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Bats

Edited by Heimo Mikkola

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Contributors

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Meet the editor

Heimo Mikkola received his PhD degree in Applied Zoology and Limnology from the University of Kuopio, Finland. Since 1988, he has been an adjunct Professor of the Eastern Finland University through which he has lately been a part-time visiting professor in the Kazakh National Agrarian University in Almaty lecturing on fisheries and aquaculture to Master's level students and on Green Biotechnology and Global Food Security to all university teachers. Before and in between his university career, he has worked abroad for well over 30 years in Africa, South America and Central and Southeast Asia mainly with the African Development Bank and Food and Agriculture Organization of the United Nations (FAO). During these years, he had an excellent free time opportunity to visit and study owls in over 130 countries of the world. Owl studies often took him to the best bat biotopes as well, and he started to collect data on bats eaten by owls. In 2014, he was given the title "Champion of Owls" in Houston, USA, mainly because of his six worldwide distributed and translated owl books.

Contents

Preface

Bats are the only mammals capable of self-powered flight and constitute more than 20% of living mammal species, and up to 110 bat species may coexist in the same ecological communities, a number that far exceeds that of any other mammalian group [1]. Bats diversified in the Early Eocene in response to an increase in prey diversity, and Eocene bat fossils have been found on most continents leaving the geographic origin a source of debate [1]. Despite their taxonomic and ecological diversity, modern bats (Order: Chiroptera) are almost exclusively nocturnal. The only other vertebrates that exploit niches for nocturnal flying predators are owls and nightjars.

My personal interest and experience with the world of bats follow closely my owl studies, which have taken me so far to 130 countries in all continents. When sleeping in a hammock on the roof of our research boat in the Colombian jungle, I was a little worried by the overhead circulating bats because in this area vampire bats are frequent visitors. However, I never had any problem because of the deplorable eating habits of these bats!

When searching for one of the rarest owls in the world, the Seychelles scops owl (*Otus insularis*), I saw a lot of Seychelles fruit bats (*Pteropus seychellensis*). These owls have a wing span of up to 1.7 m and weigh up to 900 g [2], making them to look like flying dogs and are more scary in the dark forest than the small vampire bats of South America.

When living in Abidjan, I often witnessed the invasion of up to 1 million straw-coloured fruit bats (*Eidolon helvum*) coming to harvest the city's fruit trees. It has been estimated that 3 million people have learned not only how to live with these creatures, but also how to hunt them, cook them in sweat stews and put them to use in West African voodoo ceremonies [3].

If one day I am able to return to Zambia, there is one more thing I must witness: the largest *Eidolon helvum* invasion in Africa. Over 10 million bats descend for 90 days from late October to mid-December into a small swamp forest in Kasanga National Park [4]. This is said to be the largest mammal migration on earth but is obviously only half of that compared to the Mexican free-tailed bat (*Tadarida brasiliensis*) migration in the New World! Some 20 million bats from San Antonio, Texas, move every year to winter in Mexico [5].

Bats have a poor image for the public at large. Partly because bats spend all day tucked away in places where they can't really be seen and come out at night and do strange things in strange ways. So, it is difficult for people to understand how they work and what they are doing. This book aims to improve the public image of the bat.

We have eight chapters on bats covering countries such as Algeria, Bulgaria, France, Pakistan, Poland, the UK and the USA and subjects ranging from acoustic monitoring of bat species for distribution and conservation purposes to bat-borne and bat-carried diseases, which cannot be taken lightly but should not be a reason for panic or to fear or even kill bats. With the added knowledge through this book, we should know how best to cope with bats, which need all our support in the changing environments and climates.

I want to thank the Publishing Process Manager Lada Božić for her time-consuming efforts to get all the authors to deliver their chapters after corrections. Without her active attitude, some important chapters would have been left out of the book.

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Chapter 1

Introductory Chapter: Bats Eaten by Owls

Heimo Mikkola

Additional information is available at the end of the chapter

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1. Introduction

Bats and owls are very popular hoppy and research subjects of nature loving people as shown by BatLife and Owler groups all around the world but what is the relation of bats and owls in the wild. An assessment of owl dietary studies and anecdotal accounts was made but the huge material (well over 10 million prey animals) is in print elsewhere [1]. However, the role played by owls in the mortality of Eurasian bats is shortly reviewed for this book.

