- und Reproduktionsklassen einer Art erhebliche ökologische und morphologische Unterschiede geben kann, ist eine sichere Unterscheidung von Altersklassen und Reproduktionszuständen wichtig: → *Lassen sich Altersklassen und Reproduktionszustände unterscheiden und bestimmen?*
3) Eine dauerhafte individuelle Markierung ist eine Voraussetzung, um Pseudoreplikation von Daten durch das wiederholte Vermessen der selben Individuen zu vermeiden. Die individuelle Wiedererkennung ermöglicht darüber hinaus auch das Studium von Wachstumsprozessen. Dabei sollte die Markierungsmethode möglichst keine negativen Auswirkungen auf die markierten Tiere haben: → *Welche Auswirkungen hat die individuelle Markierung mit Fledermausringen auf die untersuchten Arten?*
4) In Mitteleuropa gelten Hufeisennasen-Fledermäuse als standorttreu. Daten aus dem östlichen Mittelmeergebiet fehlen allerdings. Es erschien notwendig zu überprüfen, ob es aufgrund ausgeprägter Standorttreue möglicherweise zu lokalen oder regionalen Anpassungen in der Ökologie oder Morphologie kommen könnte. Bei einer geringen

Mobilität könnte der Genfluss zwischen Populationen eingeschränkt sein und es so zur Ausbildung lokaler Besonderheiten kommen. Dies würde eine Übertragung der gewonnen Daten auf andere Populationen der selben Art nur in eingeschränkter Form zulassen: → *Sind die bulgarischen Hufeisennasen-Fledermäuse standorttreu und kommt es zu einer deutlichen Separierung von Teilpopulationen und damit möglicherweise zu einer eingeschränkten Übertragbarkeit der Daten auf andere Populationen der selben Art?*

5) Für das Wachstum eines Individuums sind die klimatischen Bedingungen entscheidend, da diese sowohl die Beutedichte und damit die Nahrungsaufnahme und Milchproduktion durch das Muttertier beeinflussen, als auch direkt Auswirkungen auf die Stoffwechselvorgänge der zu Torpor befähigten Fledermäuse haben. Ein Vergleich zwischen verschiedenen Jahrgängen kann nur dann erfolgen, wenn voll ausgewachsene Tiere verglichen werden können: → *Bis wann ist das individuelle Wachstum junger Hufeisennasen abgeschlossen und welchen Einfluss hat die Witterung auf das Wachstum?*
6) Längenmaße von Flügelelementen sind einfach zu erheben und weisen geringe Messfehler auf. Bei Fledermäusen stellt die Unterarmlänge ein etabliertes Maß für die Körpergröße dar, die Länge des fünften Fingerstrahls für die Flügelbreite, die Länge des dritten Fingerstrahls für die Handflügellänge. Die Längen der beiden Phalangen des vierten Fingers sind wichtige Identifikationskriterien. Die Messstrecken können daher genutzt werden, um die Artzuordnung zu prüfen und um sie auf Unterschiede zwischen verschiedenen Gruppen zu testen, die möglicherweise einen Einfluss auf die Jagdökologie und Habitatwahl haben: → *Lassen sich diese Messstrecken zur Artbestimmung heranziehen und gibt es Unterschiede, die das Vorhandensein ökologischer Anpassungen vermuten lassen?*

7) Die Längenmaße am Flügel erlauben eine Abschätzung von flügelmorphologischen Anpassungen, detailliert können diese allerdings nur bei einer Auswertungsmethode erfasst werden, die Flächenmaße in standardisierter Form mit einbezieht. Dazu ist die Auswertung von standardisiert aufgenommen Flügelfotografien am genauesten. Um die gewonnenen Daten nicht nur theoretisch zwischen den Arten vergleichen, sondern auch mit tatsächlichen ökologischen Anpassungen korrelieren zu können, ist die Erfassung des Jagdverhaltens notwendig. Dies erfolgte durch die Telemetrie von freifliegenden Tieren: → *Gibt es substanzielle Unterschiede in der Flügelmorphologie der fünf Arten und lassen sich diese mit im Freiland erfassten Parametern des Jagdverhaltens korrelieren?*

Untersuchungsgebiet

Die Studien wurden in Südosteuropa mit Schwerpunkt im nordbulgarischen Donauhügelland durchgeführt. Ein Großteil der Untersuchungen wurden an und im Umfeld einer Quartierhöhle (Nanin Kamăk) am Fluss Osăm, einem Nebenfluss der Donau, bei dem Dorf Muselievo im Distrikt Pleven durchgeführt. Hier erfolgte die Telemetrie der Tiere und die Untersuchung der Wanderungsbewegungen. Weitere Daten vor allem zur Morphologie wurden im Bereich des sympatrischen Vorkommens aller fünf Arten in Bulgarien, Griechenland und der Türkei gesammelt. Die Bestimmungsmerkmale wurden an Tieren im gesamten Mittelmeergebiet (Balkanhalbinsel, Türkei, Israel, Ägypten, Marokko, Frankreich, Italien) überprüft.

