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Towards navigating the Minotaur's labyrinth: cryptic diversity and taxonomic revision within the speciose genus *Hipposideros* (Hipposideridae)

NICOLE M. FOLEY[1], STEVEN M. GOODMAN[2, 3], CONOR V. WHELAN[1], SEBASTIEN J. PUECHMAILLE[1, 4], and EMMA TEELING[1, 5]

[1]*School of Biology and Environmental Science, University College Dublin, Belfield, Dublin 4, Ireland*
[2]*Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL, USA*
[3]*Association Vahatra, BP 3972, Antananarivo 101, Madagascar*
[4]*Applied Zoology and Nature Conservation, Greifswald University, Greifswald, Germany*
[5]*Corresponding author: E-mail: emma.teeling@ucd.ie*

Recent molecular evidence has shown that the largest genus of the family Hipposideridae, *Hipposideros*, is paraphyletic with respect to *H. commersonii* sensu lato and *H. vittatus*, both belonging to a species complex referred to as the *commersonii* group. The taxonomic issues at the generic level of certain species of *Hipposideros* remain unresolved in part related to insufficient material in previous molecular studies. Herein, we expand sampling of the *commersonii* group and include *H. commersonii* sensu stricto from its type locality, Madagascar. Our phylogenetic analysis revealed that the *commersonii* group forms a highly supported monophyletic clade with *H. cyclops*, which is sister taxa to *Aselliscus* and *Coelops*. A combination of phylogenetic and comparative morphological analyses, as well as divergence time estimates, were used to provide compelling evidence to support the placement of the clade containing the *commersonii* group and that with *H. cyclops* in two resurrected genera, *Macronycteris* and *Doryrhina*, respectively. Divergence time estimates indicated that *Macronycteris* and *Doryrhina* diverged 19 mya and separated from *Coelops* and *Aselliscus* in the Oligocene, about 31 mya. The *commersonii* group underwent a rapid radiation as recently as 3 mya likely in response to favourable climatic conditions during the Late Pliocene in Africa. Phylogenetic analysis of Cyt-*b* could not resolve relationships within this morphologically conserved complex. Further sampling is necessary to fully elucidate the evolutionary history of *Doryrhina*. Given that cryptic species are widespread among bats, including within the genus *Hipposideros*, this study highlights the shortcomings of current chiropteran taxonomy to describe hidden diversity.

Key words: cryptic diversity, taxonomy, *Doryrhina*, *Macronycteris*, *Hipposideros*, phylogeny, molecular clock dating

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A taxonomic revision of the *Kerivoula hardwickii* complex (Chiroptera: Vespertilionidae) with the description of a new species

Hao-Chih Kuo[1, 6], Pipat Soisook[2], Ying-Yi Ho[3], Gabor Csorba[4], Chun-Neng Wang[1], and Stephen J. Rossiter[5]

[1]*Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei 10617, Taiwan*
[2]*Princess Maha Chakri Sirindhorn Natural History Museum, Faculty of Science, Prince of Songkla University, Hat Yai, Songkhla 90112, Thailand*
[3]*Department of Biological Sciences, National Sun Yat-sen University, Kaohsiung 80424, Taiwan*
[4]*Department of Zoology, Hungarian Natural History Museum, Baross u. 13, H-1088 Budapest, Hungary*
[5]*School of Biological and Chemical Sciences, Queen Mary University of London, London E1 4NS, United Kingdom*
[6]*Corresponding author: E-mail: haochih.kuo@gmail.com*

Since its discovery, the taxonomic status of the only species of *Kerivoula* (Chiroptera: Vespertilionidae: Kerivoulinae) to be found on Taiwan has been confused. Previous studies have assigned this species to either *Kerivoula hardwickii* or *K. titania*, both of which occur on continental SE Asia. This uncertainty supports repeated suggestions in the literature that specimens of *K. hardwickii* collected and/or sampled across SE Asia are likely to represent multiple cryptic taxa. To address these issues, we combined new and existing data from the genus *Kerivoula* on Taiwan and continental Asia, and performed diagnostic analyses in steps. First, phylogenetic reconstructions based on mitochondrial and nuclear DNA revealed a well-supported group comprising all taxa currently recognized as *K. hardwickii*, together with the Taiwanese *Kerivoula* and *Kerivoula kachinensis* to the exclusion of all other congeneric species. Second, focusing on all members of this monophyletic clade (i.e., *K. hardwickii* complex) together with *K. titania*, we used multivariate statistical methods to separate taxa based on morphometric data. Our results provide strong evidence that among these bats, the Taiwanese *Kerivoula* is a new species that also occurs on continental Asia, for which we provide a formal description and name. In addition, we show that the subspecies *K. hardwickii depressa* should be elevated to species status. We discuss our findings and the caveats of this and similar studies.