2. Bat-eating owls

The owl diet studies revealed that most owls are sometimes eating the bats although none makes a living out of them as other prey are much easier to capture. Well-studied European owl species ate a total of 19,864 bats [1]. At least 49 bat species have been identified in the diet samples (**Table 1**).

Barn Owl *Tyto alba* and Tawny Owl *Strix aluco* have captured most of all bats (47.1 and 42.6%), and Long-eared Owl *Asio otus* comes next (7.3%). Short-eared Owl *Asio flammeus* and Eagle Owl *Bubo bubo* take similar amounts of bats (1.2 and 1.3% respectively). For Tengmalm's *Aegolius funereus*, Ural *Strix uralensis* and Little Owls *Athene noctua* bats were fairly rare prey item, with less than 0.1–0.4% of this material [1]. Scops Owl *Otus scops* and Pygmy Owl *Glaucidium passerinum* ate less than 10 bats, so they are not included in **Table 1**.

Bat species	**Weight of the bat species in g**	**No of owl species as predators**	**Percentage of the Total**
Pipistrellus pygmaeus	5.1	1/8	0.26
P.pygmaeus or *P.pipistrellus*	5.3	1/8	0.19
Pipistrellus pipistrellus	5.5	6/8	16.02
Myotis mystacinus	6.1	7/8	1.51
Myotis brandtii	6.5	3/8	0.87
Pipistrellus abramus	6.5	2/8	3.41
Murina huttoni	6.7	1/8	0.01
Rhinolophus hipposideros	6.9	4/8	1.07
Pipistrellus sp.	6.9	5/8	1.57
Murina hilgendorfi	7.0	1/8	0.02
Pipistrellus kuhlii	7.3	4/8	11.85
Hypsugo savii	7.5	3/8	0.10
Asellia tridens	8.0	3/8	0.27
Myotis nattereri	8.3	6/8	3.18
Myotis emarginatus	8.7	3/8	0.52
Myotis capaccinii	8.8	2/8	0.19
Plecotus auritus	9.3	6/8	3.19
Myotis petax	9.5	1/8	0.01
Myotis annectans	9.7	1/8	0.01
Barbastella barbastellus	9.7	3/8	2.46
Plecotus sp.	9.8	3/8	0.25
Rhinopoma microphyllum	10.0	2/8	0.05
Pipistrellus nathusii	10.2	4/8	0.82
Myotis bechsteinii	10.2	4/8	0.87
Plecotus austriacus	10.3	3/8	1.52
Myotis daubentonii	10.9	5/8	1.17
Nycteris thebaica	11.5	1/8	0.02
Eptesicus nilssoni	11.6	6/8	0.48
Miniopterus schreibersii	11.9	4/8	0.50
Myotis sp.	12.1	5/8	1.40
Rhinolophus blasii	12.5	1/8	0.02
Rhinolophus eyryale	12.9	3/8	0.27
Myotis dasycneme	13.2	2/8	0.25

Bat species	**Weight of the bat species in g**	**No of owl species as predators**	**Percentage of the Total**
Rhinolophus sp.	14.6	2/8	0.02
Rhinolophus bocharius	15.1	1/8	0.03
Nyctalus leisleri	16.0	2/8	0.16
Vespertilio murinus	16.6	5/8	9.82
Vespertilio sp.	16.8	1/8	0.01
Vespertilio sinensis	17.0	1/8	0.06
Rhinolophus mehelyi	17.6	1/8	0.01
Eptesicus sp.	18.5	1/8	0.01
Hesperoptenus sp.	18.8	1/8	0.01
Otonycteris hemprichii	19.0	3/8	0.40
Eptesicus bottae	20.5	3/8	0.17
Myotis blythii	21.3	5/8	1.64
Eptesicus serotinus	23.4	5/8	7.31
Rhinolophus ferrumequinum	23.5	3/8	0.93
Taphozous nudiventris	28.0	4/8	0.23
Nyctalus sp.	28.1	1/8	0.01
Nyctalus noctula	28.3	5/8	9.12
Myotis myotis	32.8	6/8	15.24
Tadarida teniotis	38.0	3/8	0.07
Nyctalus lasiopterus	40.1	2/8	0.02
Cynopterus sphinx	46.0	1/8	0.01
Scotophilus heathi	50.0	1/8	0.01
Rousettus leschenaulti	60.0	1/8	0.01
Rousettus aegyptiacus	135.0	2/8	0.49
Total number of bats eaten			**19,864**

Table 1. Occurrence of the bat species in increasing order of weight in the diet of eight most studied owls in Eurasia [1]. Bat weights from [2–10], as an average of values given. Sp. weight is the average of the species of that family. Owl diets included: *Aegolius funereus*, *Athene noctua*, *Asio otus*, *Tyto alba*, *Asio flammeus*, *Strix aluco*, *Strix uralensis* and *Bubo bubo*.