Ergebnisse

Die wichtigsten Ergebnisse zu den Untersuchungsteilen werden hier gegliedert nach den sieben Fragestellungen bzw. Kapiteln aufgeführt:

Wie lassen sich die fünf Arten zuverlässig bestimmen und wie sicher ist diese Artbestimmung?

Eine Artbestimmung der fünf Arten ist anhand von verschiedenen Merkmalen der Nasenaufsätze zweifelsfrei möglich. Selbst die hin und wieder vorkommenden Tiere mit Missbildungen der Nasenaufsätze lassen sich meist zweifelsfrei zuordnen. Die Artmerkmale wurden zu einem Bestimmungsschlüssel zusammengefasst und an mehr als 7200 gefangenen Hufeisennasenfledermäusen im gesamten Mittelmeergebiet getestet. Lediglich ein Individuum war nicht zweifelsfrei einer Art zuzuordnen. Vermutlich handelte es sich dabei um eine zwergwüchsige Mehely-Hufeisennase (*R. mehelyi*), deren Nasenaufsatz allerdings starke Anklänge an diejenigen der Mittelmeerhufeisennase (*R. euryale*) zeigte. Bei über 2000 Individuen beider Arten traten keine weiteren Bestimmungsprobleme auf. Bis auf wenige Einzeltiere ist somit eine zweifelsfreie Artbestimmung anhand externer Merkmale an lebenden Tieren in Feld möglich.

Lassen sich Altersklassen und Reproduktionszustände unterscheiden und bestimmen?

Um Möglichkeiten der Altersbestimmung zu prüfen, wurden bei der Großen Hufeisennase (*R. ferrumequinum*) 218 Weibchen während der ersten beiden Lebensmonate individuell markiert. Davon konnten 94 Tiere insgesamt 260 mal bis zu einem Alter von 60 Monaten wiedergefangen werden. Beim Erstfang und allen Wiederfängen wurden die Form der Fingergelenke und ihrer Wachstumszonen, die Fellfarbe, Größe und Zustand der brustständigen Milchzitzen und der Haftzitzen und weitere Reproduktionsmerkmale notiert. Bei allen Fängen wurden von den Tieren Porträts und die Zitzen fotografiert. Aus den Daten und der Auswertung der Fotografien ließ sich eine Merkmalsliste erstellen, mit deren Hilfe eine Alterszuordnung bis zu einem Alter von 28 Monaten möglich ist. Die Form der Fingergelenke in Verbindung mit lockerem und hellgrauem Fell und kaum entwickelten Zitzen erlaubt eine Unterscheidung von weniger als 4 Monate alten Tieren von älteren. Bis zu einem Alter von 16 Monaten bleibt das Fell grau, erreicht aber die Dichte erwachsener Tiere, die Zitzen bleiben aber noch sehr klein. Bis zu einem Alter von 28 Monaten entwickeln sich bei den allermeisten Weibchen die sekundären Geschlechtsorgane, sie gebären ihr erstes Junges meist im Alter von etwa 24 Monaten. Bis zu ihrer dritten Überwinterung ab einem Alter von 28 Monaten bleibt das Fell im Gesicht viel dunkler als das dem adulten Haarkleid bereits sehr ähnliche gelblichbraun gefärbte sonstige Fell. Nach der dritten Überwinterung in einem Alter von 33 Monaten ist in allen Merkmalen der typische Erwachsenenzustand erreicht. Bei den anderen vier Hufeisennasen-Arten sind ebenfalls zumindest die einjährigen Tiere von mehrjährigen anhand der selben Merkmalskombination zu unterscheiden, für sie sind ein graues Fell und unentwickelte Zitzen und Haftzitzen charakteristisch. Die Männchen aller Arten sind in ihrem zweiten Sommer ebenfalls viel grauer als die Adulttiere und weisen einen dünneren Penis und wenig entwickelte Hoden und Nebenhoden auf. Somit lassen sich Individuen beider Geschlechter und aller fünf Arten im Sommerhalbjahr zuverlässig in juvenile Tiere (bis zu 4 Monate alt), einjährige bzw. nullipare Tiere (bis zu 16 Monate alt) und adulte Tiere (über 20 Monate alt) einteilen.