Key words: *Kerivoula*, new species, systematics, taxonomic revision, woolly bats

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Comparative chromosomal studies in *Rhinolophus formosae* and *R. luctus* from China and Vietnam: elevation of *R. l. lanosus* to species rank

Marianne Volleth[1, 10], Nguyen Truong Son[2], Yi Wu[3], Yuchun Li[4], Wenhua Yu[3], Liang-Kong Lin[5], Satoru Arai[6], Vladimir Trifonov[7], Thomas Liehr[8], and Masashi Harada[9]

[1]*Department of Human Genetics, Otto von Guericke University, Leipziger Strasse 44, 39120 Magdeburg, Germany*
[2]*Department of Vertebrate Zoology, Institute of Ecology and Biological Resources and Graduate University of Sciences and Technology, Vietnam Academy of Sciences and Technology, 18 Hoang Quoc Viet, Cau Giay, Hanoi, Vietnam*
[3]*College of Life Sciences, Guangzhou University, 230 Wei Huan Xi Road, Guangzhou, 510006, China*
[4]*Marine College, Shandong University, Weihai, 264209, China*
[5]*Laboratory of Wildlife Ecology, Department of Biology, Tunghai University, No. 1727, Sec. 4. Taiwan Boulevard, Xitun District, Taichung 40704, Taiwan*
[6]*Infectious Disease Surveillance Center, National Institute of Infectious Diseases, Toyama 1-23-1, Shinjuku, Tokyo 162-8640, Japan*
[7]*Institute of Human Genetics, Jena University Hospital, Friedrich-Schiller University, Kollegiengasse 10, 07743 Jena, Germany*
[8]*Institute of Molecular and Cellular Biology, Siberian Branch of RAS, 8 Ac. Lavrentieva Avenue, Novosibirsk 630090, Russia*
[9]*Laboratory Animal Center, Graduate School of Medicine, Osaka City University, Abeno, Osaka 545-8585, Japan*
[10]*Corresponding author: E-mail: Marianne.Volleth@med.ovgu.de*

For the majority of *Rhinolophus* species a karyotype consisting of either 58 or 62 chromosomes was reported. The members of the *R. trifoliatus* clade are therefore distinguished from other rhinolophids by low diploid chromosome numbers (2*n*) and a high rate of chromosomal changes. Recently, based on cytogenetic characters, a cryptic species, *R. luctoides*, was described and a subspecies, *R. luctus morio*, was elevated to species rank. In the present work, the karyotypes of a male bat from Vietnam and a female one from China, both classified as *R. luctus* by morphological characters, were studied by G-banding and fluorescence in situ hybridization with whole chromosome painting probes derived from *Aselliscus stoliczkanus*. In the male specimen from Vietnam, the composition of the 15 autosomal bi-armed pairs (2*n* = 32, FN = 60) is identical to that of *R. luctoides* from Malaysia. For reason of differences in body size and baculum length as well as in skull morphology, this specimen is provisionally treated as *R*. cf. *luctoides*. The karyotype of the female specimen from Sichuan province, China, differs from *R. luctoides* by a whole arm reciprocal translocation resulting in an altered arm composition of pairs 3 and 4. For this reason, the elevation of the Chinese subspecies of *R. luctus*, i.e. *R. lanosus*, to species rank is suggested. The karyotype of the endemic Taiwanese species *R. formosae* with a diploid number of 2*n* = 52 is mainly composed of acrocentric autosomal pairs. Of the five bi-armed pairs, only the two smallest show the same arm composition as found in the 2*n* = 32 karyotypes of other members of the *R. trifoliatus* clade. The composition of the remaining three bi-armed pairs is unique and represents an apomorphic feature for *R. formosae*.

Key words: karyotype, fluorescence in situ hybridization, *Rhinolophus lanosus*

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A review of the bacular morphology of Malagasy bats

CLAUDE FABIENNE RAKOTONDRAMANANA[1, 2] and STEVEN MICHAEL GOODMAN[2, 3, 4]

[1]*Mention Zoologie et Biodiversité Animale, Université d'Antananarivo, BP 906, Antananarivo 101, Madagascar*
[2]*Association Vahatra, BP 3972, Antananarivo 101, Madagascar*
[3]*Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605, USA*
[4]*Corresponding author: E-mail: sgoodman@fieldmuseum.org*

We present information on the morphological structure and measurements of the os penis for eight families and 28 species of bats occurring on Madagascar, most being endemic to the island. For one of these families, Miniopteridae, no bacular structure was found and for a second family, Emballonuridae, the structure was absent in one species (*Taphozous mauritianus*). For the majority of taxa, the descriptions and measurements given herein of their respective bacula are presented for the first time in the published literature. In cases when samples are sufficient for certain species, we examine intra-specific variation in bacular morphology. For species the subject of previous published phylogeographical studies and which showed clade structure associated with elevational or latitudinal clines, we investigate if intra-specific differences in bacular structure are correlated with clade associations. We examine possible correlates associated with os penis measurements and, in general, across all species or within certain families, there was not a clear correlation between body size, as measured by forearm length, and different bacular measurements.