3. Bat prey species

Most commonly owls are taking *Pipistrellus pipistrellus* (16.0%), *Myotis myotis* (15.2%), *Pipistrellus kuhlii* (11.9%), *Vespertilio murinus* (9.8%), *Nyctalus noctula* (9.1%), and *Eptesicus serotinus* (7.3%), that is, six most eaten species make 70% of the material. All these mostly eaten

Figure 1. Eagle Owl has brought to its nest a *Rousettus aegyptiacus* ♀ with a sucking baby still alive when photo was taken in 2008. Courtesy of Ezra Hadad/prof. Motti Charter, Haifa, Israel.

bats weigh less than 33 g (**Table 1**). Rest of the numerous species represents less than 5% of each of this material, and bats heavier than 33 g represent only 0.6% of this material. None of the bat species are eaten by all eight European owl species but *Myotis mystacinus* is in the diet of seven out of eight owls, when *P. pipistrellus, M. myotis, M. nattereri, Eptesicus nilssoni* and *Plecotus auratus* are the prey of six owl species (**Table 1**). The heaviest bat species eaten by two owl species is 135 g weighing *Rousettus aegyptiacus* which is illustrated in **Figure 1** as a prey of the Eagle Owl.

4. Owl predation

Bats are captured by owls probably mainly during the periods of emergence or return from roosts, but owls are in general not well adapted for catching bats. An interesting calculation from the UK shows that the predation of birds (mainly owls) would account for about 11% of the annual mortality of bats despite the apparent low representation of bats in the diets of predatory birds [11]. Owls are regulated by the availability of their food, more bats there are in the territory more they can harvest, explaining why the bat predation is higher in the south. In Britain, bats comprised only 0.03% of prey taken by Barn Owl while in Morocco the percentage is 0.05% [11].

5. Bats can defend themselves

That bats could be dangerous if consumed whole is borne out by the report of the death of an Oriental Bay Owl *Phodilus badius* picked up dead disclosing the cause to be the wing bone of the bat protruding through the stomach [12]. In Poland, on its turn, a western barbastelle bat *Barbastella barbastellus* has been observed to attack an owl [13]. And in the same country, there is an interesting observation on a Tawny Owl trying to catch *Nyctalus noctula* in the air but the bat "hid in the predator's shadow" by flying very close behind it and waiting until the owl gave up hunting. Finally, the bat flew away safely after the owl ceased searching for the lost prey [14].

6. Conclusion

It is safe to conclude that owls prey on bats rarely and opportunistically, but also that bat aggregations could be a locally important food source for some species and individual owls during certain periods. Also, the decrease in the main prey (rodent) abundance can lead owls to expand their diet and include bats.

Further work is needed to evaluate the possible effects of owl predation on bat populations, and to determine the ecological and environmental dynamics between owl species and their main prey species. Owl predation on bats deserves future research also because on one hand, it might contribute to our limited knowledge on bats biodiversity and distribution, while on the other hand, it can sometimes represent an additional risk for small populations of endangered bats.

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Chapter 2

Comparison of Driving Transect Methods for Acoustic Monitoring of Bats

Aaron S. Hogue and Andrew T. McGowan

Additional information is available at the end of the chapter

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Abstract

Acoustic monitoring for bats along driving transects typically involves recording call sequences (bat passes) continuously while driving. While this offers benefits over other survey techniques, it also poses challenges, including background noise on recordings. An alternative approach that may rectify this involves conducting sampling at discrete points along each transect instead. We compared these methods using the same bat detector, along with an additional higher sensitivity detector to determine which method yields the highest amount and quality of data per unit of time. Results from 26 18 km transects, each sampled continuously and at 10 point count sites indicate that, with a lower sensitivity detector, the two methods yield a similar number of passes per minute, percent of passes identified to species, and species documented. The higher sensitivity bat detector could not be used for continuous sampling due to background noise. However, at point count sites, the higher sensitivity detector recorded 17 times more passes per minute, 44 times more passes identified to species, and documented nearly twice as many species. Thus, while both sampling designs appear comparable, for most applications, a higher sensitivity detector trumps sampling design.