Anhand der Ausbildung der sekundären Geschlechtsorgane lassen sich die Weibchen aller fünf Arten zuverlässig als nullipar, primipar oder multipar ansprechen, innerhalb der Reproduktionszeit lassen sich Weibchen anhand der Ausprägung der Zitzen und Haftzitzen bzw. durch Abtasten des Abdomens in trächtig, laktierend oder postlaktierend einteilen. Unsicherheiten treten meist nur dann auf, wenn die Weibchen Embryonen oder die Jungtiere verloren hatten und so manchmal intermediäre Zustände zeigten.

Welche Auswirkungen hat die individuelle Markierung mit Fledermausringen auf die untersuchten Arten?

Während der Untersuchung zur Altersklassifikation und weiterer ökologischer Fragestellungen wurden über 1400 Individuen aus drei Arten (*R. ferrumequinum*, *R. mehelyi*, *R. euryale*) individuell mit Armklammern (Fledermausringen) markiert. Davon wurden in der Folge 580 Tiere wiedergefangen und die Auswirkungen der Markierung auf die Tiere konnte bewertet werden. Insgesamt waren bei über 85% der wiedergefangenen Tiere keine durch die Beringung verursachten Verletzungen zu beobachtet. Allerdings traten in allen Gruppen und Arten von den Ringen verursachte Verletzungen auf, ihr Anteil variierte indessen stark in Abhängigkeit von der Fledermausart und der Ringgröße. Die kleinere von zwei verwendeten Ringgrößen verursachte bei mehr als 60% der wiedergefangenen *R. mehelyi* Verletzungen. Selbst bei *R. ferrumequinum*, für die etablierte Ringgrößen verwendet wurden, waren 9,3 % der wiedergefangenen Tiere verletzt. Die Ursache für die auffallend hohen Verletzungsraten dürfte vor allem in der Breite des Propatagiums bei den Hufeisennasen-Fledermäusen zu suchen sein. Im Flug verursacht die Reibung durch den sich bewegenden Ring leichte Verletzungen an der Vorderkante des Propatagiums, die sich auf längere Zeit infizieren und zu schweren Verletzungen auswachsen können. Möglichkeiten, wie die Verletzungsrate verringert werden könnte, werden im entsprechenden Kapitel diskutiert.

Sind die bulgarischen Hufeisennasen-Fledermäuse standorttreu und kommt es zu einer deutlichen Separierung von Teilpopulationen?

Die Markierung der Hufeisennasen-Fledermäusen erlaubte es regionale und saisonale Wanderungen zu untersuchen. Anhand der Wiederfunde von markierten Individuen aus drei Arten (*R. ferrumequinum*, *R. euryale* und *R. mehelyi*) ließen sich einige Muster herausarbeiten. Der Großteil der Wiederfänge erfolgte am Beringungsort oder an nahe gelegenen Ausweichhangplätzen. Zur Überwinterung wanderten die Großen Hufeisennasen im Mittel 57 km und maximal 90 km in Richtung Balkan-Gebirge. Es konnten keine signifikanten Unterschiede in der Entfernung der Winterquartiere vom Sommerhangplatz zwischen Männchen und Weibchen oder Adulten und Jungtieren gefunden werden. Für die beiden anderen Hufeisennasen-Fledermäuse wurden ebenfalls weite Überflüge verzeichnet. Die Mittelmeer-Hufeisennase wechselte Quartiere in Entfernungen von bis zu 60 km. Bei der bislang wenig untersuchten Mehely-Hufeisennase konnten erstmals Wanderungen von über 90 km dokumentiert werden. Anhand der Ergebnisse und einer Zusammenstellung publizierter Studien ist davon auszugehen, dass alle europäischen Hufeisennasen zwar weitgehend ortstreu sind, es dennoch zu regelmäßigen Überflügen in einem 100 km Radius kommen kann und auch einzelne Weibchen in andere Wochenstubenverbände übersiedeln können. Da die Paarung größtenteils im Winterquartier erfolgt und zwischen Sommer- und Winterquartier teilweise erhebliche Strecken zurückgelegt werden, ist davon auszugehen, dass es zu einer erheblichen genetischen Durchmischung innerhalb der Populationen kommt. Somit kann davon ausgegangen werden, dass es, von dem möglichen Einfluss geographischer Barrieren abgesehen, zu keiner deutlichen Separierung von Teilpopulationen kommt. Demnach sollten die gewonnenen ökologischen und morphologischen Daten auch auf andere Populationen der selben Art übertragbar sein.