Key words: intra-specific, inter-specific, Madagascar, os penis, variation

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Morphometric patterns of secondary sexual dimorphism and seasonal differences in *Rousettus madagascariensis* from northern Madagascar

Steven M. Goodman[1, 2, 4], Faneva I. Rajemison[2, 3], and Olivà S. Noroalintseheno Lalarivoniaina[2, 3]

[1]*Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, Illinois 60605, USA*
[2]*Association Vahatra, BP 3972, Antananarivo 101, Madagascar*
[3]*Département de Biologie Animale, Université d'Antananarivo, BP 906, Antananarivo 101, Madagascar*
[4]*Corresponding author: E-mail: sgoodman@fieldmuseum.org*

On the basis of four visits to the Grotte des Chauves-souris (12°57'S, 49°07'E), Parc National d'Ankarana, northern Madagascar, we examine patterns of sexual dimorphism and seasonal differences in body mass of *Rousettus madagascariensis*, an endemic Malagasy Pteropodidae. Two visits per season were made over the course of two years, dry season (September 2014 and 2015) and rainy season (January 2015 and 2016). Individuals of this species were trapped when exiting the cave after dusk or entering before dawn. Animals were aged, sexed, and then individually marked before being released. In total, 271 adult males and 289 adult females were captured. Although some overlap was found in measurement ranges, males showed significantly larger mean forearm length and body mass than females, including separate analyses of the four different capture periods and in the combined season dataset. For the September 2015 visit, for which a considerable number of adults of both sexes were captured at dusk and dawn, animals entering the cave before dawn were significantly heavier in body mass than those exiting after dusk. When body mass data were pooled within a season, significant differences were found between the rainy and dry seasons in males, as well as females, indicating fluctuating aspects. Further analyses of intra-season and inter-season showed differences in body mass, presumably associated with the availability of fruit resources. Further, the sex ratios of captured individuals were not equal during different capture sessions and inferences are presented on aspects of the breeding biology of this species.

Key words: *Rousettus madagascariensis*, morphometrics, secondary sexual dimorphism, Madagascar

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How does Africa's most hunted bat vary across the continent? Population traits of the straw-coloured fruit bat (*Eidolon helvu*m) and its interactions with humans

Alison J. Peel[1, 2, 3, 18], James L. N. Wood[1], Kate S. Baker[1, 2], Andrew C. Breed[4], Arlindo de Carvalho[5], Andrés Fernández-Loras[2], Harrison Sadiki Gabrieli[6], Guy-Crispin Gembu[7], Victor A. Kakengi[8], Potiphar M. Kaliba[9], Robert M. Kityo[10], Tiziana Lembo[11], Fidel Esono Mba[12], Daniel Ramos[13], Iñaki Rodriguez-Prieto[14], Richard Suu-Ire[15, 16], Andrew A. Cunningham[2], and David T. S. Hayman[1, 2, 17]

[1]*Department of Veterinary Medicine, University of Cambridge, Cambridge, CB3 0ES, United Kingdom*
[2]*Institute of Zoology, Zoological Society of London, Regent's Park, London, NW1 4RY, United Kingdom*
[3]*Environmental Futures Research Institute, Griffith University, Brisbane, Queensland, 4111, Australia*
[4]*Animal and Plant Health Agency (APHA), Addlestone, Surrey, KT15 3NB, United Kingdom*
[5]*Direção Geral de Ambiente, Avenida Kwame Krhuma-Caixa Postal 1023, São Tomé, São Tomé e Príncipe*
[6]*Tanzania Veterinary Laboratory Agency (TVLA), Ministry of Livestock Development and Fisheries (MLDF), P.O. Box 1026, Tanga, Tanzania*
[7]*Faculté des Sciences, Université de Kisangani, Kisangani, République Démocratique du Congo*
[8]*Tanzania Wildlife Research Institute, Box 661, Arusha, Tanzania*
[9]*Museums of Malawi, P.O. Box 30360, Chichiri, Blantyre 3, Malawi*
[10]*College of Natural Sciences, School of BioSciences, Department of Biological Sciences. Makerere University, P.O. Box 7062, Kampala, Uganda*
[11]*Institute of Biodiversity, Animal Health and Comparative Medicine, College of Medical, Veterinary and Life Sciences, University of Glasgow, Graham Kerr Building, Glasgow, G12 8QQ, Scotland*
[12]*Instituto Nacional de Desarrollo Forestal y Manejo del Sistema de Áreas Protegidas (INDEFOR-AP), Calle Jesús Bakale S/N, Bata, Equatorial Guinea*
[13]*Parque Natural do Príncipe, Avenida Amilcar Cabral, Cidade de Santo António, Ilha do Príncipe, São Tomé e Príncipe*
[14]*Department of Evolutionary Ecology, Museo Nacional de Ciencias Naturales, CSIC 28006 Madrid, Spain*
[15]*Wildlife Division, Ghana Forestry Commission, Accra, Ghana*
[16]*Faculty of Animal Biology and Conservation Science, University of Ghana, Box LG 571, Legon, Accra, Ghana*
[17]*Molecular Epidemiology and Public Health Laboratory, Hopkirk Research Institute, Massey University, Private Bag, 11 222, Palmerston North 4442, New Zealand*
[18]*Corresponding author: E-mail: alisonpeel@gmail.com*