Keywords: acoustic monitoring, bats, continuous sampling, point count sampling, driving transects

1. Introduction

1.1. Importance and status of bats

Bats are an extremely important part of ecosystems across the globe, providing a variety of ecological services such as pollination, seed dispersal, and regulation of insect populations [1–3].

Their role in many ecosystems is so vital that some have suggested using bats as bio-indicators [4]. As most bats are insectivorous, one of their most significant contributions lies in reducing vegetation damage from insect herbivory in native ecosystems [2, 5, 6]. This has profound economic and social ramifications for human civilization as well. One of the biggest challenges faced by humanity in the coming decades will be the production of enough food to feed a growing population without dramatic losses in habitat and biodiversity [7]. While bats alone will not solve this problem, by devouring large numbers of agricultural pests, these small flying mammals reduce crop losses, thereby enhancing food production on existing agricultural lands [3, 8]. This, in turn, provides significant economic benefits by saving farmers billions of dollars (in US dollars, [9, 10]).

In light of the value bats have to ecosystems and modern civilization, it should be of great concern that they face a growing array of threats. These include persecution, hibernacula damage and disturbance, loss of foraging and roosting habitat, pesticide exposure, and many others [4, 11]. The net effect of all these threats is that roughly a quarter of all bat species are threatened [12]. In North America, aside from habitat loss, two of the biggest emerging threats are White Nose Syndrome (WNS) and wind turbine facilities. WNS is caused by a fungal infection spread among bats in their winter hibernacula [13]. First observed at a hibernaculum in New York in 2006, WNS has since spread across eastern North America, killing millions of bats and wiping out entire populations in some cases [14, 15]. Similar threats may be posed by wind power. With the recent push toward renewable energy, many countries have seen a tremendous growth in the number of wind power facilities. While wind turbines vary widely in their impact on bats depending on their geographic location, in some parts of North American, turbine facilities are estimated to be killing bats in the hundreds of thousands annually [16, 17]. With the slow rate at which bats reproduce [18], these numbers could be devastating to bat populations over the long term. For these and many other reasons, extensive monitoring of the status of bat populations in all affected areas is needed. Given the highly variable and broad geographic distribution of these threats, effective techniques for systematically surveying bats across large geographic areas are needed.

1.2. Challenges in studying bats across large geographic areas

As nocturnal, flying mammals, bats are uniquely challenging animals to study. However, a variety of survey techniques have been developed to overcome many of these challenges, including mist nets, radio telemetry, and ultrasonic detectors [19–21]. While each technique has its own benefits and drawbacks, ultrasonic detectors (also known as "bat detectors") have proven to be a powerful tool for examining insectivorous bat species composition and habitat use, and are among the most widely utilized tools for these purposes [22, 23].

Aerial-foraging insectivorous bats, which constitute the majority of species globally, use echolocation to navigate and find insect prey [24]. They do so by periodically emitting a sequence of ultrasonic calls (sounds above the limit of human hearing, roughly 20 kHz) and listening for the echo [25]. Information provided in the returning echoes of these call sequences enable bats to discern a variety of factors such as size, shape, location, and movement of objects in the environment, all of which are crucial for navigation and acquiring prey [26]. Another important aspect of bat calls is that they typically differ between species, likely to ensure species have their own "bandwidth" to facilitate effective communication among conspecifics [27]. These differences between species mean ultrasonic detectors are not only valuable in recording the presence of bats, but also in enabling investigators to determine which species are present. Bat detectors offer many other advantages as well. They are also easily deployed, they do not disturb bats, they can be used in areas where mist netting is difficult or marginally effective, and if financial resources permit multiple detectors, they can be used to survey many sites simultaneously with limited personnel [22, 23, 28]. For these reasons, among many others, bat detectors remain one of the most popular tools for studying bats.

However, these devices are not without limitations. For instance, an individual detector placed at a single location can only provide data for one site. If one wishes to survey a large area or multiple habitats each night, numerous detectors would be needed. This can dramatically increase the cost of a project, placing it out of reach for many investigators [29].

One technique that may help overcome this problem is the use of transects [19, 30, 31]. By moving a single detector through different habitats, a larger area can be sampled each night compared to stationary approaches. While most transect studies have employed walking transects, they are constrained in the amount of area that can be sampled by the slow pace of walking. As bats can typically fly faster than a walking observer, no two call sequences recorded along a given transect can be viewed as independent of each other. Additionally, randomly and systematically sampling across numerous habitat types on a large geographic scale becomes exceedingly difficult in areas where most properties are privately owned and require permission to sample. Driving transects solve these problems [31–33].