Bis wann ist das individuelle Wachstum junger Hufeisennasen abgeschlossen und welchen Einfluss hat die Witterung auf das Wachstum?

Für die weitergehenden Untersuchungen zur Flügelmorphologie war es wichtig zu untersuchen, wann das Wachstum von Jungtieren abgeschlossen ist, und ob es aufgrund klimatischer Faktoren möglicherweise Größenunterschiede zwischen verschiedenen Jahrgängen der selben Art gibt. Dazu wurde das Wachstum bei drei Arten (*R. ferrumequinum*, *R. euryale* und *R. mehelyi*) untersucht und die Messwerte verschiedener Geburtsjahrgänge verglichen. Bulgarische Hufeisennasen-Fledermäuse werden in der Regel in den ersten drei

Juni-Wochen geboren und verlassen das Quartier erstmals in einem Alter von etwa drei Wochen. Mit dem Beginn des selbstständigen Beuteerwerbs ab Ende Juli erreichen die Jungtiere aller drei Arten bereits mehr als 95% der adulten Flügelmaße in vier Messstrecken. Individuell markierte Jungtiere der Großen Hufeisennase (*R. ferrumequinum*) erreichten in den meisten Flügelmaßen Adultdimensionen in der zweiten Augusthälfte. Entsprechend wichen dann auch die gemittelten Maße aller Jungtiere ab Ende August nicht mehr von denen adulter Tiere ab. Ein vergleichbares Muster wurde auch bei *R. mehelyi* und *R. euryale* gefunden. Darüber hinaus konnten eindeutige Größenunterschiede zwischen verschiedenen Geburtsjahrgängen nachgewiesen werden, die mit Klimabedingungen während der Wachstumsphase in Zusammenhang zu bringen sind. Anhand dieser Daten konnte erstmals ein Einfluss des Klimas auf das Wachstum von Individuen im Zentrum ihres Verbreitungsgebietes gezeigt werden. Bisherige Untersuchungen konnten solch einen Einfluss lediglich auf Population an den nördlichen Verbreitungsgrenzen der Arten nachweisen. Aus diesen Daten ließ sich ablesen, dass Jungtiere zwar ab Ende August ihre endgültige Größe erreichen, aufgrund klimatischer Bedingungen zur Wachstumszeit aber teilweise erheblich von den mittleren Messwerten der Adultpopulation abweichen können. Daher schien es sinnvoll, für weitere Vergleiche nur mehrjährige adulte Tiere heranzuziehen, die bei einem genügend großen Stichprobenumfang die Maße vieler Jahrgänge repräsentieren.

Lassen sich die Messstrecken am Flügel zur Artbestimmung heranziehen und gibt es Unterschiede, die das Vorhandensein ökologischer Anpassungen vermuten lassen?

Zur Bewertung der intra- und interspezifischen Variabilität von Messstrecken am Flügel wurden fünf Längenmaße der fünf europäischen Arten untersucht. Dazu wurden 3081 adulte Individuen in Bulgarien, Griechenland und der Türkei vermessen. Die Daten belegen, dass sich die Flügel der fünf Arten in ihrer Größe substanziell unterscheiden. Trotz einer ähnlichen Form konnten auch größenunabhängige Unterschiede in der Flügelform gefunden werden. So haben die beiden kleinsten Arten, *Rhinolophus hipposideros*, und etwas weniger stark ausgeprägt auch *R. blasii*, sehr kurze Handflügel, was einen sehr manövrierfähigen Flug dicht an und in der Vegetation ermöglicht. Die größte Art *R. ferrumequinum* und die zweitgrößte, *R. mehelyi*, haben deutlich längere Handflügel, dies ermöglicht schnelle und energiesparende Transferflüge über längere Distanzen, schränkt aber die Fähigkeit zu kleinräumig manövrierfähigen Beuteflügen ein. Die Bedeutung sowohl der Körpergröße und Flügelgröße, als auch der Flügelform für eine Nischenaufteilung zwischen den Arten wird in der entsprechenden Arbeit (Kapitel 6) diskutiert.

Innerhalb der Arten konnten sowohl Unterschiede zwischen den Geschlechtern, als auch zwischen Regionen innerhalb Südosteuropas gefunden werden. In den meisten Maßen waren die Weibchen deutlich größer als die Männchen. Populationen von *R. mehelyi* zeigten darüber hinaus im Gegensatz zu *R. ferrumequinum* und *R. euryale* auch geographische Unterschiede. Dabei ist derzeit unklar, ob dies als Anpassungen an Habitatunterschiede zu werten ist, oder ob andere Ursachen zugrunde liegen.