The straw-coloured fruit bat, *Eidolon helvum*, is a common and conspicuous migratory species, with an extensive distribution across sub-Saharan Africa, yet hunting and habitat loss are thought to be resulting in decline in some areas. *Eidolon helvum* is also a known reservoir for potentially zoonotic viruses. Despite *E. helvum*'s importance, ecological and behavioural traits are poorly described for this species. Here we present extensive data on the distribution, migration patterns, roost size, age and sex composition of 29 *E. helvum* roosts from nine countries across tropical Africa, including roosts not previously described in the literature. Roost age and sex composition were dependent on timing of sampling relative to the annual birth pulse. Rather than a single 'breeding season' as is frequently reported for this species, regional asynchrony of reproductive timing was observed across study sites (with birth pulses variably starting in March, April, September, November or December). Considered together with its genetic panmixia, we conclude that the species has a fluid, fission-fusion social structure, resulting in different roost 'types' at different times of the year relative to seasonal reproduction. Bat-human interactions also varied across the species' geographical range. In the absence of significant hunting, large urban colonies were generally tolerated, yet in regions with high hunting pressure, bats tended to roost in remote or protected sites. The extensive quantitative and qualitative data presented in this manuscript are also valuable for a wide range of studies and provide an historical snapshot as its populations become increasingly threatened.

Key words: age composition, demography, fission-fusion, hunting, straw-coloured fruit bat

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The bat fauna from southwestern Brazil and its affinities with the fauna of western Amazon

VALÉRIA DA C. TAVARES[1, 2, 5], CARLA C. NOBRE[2], CESAR F. DE S. PALMUTI[3], EDUARDO DE P. P. NOGUEIRA[3], JOSIMAR D. GOMES[3], MARCELO H. MARCOS[3], RICARDO F. SILVA[3], SOLANGE G. FARIAS[3], and PAULO E. D. BOBROWIEC[4]

[1]*Programa Nacional de Pós-Doutorado (PNPD) CAPES, Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais (UFMG), Belo Horizonte, MG, 31270-901, Brazil*
[2]*Programa de Pós-graduação em Zoologia, Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais (UFMG), Belo Horizonte, MG, 31270-901, Brazil*
[3]*Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais (UFMG), Belo Horizonte, MG, 31270-901, Brazil*
[4]*Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia (INPA), Av. André Araújo 2936, CP 2223, Manaus, AM, 69080-971, Brazil*
[5]*Corresponding author: E-mail: val.c.tavares@gmail.com*

Historically for bats, the southwestern Brazilian Amazon has had scant biological data available, which compromised large-scale comparisons and macroecological studies that could support conservation initiatives in the area. We tested faunal similarity among 26 well-sampled bat assemblages distributed throughout the Amazon, including our database from surveys in the upper Madeira River region, a core area of the southwestern Brazilian Amazon. To document bats we conducted nocturnal mist-net sampling under standardized Rapid Assessments for Long-term Ecological Research (RAPELD) protocols in forests and farmlands, and diurnal search of roosts in rocky outcrops located along the riverbed of the Madeira River. We captured 2930 bats representing 66 species, 20 of which were previously unreported for the region. Thirty-four species recorded were exclusive to forests, and two to the rocky outcrops of the Madeira River. Frugivores outnumbered the other trophic guilds, followed by the gleaning insectivores in forests, and then aerial insectivores in the farmlands. The southwestern Brazilian Amazon fauna is more similar to others from the western Amazon and less similar to the bat fauna from the eastern Amazon and the Guianas. This geographic association is undoubtedly related to a more recent history of formation of the terrestrial ecosystems of the western Amazon lowlands. With 87 species currently known, the southwestern Brazilian Amazon is now one of the richest areas in the world for bats, which helps to understand the limits of the distributional patterns between eastern and western Amazon bat faunas.

Key words: diversity, biogeography, Neotropics, rocky outcrop bats, conservation hotspots, RAPELD, species distribution

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Population trends of cave-dwelling bats in the Eastern Iberian Peninsula and the effect of protecting their roosts

Marjorie Carolina Machado[1, 4], Miguel Angel Monsalve[2], Antonio Castelló[3], David Almenar[3], Antonio Alcocer[3], and Juan Salvador Monrós[1]

[1]*Institute Cavanilles of Biodiversity and Evolutionary Biology, University of Valencia, Calle Catedrático José Beltrán Martínez, nº 2, 46980 Paterna, Valencia, Spain*
[2]*Servicio de Vida Silvestre, VAERSA-Generalitat Valenciana, Los Pinares, nº 106, 46012 El Saler, Valencia, Spain*
[3]*CADEC, Taller de Gestión Ambiental S.L., Carrer de Benaguasil, nº 19, 46015 Valencia, Spain*
[4]*Corresponding author: E-mail: marjomachado@hotmail.com*