While driving transects represent an important addition to the tools available for studying bats in the wild, several questions remain. Most previous studies have used continuous sampling. Continuous sampling involves leaving the detector recording while driving along the transect. Although this allows for data collection along the entire length of each transect, there are potential problems. For example, if habitat types vary along each transect (which is often the case in many modern mosaic landscapes), the types of statistical techniques that can be used to test predictions about habitat use with data collected continuously are limited. In addition, sounds from vehicle movements, including airflow over the microphone, may cause significant problems with the resulting audio files. These include constantly triggering the detector to record in the absence of bats or producing extensive background noise that prevents call sequences from being detectable or making it impossible for call analysis software to identify the species emitting the calls. One possible solution to these problems would be to restrict sampling to specific points along each transect at established intervals (point count sampling). While the latter have been used extensively in bird research [34, 35], they are rare for bats. Moreover, the absence of direct comparisons of these two methods makes it difficult to determine which sampling methodology is superior. The purpose of this study was to fill this void by comparing continuous versus point count sampling along the same driving transects using two detectors varying in microphone sensitivity. In particular, we assess whether the two types of detectors and methods are comparable in number of bat passes recorded per unit of time, percent of recorded bat passes able to be identified to species, and total number of species identified.

2. Methods

2.1. Bat detectors

We recorded bats using an EM3 EchoMeter (Wildlife Acoustics Inc., Maynard, MA, USA) fitted with a Garmin GPS device that stamps all call sequence recordings with the coordinates. Since the calls of most aerial foraging insectivorous bats are above 20 kHz [36], we set the minimum frequency to begin recording (trigger threshold) to 20 kHz. This minimizes false triggers by insects, road noise and other sounds. As bat call sequences typically last only few seconds, maximum time length for individual recordings was set to 3 s to ensure file sizes of recordings were easily managed by the call-analysis software (see below). To minimize triggering by indiscernible, distant, low intensity sounds, we set the threshold amplitude to 18 db. Lastly, to determine if detector microphone sensitivity influences whether, and to what extent, background noise during driving adversely impacts the number and quality of bat passes recorded, we decided to add a second detector known for being highly sensitive. We selected the miniMIC ultrasonic microphone (Binary Acoustic Technology Inc. Tucson, Arizona, USA). The miniMIC was connected to a Dell Venue tablet via USB and call sequences were recorded using Spectral Analysis, digital Tuning and Recording Software (SPECT'R, Binary Acoustic Technology Inc. Tucson, Arizona, USA). Settings were as described for the EM3.

2.2. Sampling location

The study was conducted in the states of Maryland and Delaware on the Delmarva Peninsula, which is located along the mid-Atlantic coast of the United States between the Atlantic Ocean and the Chesapeake Bay. The peninsula consists primarily of a mosaic of agriculture (48%) and forests (37%, mostly mixed hardwood-pine and loblolly pine—*Pinus taeda*—plantations) [37]. The remainder is comprised of coastal marshes and scattered suburban and urban developments [37].

2.3. Sampling protocol

We established 28 transects that were evenly spaced across the Delmarva Peninsula as described by McGowan and Hogue [38]. Each transect contained 10 sampling points spaced 2 km apart (in straight line distance) for a total of 280 sites. We restricted transects to 2 lane roads, and sampling points to the nearest safe roadside location to stop for sampling. We sampled each transect once between June and August of 2014, yielding a total of 28 sampling nights. Transects were selected randomly for sampling without replacement using the random number generator in R Statistical Software [39]. The direction of travel along each transect was also randomly chosen. Unfortunately, due to equipment failure, two transects had to be excluded from analyses, dropping our total sampling nights (and transects) to 26.