Aus den Maßen ließ sich eine Diskriminanzfunktion erstellen, die anhand von nur zwei der fünf Messstrecken eine korrekte Artzuordnung von 98% der 3081 untersuchten Tiere ermöglicht. Diese Diskriminanzfunktion könnte vor allem für die Artbestimmung von Museumsbelegen hilfreich sein.

Gibt es substanzielle Unterschiede in der Flügelmorphologie der fünf Arten und lassen sich diese mit im Freiland erfassten Parametern des Jagdverhaltens korrelieren?

Ziel war es, Flächenmaße der Flügel der fünf Arten zu vergleichen und für die Bewertung von Flugleistungen wichtige Parameter zu berechnen und in einem nächsten Schritt mit jagdökologischen Daten zu vergleichen. Dazu wurden mit Hilfe einer Flügelfotoapparatur die ausgestreckten Flügel von 479 Hufeisennasenfledermäusen fotografiert. Mit Ausnahme von *R. hipposideros* wurden dazu mindestens 50 adulte

Männchen und 50 adulte Weibchen je Art herangezogen. Die Flügelfotografien wurden digitalisiert und in einem Programm zur Flächenauswertung analysiert. Aus den Flächenmaßen wurden die Parameter Flügelflächenbelastung (wing loading), Flügelstreckung (aspect ratio) und Flügelspitzen-Index (tip shape index) abgeleitet. Für jede Art wurde der Messfehler ermittelt, in dem jeweils ein Individuum 20 mal fotografiert und ausgemessen wurde: In den abgeleiteten Flügelmaßen betrug die durch Messfehler verursachte Standardabweichung 2-3 % der Werte, womit erstmals ein Fehlerbereich für die Methode angegeben wird. Um die Flügelflächenbelastung (wing loading) zwischen Individuen, die in verschiedenen Jahreszeiten gefangen wurden, vergleichen zu können, wurde ein Standardgewicht für Männchen, nichtreproduktive und laktierende Weibchen je Art berechnet.

Die Auswertung der Daten ergab, dass sich die Flügelflächen der fünf Arten in ihrer Größe deutlich unterscheiden, ein Geschlechtsunterschied war dahingegen nur in der Handflügelfläche nachweisbar, dabei waren Weibchen größer als Männchen. Auch bei den abgeleiteten Parametern gab es signifikante Unterschiede, allerdings erklären die Faktoren Art und Geschlecht hier nur einen geringen Teil der Variabilität.

Aus den Flächenmaßen und den abgeleiteten Parametern wurden Vorhersagen über das Jagdverhalten, die Habitatwahl und die Fluggeschwindigkeit auf Transferstrecken getroffen. Diese Vorhersagen wurden mit den entsprechenden Werten verglichen, die mit Hilfe der Radiotelemetrie an freifliegenden Fledermäusen aller fünf Arten in Bulgarien gewonnen wurden. Dabei wurden vor allem adulte Weibchen aller fünf Arten mit sehr leichten Telemetriesendern ausgestattet und über mehrere Nächte verfolgt. Dabei wurden Daten zur Geschwindigkeit des Transferflugs, zur Jagdmethode (Wartenjagd versus Jagdflug) und zur Habitatwahl aufgenommen und ausgewertet.

Beim Vergleich der theoretischen Vorhersagen und der im Freiland erhobenen Daten zum Jagdverhalten konnten nur wenige signifikante Korrelationen gefunden werden. Lediglich das individuelle Körpergewicht und die Flügelflächenbelastung korrelierten signifikant mit der prozentualen Zeit der Wartenjagd an der gesamten Jagdzeit und die Spannweite und Länge des Handflügels korrelierten negativ mit der Nutzung von dichter Vegetation als Jagdhabitat.

In drei der fünf Arten stimmte die theoretisch vorhergesagte energiesparendste Fluggeschwindigkeit mit der tatsächlich bei Transferflügel festgestellten überein, die Abweichungen der beiden anderen Arten hinsichtlich ihrer Fluggeschwindigkeiten dürften in der Datenlage beziehungsweise in ihrem Jagdverhalten zu suchen sein.

Diskussion

Die jeweiligen Einzelergebnisse werden in den entsprechenden Kapiteln der Dissertation diskutiert. Zusammenfassend konnten flügelmorphologische Unterschiede zwischen den sympatrisch vorkommenden Arten gefunden werden, die als Anpassungen an das Jagdverhalten und die Habitatnutzung zu werten sind.