Populations trends of cave-dwelling bats in the Eastern Iberian Peninsula and the effect of placing a perimeter fencing around their roosts (to avoid human disturbance on breeding colonies) were evaluated from 1997 to 2014. The species with the highest relative abundance was *Miniopterus schreibersii* (62.4%), followed by *Myotis myotis*/*blythii* (18%), and both populations showed positive trends. On the other hand, *Myotis capaccinii* (6.2%), *M. escalerai* (4.8%) and *M. emarginatus* (0.9%) showed significant, but minor increases, particularly in recent years. *Rhinolophus mehelyi* (0.2%) displayed no significant trends, while a moderate population decline was recorded for *R. euryale* (5.1%). *Rhinolophus ferrumequinum* (2.2%) and *R. hipposideros* (0.1%) showed positive growth trends. The main assemblages in the evaluated roosts were formed by *Myotis myotis*/*blythii*, *Miniopterus schreibersii* and *R. ferrumequinum*. This denotes their less specific requirements or greater flexibility when selecting roosts, compared with other species, except for *M. capaccinii* and *R. mehelyi*. No significant differences were found between roosts with different levels of protection, but there were positive trends in the protected roosts. Most non-fenced cavities showed negative trends during the period evaluated. We did not rule out other factors, such as requiring habitats with optimum food sources next to maternal roosts, which could affect population growth. The selectivity of some species of bats for certain caves will be essential for the preparation of management plans for certain roosts. Four of the seven risk factors documented for European bats affect studied population. *Myotis blythii*, *M. myotis* and *Rhinolophus euryale* would be most affected by a reduction in the areas they currently occupy.

Key words: assemblages, cave-dwelling bats, mediterranean, monitoring, perimeter fencing, roosts

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Small in size but rich in bats — species diversity and abandoned man-made structures put Asinara Island (Sardinia) into conservation focus for bats in the Mediterranean region

Rebecca Winter[1, 4], Mauro Mucedda[2], Ermanno Pidinchedda[2], Uwe Kierdorf[1], Sabine Schmidt[3], and Jasmin Mantilla-Contreras[1]

[1]*Department of Biology, University of Hildesheim, Universitätsplatz 1, 31141 Hildesheim, Germany*
[2]*Centro Pipistrelli Sardegna, Via Giacomo Leopardi 1, 07100 Sassari, Italy*
[3]*Institute of Zoology, University of Veterinary Medicine Hannover, Foundation, Bünteweg 17, 30559 Hannover, Germany*
[4]*Corresponding author: E-mail: winterebecca@web.de*

During the last decades, the important role of bats in ecosystems and the threats to many bat species were increasingly recognized, and bats were integrated into several conservation acts. Protected areas like national parks may play a major role in bat conservation if species requirements are included in management plans. With its high bat diversity and many unexplored off-shore islands, Sardinia has a high potential for the protection of European bats and for research on their ecology. We conducted the first survey of the bat fauna on the Sardinian off-shore island and National Park Asinara, a formerly inhabited island. We applied a multi-method approach over two years to create a proper species inventory and to obtain data on the use of man-made structures by the bats. We recorded bat calls at different sites in summer and winter, captured bats via mist-netting, and performed roost surveys of man-made structures. Ten species were identified, three of them are highly protected, namely *Rhinolophus hipposideros*, *R. ferrumequinum* and *Miniopterus schreibersii*. Thirty-nine day roosts and 14 night roosts of, in total, five species were found in man-made structures. Many structures provided day and night roosts for different bat species. Although forest and water bodies are limited, and intensive grazing has created several open areas on the island, a remarkably high bat diversity developed, making Asinara an important off-shore retreat area for bats in Italy. Our findings indicate an essential role of the abandoned buildings, and artificial ponds, of the island for bat conservation. The results of this study provide a basis for future bat conservation measures on Asinara Island.

Key words: bat conservation, Italy, off-shore islands, species inventory

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Evidence of the migratory bat, *Pipistrellus nathusii*, aggregating to the coastlines in the Northern Baltic Sea

Asko Ijäs[1, 5], Aapo Kahilainen[2], Ville V. Vasko[3], and Thomas M Lilley[4]

[1]*Brahea Centre, Centre for Maritime Studies, University of Turku, 28101 Pori, Finland*
[2]*Metapopulation Research Centre, Department of Biosciences, University of Helsinki, 00014 Helsinki, Finland*
[3]*Department of Biology, University of Turku, 20014 Turun yliopisto, Finland*
[4]*Biodiversity Unit, University of Turku, 20014 Turun yliopisto, Finland*
[5]*Corresponding author: E-mail: asko.ijas@gmail.com*

Similar to birds, bats also perform long-distance migration between their breeding and wintering sites. In Northern Europe, migratory bat species are often detected along the coastline of the Baltic Sea particularly during migration seasons in the spring and autumn. In spite of regular monitoring of bat migration at coastal sites, the overall distribution of migratory bats in Northern Europe and variability between sites and seasons are still very poorly known. In this study we used automated bat detectors to compare the activity of migratory bat species between coastal and inland monitoring sites along the west coast of Finland (61.5–61.9°N, 21.3−22.3°E). Our main goal was to test whether the activity of migratory bat species is associated with the coastline or whether these species also occur inland. Of migratory bat species observations, 98.6% were covered by *Pipistrellus nathusii*, which was detected at all our monitoring sites. The activity of the species decreased rapidly, with increasing distance from the coastline towards inland, indicating a sharp activity gradient along the coastline of the Baltic Sea. Because the activity of *P. nathusii* occurred in migration season and no similar spatial pattern was detected among sedentary species, our results suggest that the aggregation of *P. nathusii* at the coastline is related to migration as such rather than regular foraging behavior of this species. Our study has direct implications to the wind power planning in Northern Europe. Based on our study we conclude that the impact of wind power on both migratory (namely *P. nathusii*) and sedentary bat species (namely *Eptesicus nilssonii*) should be taken into account in wind power planning and impact mitigation in Northern Europe, especially if new wind farms are located along the coastline of the Baltic Sea. When the turbines are located further inland, more attention in the planning process should however be given to the sedentary bat *E. nilssonii*.