We sampled each transect for bats using two approaches: point count and continuous sampling. Point count sampling occurred for 12 min at each of the 10 sampling points along each transect. Continuous sampling was carried out by leaving the detectors to operate as we drove the vehicle at speeds of 32–48 km/h along the transect between point count sites. We sampled each transect during peak bat activity, beginning 30 min after sunset and continuing until the transect was completed several hours later. For the continuous approach, we allowed the EM3 and miniMIC to operate atop a telescoping pole connected to the vehicle at a height of 2 m while we drove between sampling points. This allowed the detectors to be at a moderately elevated height while preventing damage from overlying bridges and road signs. Upon arriving at sampling points, we stopped the vehicle and extended the pole to 4 m and recorded for 12 min. We then collapsed the pole and drove the transect until reaching the next sampling point, repeating the process until all 10 points were sampled. In all cases, the detectors were pointed toward the immediately adjacent habitat to the right the road. Following recommendations of previous studies, we restricted sampling to nights without rain, temperatures above 10°C, and wind speeds less than 20 km/h [21, 40]. Call sequences recorded while driving were allocated to the continuous sampling data pool. Those recorded within the 12 min at each site were allocated to the point count sample. In total, we logged 52 h of recording time at stationary sampling points and just over 27 h from continuous sampling.

2.4. Analyses

We defined a bat pass as a sequence of one or more echolocation calls with <1 s between sequential calls [24]. Based on currently available technology, researchers are not able to distinguish individual bats of the same species from their calls. As a result, it is not possible to determine the absolute number of bats at a given location with bat detectors [19, 41]. Instead, the number of bat passes may be viewed as a measure of overall bat activity rather than number of individuals [19, 41]. We attempted to identify all bat passes to species using Sonobat 3.2 automated classifier (SonoBat, Arcata, CA, USA). As recommended by official Sonobat Guidelines, a probability threshold of 90% was set for accurate species identification.

For comparisons between continuous versus point count methods (EM3 detector only, see Section 3), we tallied the total number of bat passes recorded along each transect while continuously sampling and separately for point count sampling. We then divided these numbers by the amount of time spent recording using each method to yield passes per minute. Since the data were not normally distributed, we compared passes per minute between the two methods at the 26 transects using a two-tailed Wilcoxon signed-rank test ($N = 26$, $\alpha = 0.05$) in R Statistical Software [39].

For reasons discussed below (Section 3), comparisons between the two detectors were not possible using continuously sampled data. We therefore limited analyses to the point count data. Since these data were recorded at 260 discrete sampling points, each sampled simultaneously by both detectors for 12 min, we were able to treat each site as a separate data point. Specifically, we compared total bat passes recorded at each site between the two detectors. Since the data were not normally distributed, we used a two-tailed Wilcoxon signed-rank test ($N = 260$, $\alpha = 0.05$) in R Statistical Software [39] to test for statistically significant differences. We also compared data on percent of bat passes identified to species and total number of species identified between the different detectors and sampling methodologies.

3. Results

The concern that the more sensitive bat detector (miniMIC) would be more adversely impacted by road noise or airflow was fully realized. The detector was sensitive to wind resistance at speeds over 10 km/h, recording tens of thousands of audio files, all obscured with background noise. This made analysis of these data impossible. Therefore, comparisons of continuous and point count sampling results could only be performed with data obtained from the EM3 detector.

Average passes per minute recorded along the 26 transects was not significantly different between continuous sampling versus point count sampling (0.076 vs. 0.067 passes/min, respectively, P = 0.097, **Table 1**). Comparisons of the proportion of bat passes identified to species and total number of species documented using the two approaches revealed largely similar results as well. Of all the passes recorded for the entire sample during continuous sampling, 20% were able to be identified to species, yielding an overall rate of 0.015 passes per minute identified to species (**Table 1**). At point count sites, 24.5% of passes were able to be identified to species, yielding a rate of 0.016 passes per minute identified to species (**Table 1**). Both approaches also documented the same four species: big brown bat (*Eptesicus fuscus*), red bat (*Lasiurus borealis*), evening bat (*Nycticeius humeralis*), and silver-haired bat (*Lasionycteris noctivagans*).

Since data obtained with the more sensitive miniMIC detector during continuous sampling could not be analyzed, comparisons of the two detectors were restricted to point count sampling. Here, considerable differences were uncovered. The average number of bat passes recorded at each site were significantly higher using the miniMIC detector compared to the less sensitive EM3 detector (mean = 13.17 vs. 0.812 bat passes per site, respectively, N = 260, P < 0.001, **Table 2**). This translates to an average of 1.098 passes per minute for the miniMIC versus 0.067 for the EM3 (**Table 2**). Magnified over 52 hours of recording at the 260 sites, this resulted in a considerably higher number of total bat passes recorded with the miniMIC (3550) compared to the EM3 (211) (**Table 2**). Furthermore, due to the superior resolution of the audio files obtained with the miniMIC, a considerably higher proportion of bat passes were able to be identified to species (64.1% vs. 24.5%, **Table 2**). The combination of a higher number of calls recorded with a higher proportion identified to species meant that the miniMIC

	Continuous sampling	**Point count sampling**
Mean (SD) passes/minute	0.076 (0.073)	0.067 (0.128)
Percent passes identified to species	20.0%	24.5%
Passes/minute identified to species	0.015	0.016
Total number of species identified	4	4

Passes per minute were not statistically different between the two approaches (Wilcoxon test, N = 26, P = 0.097).