Die Schwierigkeiten, die aus der Flügelmorphologie gewonnenen Daten mit den im Feld erhobenen Daten zum Jagdverhalten in Einklang zu bringen, werden vor allem auf die hohe intraspezifische Variabilität und die Flexibilität des Jagdverhaltens zurückgeführt. Die Flügelmorphologie unterliegt bei den fliegenden und insektenjagenden Fledermäusen sicherlich einem hohen Anpassungsdruck, dennoch erlaubt eine gegebene Flügelform innerhalb gewisser Grenzen eine erhebliche Variabilität des Jagdfluges. So scheinen vor allem die Größenunterschiede zwischen den fünf Arten einen Einfluss auf den Jagdstil und die Habitatwahl zu haben, während die Bedeutung der Feinmodifikationen im Bau der Flügel kaum zu bestimmen ist. So nimmt die Nutzung von offeneren und weniger dicht bewachsenen Jagdhabitaten und der Anteil der Wartenjagd mit zunehmender Körpergröße, Flügelspannweite und Handflügellänge zu, dagegen sind die kleinen und kurzflügligen Arten nahezu ausschließlich Flugjäger nahe oder in der dichten Vegetation.

Damit scheint die Gilde hinsichtlich der Flügelmorphologie vor allem durch Größenunterschiede strukturiert, die wiederum Unterschiede in der Habitatwahl und Jagdstrategie bedingen. Somit werden ein Nischenüberlapp und eine interspezifische Konkurrenz reduziert und unter den gegebenen Bedingungen ist eine Koexistenz der fünf Arten offensichtlich möglich. Über die Größenunterschiede hinaus tragen sicherlich weitere größenunabhängige Besonderheiten zu einer Strukturierung der Gilde bei, deren Einfluss bei der vorliegenden Untersuchung aber nicht vollständig zu bestimmen war.

Vermutlich spielen neben der Ökomorphologie des Flugapparates sensorische und weitere morphologische Anpassungen ebenfalls eine große Rolle und sollten detailliert untersucht werden. Erst in der Zusammenschau zahlreicher morphologischer, sensorischer und ökologischer Teilaspekte wird es möglich sein, die Koexistenzmechanismen umfassend zu verstehen.

Veröffentlichung und Eigenanteil

Mit Ausnahme des ersten Teils sind alle Teilmanuskripte der Dissertation für die Veröffentlichung in wissenschaftlichen Fachzeitschriften vorgesehen. Der Bestimmungsschlüssel (Kapitel 1) ist bereits in elektronischer Form im Internet veröffentlich (Dietz & von Helversen 2004) bzw. ist Teil eines Bestimmungsschlüssels in einem populärwissenschaftlichen Buch (Dietz et al. 2007b). Das Kapitel 2 ist bislang noch nicht veröffentlicht, wird aber in Bälde eingereicht. Das Kapitel 3 ist eingereicht und bereits zur Veröffentlichung akzeptiert und wird in Kürze in gedruckter Form erscheinen. Die Kapitel 4-6 sind bereits in referierten internationalen wissenschaftlichen Zeitschriften erschienen (Dietz et al. 2006a; Dietz et al. 2006b; Dietz et al. 2007a). Das Kapitel 7 ist bislang nicht veröffentlicht, wird aber demnächst bei einer referierten internationalen wissenschaftlichen Zeitschrift zur Veröffentlichung eingereicht.

Die den Teilmanuskripten der Dissertation zugrunde liegenden Projekte wurde von mir geplant, die verwendeten Methoden selbstständig erarbeitet und etabliert, die Daten eigenständig erhoben und ausgewertet. Die Dissertation beziehungsweise die zugrunde liegenden Manuskripte wurde von mir geschrieben. Für ihren wissenschaftliche Beitrag danke ich den beteiligten Personen: sie haben Anteil an den Veröffentlichungen als Mitautoren:
Prof. Dr. H.-U. Schnitzler wird bei der Veröffentlichung über die Flügelmorphologie (Kapitel 7) Mitautor sein, er war der Betreuer der Dissertation und steuerte wertvolle Diskussionsteile über die möglichen Strukturierungsmechansimen von Gilden bei. Dr. B.M. Siemers ist, beziehungsweise wird Mitautor bei den meisten der Veröffentlichungen (Kapitel 3-7) sein: er stellte technische Ausrüstung und finanzielle Unterstützung bereit, war Betreuer der Arbeit und erbrachte wertvolle Kommentare und Diskussionsbeiträge zu den genannten Manuskriptteilen. Bei den Kapiteln 2-7 ist beziehungsweise wird I. Dietz Mitautorin sein: sie

nahm an der Feldarbeit und der Datenaufnahme teil, erbrachte vielfältige Hilfe und Diskussionsbeiträge. Bei den Kapiteln 3 und 7 ist beziehungsweise wird Dr. T. Ivanova Mitautorin sein, da sie bei Teilen der Feldarbeit beteiligt war und wichtige Hilfe bei der Organisation des Projektes in Bulgarien bereitstellte. Prof. Dr. O. von Helversen und D. Nill sind Mitautoren bei den beiden Veröffentlichungen, die aus dem Kapitel 1 stammende Informationen enthalten, da sie andere als die in die Dissertation aufgenommene Teile der Veröffentlichungen erstellt haben.