Key words: bat migration, acoustic monitoring, wind power, Finland

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Seasonal activity pattern and habitat use by the Isabelline serotine bat (*Eptesicus isabellinus*) in an arid environment of Tunisia

RIDHA DALHOUMI[1, 3], NICOLAS MORELLET[2], PATRICIA AISSA[1], and STÉPHANE AULAGNIER[2]

[1]*Laboratoire de Biosurveillance de l'Environnement, Faculté des Sciences de Bizerte, Université de Carthage, 7021 Zarzouna, Tunisie*
[2]*Comportement et Ecologie de la Faune Sauvage, Université de Toulouse, Institut National de la Recherche Agronomique, CS 52627, 31326 Castanet-Tolosan cedex, France*
[3]*Corresponding author: E-mail: ridhadalhoumi@gmail.com*

The seasonal activity of the Isabelline serotine bat *Eptesicus isabellinus* was studied in eight habitats of the Bou Hedma National Park, central Tunisia. From June 2010 to June 2011 two techniques, mist-netting and echolocation call recording, were implemented. This bat species was captured throughout the year but only at water bodies and particularly at Nouh basin. Captures peaked in late spring — early summer, and declined in winter. Pregnant females were captured from April to June, and lactating females in May and June. Echolocation calls were recorded throughout the year, but not every month in all habitats. Most activity was reported at water bodies and street lamps. Activity peaked in late spring and early autumn, and declined during winter period. Terminal buzzes were mainly detected at basins, peaking in late spring — early summer and early autumn. Our study provided further insights on the importance of water bodies which should draw particular attention in the management plan of the national park and in the whole country.

Key words: Chiroptera, Bou Hedma National Park, Tunisia, mist-netting, acoustic ecology, water bodies

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Description of whole-night activity patterns for Neotropical bat species

Caio Graco Zeppelini[1, 2, 6], Isabela Jerônimo[2], Karlla Morganna Costa Rego[3], Maria Paula Aguiar Fracasso[4], and Luiz Carlos Serramo Lopez[5]

[1]*Programa de Pós-Graduação em Ciências Biológicas, Departamento de Sistemática e Ecologia, Centro de Ciências Exatas e da Natureza, Universidade Federal da Paraíba, Cidade Universitária, s/n Castelo Branco, 58051-900 João Pessoa, Brazil*
[2]*Laboratório de Mamíferos, Departamento de Sistemática e Ecologia, Centro de Ciências Exatas e da Natureza, Universidade Federal da Paraíba, Cidade Universitária, s/n Castelo Branco, 58051-900 João Pessoa, Brazil*
[3]*PRODEMA (Programa Regional de Pós-Graduação em Desenvolvimento e Meio Ambiente), Universidade Federal da Paraíba, Cidade Universitária, s/n Castelo Branco, 58051-900 João Pessoa, Brazil*
[4]*Departamento de Engenharia e Meio Ambiente, Centro de Ciências Aplicadas e Educação, Universidade Federal da Paraíba, Rua da Mangueira, s/n Centro, 58297-000 Rio Tinto, Brazil*
[5]*Programa de Pós-Graduação em Ciências Biológicas, Departamento de Sistemática e Ecologia, Centro de Ciências Exatas e da Natureza, Universidade Federal da Paraíba, Cidade Universitária, s/n Castelo Branco, 58051-900 João Pessoa, Brazil*
[6]*Corresponding author: E-mail: czeppelini@gmail.com*

Nocturnal activity is a key factor in the success of bats, along with several other ecological characteristics of the group. Studying the activity patterns of bats can help to understand ecological and behavioural aspects of bat assemblies, especially in the Neotropics, where the group presents high species richness. The activity patterns of five species of Neotropical bats, sampled in a Reserve in the Brazilian Northeastern Region, were analysed. A general trend emerged, with an activity peak in the first half of the nocturnal observation. The overlap of activity patterns in closely related species (*Artibeus planirostris* and *A. lituratus*) agrees with previous findings that the nocturnal activity peaks in frugivorous bats have not evolved to relieve competition. The present work provides the first whole-night activity data for *Dermanura cinerea*. The results demonstrate the importance of whole-night sampling studies; not only as an opportunity to assess different ecological and behavioural data but also to efficiently register the abundance and richness of the assembly.

Key words: activity, Neotropics, Phyllostomidae, *Dermanura cinerea*, behaviour

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Social activity of lesser horseshoe bats (*Rhinolophus hipposideros*) at nursery roosts and a hibernaculum in North Wales, U.K.