Table 1. Comparison of bat detection rates between continuous versus point count sampling along 26 transects using the EM3 bat detector.

	EM3 detector	miniMIC detector
Mean (SD) passes at each site	0.812 (5.15)	13.17 (24.24)
Mean passes/minute	0.067	1.098
Total passes recorded	211	3550
Percent passes identified to species	24.5%	64.1%
Passes/minute identified to species	0.016	0.724
Total passes identified to species	52	2276
Total number of species identified	4	7

The miniMIC documented significantly more calls than the EM3 (Wilcoxon test, N = 260, P < 0.001).

Table 2. Comparison of bat detection rates between the two different bat detectors at 260 point count sampling sites.

obtained vastly more calls identified to species throughout the study compared to the EM3 (2276 vs. 52, respectively, **Table 2**). Lastly, the miniMIC not only documented the four species found with the EM3 (see above), but it also uncovered three additional species: hoary bat (*Lasiurus cinereus*), tricolored bat (*Perimyotis subflavus*), and one or more species in the genus *Myotis* (we were unable to confidently identify the specific species).

4. Discussion

Bats face a growing array of threats. Many of these threats have complex and overlapping geographic distributions. Given the uncertainty of how these threats interact and impact bats across the landscape, it is becoming increasingly important to monitor populations across large geographic areas. Driving transects offer one the most cost effective and least labor-intensive tools for doing this. However, driving transects can be implemented in different ways and it is important to determine which approach is superior in terms of the amount and quality of data obtained.

When comparing results from a single detector capable of yielding analyzable audio files from both continuous and point count sampling, these two methods appear comparable. Specifically, mean number of passes per minute, percent of passes identified to species, passes per minute identified to species, and number of species identified were similar between the two approaches (**Table 1**). They also documented the same four species. If this holds with other detectors that are similarly unaffected by airflow or driving noises, we conclude that either driving transect technique can be a viable option. With such detectors, the needs of the particular project should dictate which option is selected. For example, if one seeks to test hypotheses about habitat use or other factors, the ability to use a variety of standard statistical techniques such as ANOVA (or nonparametric equivalents) for data from discrete sampling points may indicate the point count method is preferable. If, on the other hand, one simply seeks to document the bat fauna of an area, particularly in places it may not be safe to stop and record for extended periods, continuous sampling might be preferable.

The above conclusions are based on the use of a detector capable of operating while driving at speeds above 10 km/h without significant airflow or driving noise interference. We recommend testing any detectors intended for continuous sampling on driving transects to ensure they yield audio files of adequate quality for extracting bat passes and identifying them to species. Data obtained from the miniMIC suggests not all bat detectors may be capable of this. It remains unclear whether other high-sensitivity detectors are similarly affected, or whether accessory devices such as wind screens can mitigate these issues. Future work should test a variety of high sensitivity bat detectors with different types of wind screens to determine if it is possible to use these devices for continuous sampling. If not, our data suggest overall detector sensitivity is vastly more important than driving transect sampling design.

Overall, the more sensitive miniMIC recorded nearly 17 times more bat passes than the EM3 (**Table 2**). Factoring in that nearly 3 times as many of the miniMIC passes could be identified to species, this yielded nearly 44 times more calls identified to species and nearly twice as many bat species identified (**Table 2**). These differences are substantial and have profound implications for the types of conclusions that can be drawn from comparably designed studies. The failure of the less sensitive detector to record numerous bat passes at each site lowers the power of a study. It means any differences that may exist in activity among species or habitats may fail to be detected or may not be identified as significantly different due to the small amount of resulting data. Perhaps even more importantly, the fact that nearly half the species present were effectively missed by the less sensitive detector could alter conclusions about species presence, distribution, habitat associations, and many other ecological questions. The findings from the lower sensitivity detector are particularly troubling for research related to species conservation, as the very species typically of greatest concern (rare and threatened species) are the ones most likely to be missed. All three of the additional species recorded with the miniMIC are uncommon or rare in the sampled area [38]. This is especially true of the genus *Myotis*. Most *Myotis* species in eastern North America have been devastated by White Nose Syndrome, with concerns that at least one species is in danger of becoming regionally extinct in the coming decades [42]. Failing to detect these species in areas where they persist could adversely impact conservation efforts. For example, the presumed absence of such species in a given area may fail to trigger recovery measures normally implemented by governmental and nongovernmental organizations when rare or threatened species are detected. It could also lead to the diversion of much needed conservation resources away from areas where the species persist because they are presumed absent. Given these concerns, if future research confirms that higher sensitivity detectors are not viable options for continuous sampling, the greater amount and quality of data obtained from such detectors strongly suggests priority should be given to using these types of detectors at point count sites rather than using lower sensitivity detectors for continuous sampling.