Liste der bereits veröffentlichten Teile der Dissertation

DIETZ, C. AND O. VON HELVERSEN. 2004. Identification key to the bats of Europe. 72 pp. Electronical publication, version 1.0, available at www.uni-tuebingen.de/tierphys/Kontakt/mitarbeiter_seiten/dietz.htm.

DIETZ, C., I. DIETZ AND B. M. SIEMERS. 2006a. Wing measurement variations in the five European horseshoe bat species (Chiroptera: Rhinolophidae). Journal of Mammalogy 87: 1241-1251.

DIETZ, C., I. DIETZ, T. IVANOVA AND B.M. SIEMERS. 2006b. Effects of forearm bands on horseshoe bats (Chiroptera: Rhinolophidae). Acta Chiropterologica 8: 523-535.

DIETZ, C., I. DIETZ AND B. M. SIEMERS. 2007a. Growth of horseshoe bats (Chiroptera: Rhinolophidae) in temperate continental conditions and the influence of climate. Mammalian Biology 72: 129-144.

DIETZ, C., O. VON HELVERSEN AND D. NILL. 2007b. Handbuch der Fledermäuse Europas und Nordwestafrikas, 399 pp.; Kosmos, Stuttgart, Germany.

Danksagung

Bei Prof. Dr. Hans-Ulrich Schnitzler und Dr. Björn Siemers möchte ich mich herzlich dafür bedanken, dass sie diese Arbeit ermöglicht und nach Kräften unterstützt haben. Beiden danke ich für die vielen Freiheiten, die ich genießen durfte, und das großzügige Darüberhinwegsehen, wenn ich mal wieder alles andere interessanter fand als das eigentliche Promotionsthema. Besonderer Dank geht an Björn Siemers für die konstruktiven Diskussionen und Korrekturen an den Manuskripten und die viele Ideen wie die Daten am Besten darzustellen wären.

Dr. Teodora Ivanova und der Bulgarischen Fledermausgruppe danke ich für die Möglichkeit, in Bulgarien arbeiten zu dürfen, die Bereitstellung von Genehmigungen und das Teilen ihres Wissens um Fledermäuse und deren Quartiere. Dessi Merdschanova, Spartak Merdschanov und Kamen Christov danke ich für ihre herzliche Freundschaft und die Treue, über Jahre hinweg bei jedweder Feldarbeit mitzuhelfen und bis and die Grenzen der Kräfte zu gehen, um die Projekt durchzuführen. Ivailo Borrisov, Antoaneta Gueorguieva, Dessislava Harizanova, Todor Troanski, Nikolai Simov und Stanimira Staneva danke ich für die Hilfe im Feld, viele Diskussionen und die nette gemeinsame Zeit. Ein herzliches Dankeschön geht an Boyan Petrov für logistische Unterstützung, ein offenes Ohr und praktische Hilfe in Notlagen und seine Freundschaft. Eleonora Dimanova, oder einfach „Lelja Nora“ gilt der herzlichste Dank für die liebevolle Aufnahme in ihre Familie, das Verpflegen mit bulgarischen Köstlichkeiten, das geduldige Beibringen der bulgarischen Sprache, den eleganten Einsatz von Händen und Füßen zum Erklären selbst komplizierter Sachverhalte, ihr Verständnis für die Merkwürdigkeiten der Fledermausforschung, ihre Begeisterung für technische Spielereien und ihre Liebe.

Prof. Dr. Otto von Helversen, Dietmar Nill, Eleni Papadatou und Torsten Pröhl danke ich für ihre Hilfe bei Feldaufenthalten in Griechenland, Otto von Helversen für die scharfsinnigen und spitzfindigen Diskussionen, die für ein kritisches Hinterfragen des eigenen Wissens und der Daten so wichtig sind, Dietmar Nill für Tipps und Tricks rund ums Fotografieren, Eleni Papadatou für das Besorgen von Genehmigungen in Griechenland und das Zeigen von Quartieren und für ihr Lachen, und Torsten Pröhl einfach dafür, dass er in allen Lebenslagen so fröhlich ist und so eine nette unbeschwerte Art des Reisens hat.