MARGARET M. ANDREWS[1, 4], AMELIA M. HODNETT[2], and PETER T. ANDREWS[3]

[1]*Liverpool John Moores University, Byrom Street, Liverpool L3 3AF, United Kingdom*
[2]*Gavia Environmental, Perth, PH1 3FX, United Kingdom*
[3]*Department of Physics, Liverpool University, Liverpool L69 5BX, United Kingdom*
[4]*Corresponding author: E-mail: m.m.andrews@livjm.ac.uk*

To better understand the importance of social activity, ultrasonic calls made by lesser horseshoe bats (*Rhinolophus hipposideros*) in North Wales, U.K. were recorded during extended pre-set periods since 2010 inside and outside nursery roosts from May to July and in a hibernaculum in October. Ultrasonic calls with fundamental frequencies between 15–42 kHz were identified as seven categories of infant development calls and 15 categories of adult ultrasonic social calls according to the frequency and duration of the fundamental, the number of harmonics and the number of calls in a sequence. Activities were monitored remotely using infrared video cameras with simultaneous time expansion sound recorders. Distinctive polyharmonic isolation calls of newborn *R. hipposideros* enabled timing of births to be determined and infant echolocation marked the time when they started to fly. Trill advertisement calls in the hibernaculum indicated mating behaviour in October. Comparison of call-triggered recording times enabled variable levels of activity to be determined quickly. The longest sonogram times were in July (50.2 min/h) and in June (49.1 min/h). During these recordings, 95 and 90 adults returned to the roost after foraging and there were 16 and 42 babies, respectively. In May sound and video recordings outside a nursery roost revealed ultrasonic social calls during the emergence of 200 adult *R. hipposideros* when the light level was low at two lux, which showed that *R. hipposideros* were engaged in social activity, not light sampling. Surveys of ten nursery roosts showed that this social behaviour was typical of *R. hipposideros* in Wales.

Key words: lesser horseshoe bat, infant, ultrasonic, social calls, roosts

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Acoustic call library and detection distances for bats of Swaziland

ARA MONADJEM[1, 2, 3, 5], JULIE T. SHAPIRO[2], FEZILE MTSETFWA[1], APRIL E. RESIDE[4], and ROBERT A. MCCLEERY[2]

[1]*All Out Africa Research Unit, Department of Biological Sciences, University of Swaziland, Private Bag 4, Kwaluseni, Swaziland*
[2]*School of Natural Resources and Environment and Department of Wildlife Ecology and Conservation University of Florida, Newins-Ziegler Hall, Gainesville FL 32611, USA*
[3]*Mammal Research Institute, Department of Zoology & Entomology, University of Pretoria, Private Bag 20, Hatfield 0028, Pretoria, South Africa*
[4]*Centre for Biodiversity and Conservation Science, University of Queensland, Brisbane, Queensland 4072, Australia*
[5]*Corresponding author: E-mail: aramonadjem@gmail.com*

Bats are a critical component of most terrestrial systems, yet accurately assessing species richness and abundances remains a challenge. The use of acoustic monitoring has increasingly been used to assess bat communities. Compared with more traditional trapping surveys, acoustic monitoring is relatively easy to use and vastly increases the amount of data collected. However, the ability to accurately identify bat calls from acoustic detectors is limited by the availability of regional call libraries describing the calls of local species. Further, the lack of knowledge of detection distances for different species limits the ability to compare activity levels or abundances between species. We developed an echolocation call library based on zero-crossing recordings with Anabat Express detectors that can be applied broadly to bat acoustic detector surveys across the savanna systems of Swaziland and South Africa, and potentially the broader region of Southern Africa. We also compared detection distances for different species and provide a correction factor that will increase our ability to accurately compare activity between different species.

Key words: acoustic survey, Anabat, Chiroptera, bat call library, Swaziland, detection distance

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Within-site variability of field recordings from stationary, passively working detectors

CLAUDIA ELISA KUBISTA[1, 2] and ALEXANDER BRUCKNER[1]

[1]*Department of Integrative Biology and Biodiversity Research, Institute of Zoology, University of Natural Resources and Life Sciences, Gregor-Mendel-Strasse 33, A-1180 Wien, Austria*
[2]*Corresponding author: E-mail: claudia.kubista@boku.ac.at*

Passively working devices (with no operator input) that register bat calls in real time are very important in conservation and environmental risk assessment, but data on their performance and limits under field conditions are mostly missing. We characterized the recording variability among three batcorders placed in proximate vicinity (ca. 10 m apart) to each other at 157 sites in Austria (central Europe). We found this variability perplexingly high, both for bat activity and species richness estimates. Specifically, the ratio of the highest to the lowest total sequence length (all species combined) was over fivefold in 23%, and over tenfold in 8% of the sites. In only 17% of the sites, we found the same number of species for all three devices — in most sites it varied between one and five species. The maximum call ranges of the recorded bat species affected the recording variability between the devices only for short ranges (5 m) but showed similar or relatively low variability for longer ranges. There was significantly less recording variability in sites with no woody vegetation present than in sites with open to dense vegetation structure. The results clearly indicate that the common practice of deploying only one device per site and night very likely leads to several of the resident bat species being missed and produces unreliable activity estimates.