Eran Levin, Kathy Meakin, Ladousine Oussouilh, Prof. Dr. Samy Zalat und Francis Gilbert danke ich für die Begleitung bei Fangexkursionen in Israel, Marokko und Ägypten, das Organisieren von Genehmigungen und ihre Begeisterung für Fledermäuse.

Den Mitgliedern des Lehrstuhls für Tierphysiologie der Uni Tübingen danke ich für ihre Freundschaft, das Aushalten zahlreicher frecher Sprüche und anderer Nettigkeiten, die vielen guten Diskussionen und die Hilfe in kleinen und großen Nöten.

Dr. Peter Pilz und Klemen Koselj danke ich für viele gute Anregungen zur Statistik und zur Datenerhebung, Klemen Koselj insbesondere für seine kritischen Nachfragen und berechtigte Zweifel an anekdotischen Feldbeobachtungen.

Ein herzliches Dankeschön geht an meine Zimmergenossinnen Andrea Schaub und Wiebke Pflästerer dafür, dass sie trotz weitgehender Abwesenheit meinerseits den Schreibtisch freigehalten haben und immer für Blödsinn, Spinnereien, eine fröhliche Lästerrunde und technische Neuerungen aller Art zu haben waren. Als ebenbürtige Sparringspartner im gegenseitigen Austausch zynisch-sarkastischer Freundlichkeiten vermisse ich Euch jetzt schon!

Für die stetige Unterstützung in vielerlei Hinsicht geht mein herzlicher Dank an meine Eltern Christine und Ludwig Dietz; für die zeitraubenden und umfassenden Reparaturen des VW-Busses vor und nach jeder Feldsaison bedanke ich mich bei meinem Schwiegervater Alfons Schunger und meinem Schwager Tony Schunger – ohne Euch wäre Vieles nicht möglich gewesen!

Ganz besonderer Dank gilt meiner Frau Isabel Dietz für ihre beständige Kameradschaft, ihre fortwährende Begeisterung zur Feldarbeit und ihre Fröhlichkeit, die sich weder durch die dumpfe Hitze oder die immer hungrigen Schnakenschwärme des Donautieflandes, noch durch Autopannen in der Türkei oder Marokko, Dauerregen in Griechenland oder den für das Sommerhalbjahr üblichen Schlafmangel verringert hat. Herzlichen Dank für die immer gute Laune, Rundumversorgung in allen Lebenslagen, zahllose Ideen, stetigen Rückhalt, das Zurückholen auf den Boden der Tatsachen, wann immer nötig, oder einfach dafür, dass es Dich gibt!

Die Arbeit wurde durch die Graduiertenförderung des Landes Baden-Württemberg und die Rheinhold-und-Maria-Teufel-Stiftung gefördert.

Lebenslauf

Christian Dietz

geboren am 15.07.1974 in Tübingen
verheiratet seit dem 03.11.2005 mit
Isabel Dietz, geb. Schunger

Schulbildung

1981-1994	Besuch der Gutermann-Grundschule in Horb und des Martin-Gerbert-Gymnasiums in Horb. Abitur am Martin-Gerbert-Gymnasium in Horb.

Studium

1994-1995	Studium der Fächer Biologie und Chemie an der Eberhard Karls Universität Tübingen.
1995-2000	Studium der Fächer Biologie und Geographie an der Eberhard Karls Universität Tübingen.
2000	1. Staatsexamensarbeit „Untersuchung von Brücken und Wasserdurchlässen als Fledermausquartiere im Jahresverlauf" bei Prof. Dr. E. Müller.

Promotion

2001-2005	Promotion am Lehrstuhl für Tierphysiologie bei Prof. Dr. H.-U. Schnitzler und Dr. B. Siemers.

beruflicher Werdegang

2005-2007	Referendariat am Staatlichen Seminar für Didaktik und Lehrerbildung (Gymnasien) in Tübingen in den Fächern Biologie und Geographie. Zusatzausbildung für das Fach Naturwissenschaften und Technik.
2005-2006	Referendar im 1. Ausbildungsabschnitt am Eugen-Bolz-Gymnasium Rottenburg. 2. Staatsexamensarbeit „Humanevolution in der Kursstufe".
2006-2007	Referendar im 2. Ausbildungsabschnitt am Gymnasium Haigerloch und 2. Staatsexamen.
seit 2007	Studienassessor am Gymnasium Haigerloch.