Key words: bat species, detection probability, ultrasound detectors, batcorder system, vegetation clutter

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Assessing bat roosts using the LiDAR system at Wind Cave Nature Reserve in Sarawak, Malaysian Borneo

NURSYAFIQAH SHAZALI[1], TEONG HAN CHEW[2], MOHD SHAHIR SHAMSIR[2], ROBERTA CHAYA TAWIE TINGGA[3], MOHD-RIDWAN A. R.[3], and FAISAL ALI ANWARALI KHAN[1, 4]

[1]*Department of Zoology, Faculty of Resource Science and Technology, Universiti Malaysia Sarawak, 94300 Kota Samarahan, Sarawak, Malaysia*
[2]*Department of Biosciences and Health Sciences, Faculty of Biosciences and Medical Engineering, Universiti Teknologi Malaysia, 81310 Skudai, Johor, Malaysia*
[3]*Centre for Pre-University Studies, Universiti Malaysia Sarawak, 94300 Kota Samarahan, Sarawak, Malaysia*
[4]*Corresponding author: E-mail: fanwaral@gmail.com*

Conventionally, bat roost counts and roost size estimation are potentially a disruptive, repetitive method and are time consuming. Introduction of the Light Detection and Ranging (LiDAR) scanning system, an optical remote sensing technology, for scientific purposes have open many research possibilities especially on cave wildlife surveys. Scanned images at high resolution provide new effective biological tools for assessing bat roosts inside caves on walls or ceiling in total darkness. LiDAR system was applied to census bats that roost in Wind Cave Nature Reserve, Sarawak, Malaysia, based on laser return intensity values from the images. Bats that roost in large clusters, specifically *Penthetor lucasi* were determined through automated counting using connected components labelling, a graph theory algorithm mostly used in image analysis applications. Roost surface area of bats species was calculated based on point clouds extracted and using simple trigonometry. Wind Cave was successfully modelled into three dimensional (3D) cave images with bats roosting inside the cave. The roost sites of bats in the cave were represented in coloured point clouds that represent the species. Through LiDAR images, bats in Wind Cave consisted of about 979 individuals of *P. lucasi* and 1,907 individuals of insectivorous bats from nine species representing four families. There is a positive correlation between group size and roost area. For every additional bat, roost area is expected to increase by an average of 1.75 m^2. Our result suggested that terrestrial LiDAR technology is capable of assessing bat roosts in their natural habitat to determine their roost size and number of individuals that roost in the cave. Terrestrial LiDAR application is most complementary when integrated with field surveys to produce more reliable outcomes which open up possibilities of effective conservation action plans.

Key words: cave mapping, Chiroptera, population count, roost pattern, roost survey, terrestrial laser scanning, 3D images

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The dynamics of Mediterranean horseshoe bat (*Rhinolophus euryale*, Chiroptera) gut microflora during hibernation

LENKA MALINIČOVÁ[1, 5], ĽUDMILA HREHOVÁ[1], EDITA MAXINOVÁ[1, 2], MARCEL UHRIN[1, 3], and PETER PRISTAŠ[1, 4]

[1]*Institute of Biology and Ecology, Faculty of Science, Pavol Jozef Šafárik University in Košice, Šrobárova 2, 04154 Košice, Slovakia*
[2]*Department of Zoology and Animal Cell Biology, Faculty of Science and Technology, University of the Basque Country, UPV/EHU, Barrio Sarriena s/n, 48940 Leioa, Bizkaia, Basque Country*
[3]*Department of Forest Protection and Wildlife Management, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Kamýcká 1176, CZ–165 21 Praha 6, Czech Republic*
[4]*Institute of Animal Physiology, Slovak Academy of Sciences, Šoltésovej 4–6, 04001 Košice, Slovakia*
[5]*Corresponding author: E-mail: lenka.malinicova@upjs.sk*

Hibernation is an extraordinary phenomenon evolved in many animals including some mammals, allowing them to survive unfavorable environmental conditions. This period represents a phase of fasting, which is known to affect the gut microflora in non-hibernating mammals. Since during hibernation the physiological parameters (e.g., body temperature) differ from values in non-hibernating individuals, the food starvation is not the only parameter affecting the gut microflora. However, little is known about gut microflora in hibernating mammals. This study is focused on the examination of the gut microflora of Mediterranean horseshoe bat (*Rhinolophus euryale*) during hibernation. Faecal samples were collected during the winter from November 2014 to March 2015 and subsequently subjected to cultivation, non-cultivation analyses and morphological examination. Cultivation analysis revealed that the numbers of total cultivable bacteria, enterobacteria and enterococci in the faecal samples decreased during the hibernation and restored to pre-hibernation numbers at the end of hibernation. Results of non-cultivation analysis showed time-dependent (but surprisingly almost not individual-specific) changes in the gut microflora and decrease in bacterial variability dependent on hibernation stage. Changes in microflora were accompanied by changes in faecal content identified by morphological analysis. Our results demonstrate that hibernation affects the gut microflora of bats in significant degree in both quantitative and qualitative scale.

Key words: hibernation, faeces, gut microflora, Chiroptera