It is important to note that even with a high sensitivity detector operated at point count sites, driving transects have limitations. Some areas or habitats may lack adequate road access. Depending on how limited road access is, this may put analysis of certain habitats off limits, or cause them to be significantly underrepresented in the sample. In such cases, the use of other techniques such as walking transects, mist nets, or unmanned stationary bat detectors may be indicated. Roads are also, by definition, human-altered environments. Their presence and usage can have a variety of impacts on adjacent environments [43]. Even if much of the surrounding habitat is largely intact, the presence of roads effectively creates a habitat edge. Some species are adapted to interior habitat conditions and avoid or are otherwise negatively impacted by edge conditions [44]. While this is often not a significant problem with insectivorous bats, since many species prefer edges like forest edges [30, 45–47], if there is reason to believe research questions about focal species in the study area might be adversely impacted by sampling at habitat edges, driving transects may not be appropriate. For the region sampled in the present study, driving transects have proven comparable in documenting the bat fauna to unmanned stationary bat detectors placed in both interior and edge conditions of different habitats [38].

5. Conclusions

Like many mammals, bats across the globe face a variety of threats that imperil their very existence. In North America, many of these threats are both increasing and span large geographic areas. The growing and expansive nature of these threats requires the urgent development and deployment of sampling techniques capable of effectively and efficiently documenting changes in the status of bat populations across large areas. Driving transects have been proposed and implemented as a tool for doing precisely that. Unfortunately, previous studies failed to examine the implications of using different sampling methodologies or detectors on the results obtained.

In this study we showed that, with a lower sensitivity detector that is unaffected by wind and driving noise, sampling continuously while driving yields similar results to sampling at discrete sampling points. However, detector sensitivity proved to be much more important than sampling technique in terms of the amount and quality of data obtained. That is, the higher sensitivity detector documented substantially higher numbers of bat passes and species than the lower sensitivity detector. The downside to the former is that data obtained while driving could not be analyzed due to significant interference from driving noise and airflow over the microphone at speeds above 10 km/h. Based on our findings, for most studies using driving transects to study bat populations, we suggest detector sensitivity should take priority over sampling design. If future studies are unable to resolve the problems of using high sensitivity detectors while continuously sampling along driving transects, this would necessitate using point count sampling instead. We recommend selecting the detector capable of obtaining the greatest amount and quality of call sequence recordings under a given research design, then conducting preliminary trials with continuous and point count sampling. If airflow or driving noises significantly diminish the data available with continuous sampling, as in the current study, point count sampling would be the more appropriate sampling regime to use for most applications.

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Chapter 3

The Bat: A Benefactor Animal Poorly Understood in Algeria

Mourad Ahmim

Additional information is available at the end of the chapter

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Abstract

Bats are very interesting mammals; they are man's helpers because they fight against the proliferation of insects harmful to agriculture and public health. They play an important role in the agricultural economy too because they allow farmers to save money as they do not use pesticides and also their product is organic. Even the feces of bats serve as a fertilizer of excellent quality. With all these assets, bats remain poorly known in Algeria, and protection work is highly recommended.

Keywords: bats, interesting mammals, man's helpers, economy, public health

1. Introduction to the knowledge and the importance of bats

The last few decades have witnessed the progressive impact of humans on global biodiversity [1], not only through simple loss of habitat but also through habitat fragmentation and a reduction in the quality of the habitat that remains [2, 3]. As a result, many species, including bats, are currently threatened with extinction around the world. The 1232 species of bats are found across most of the world other Antarctica and some remote oceanic islands [4]; the number and diversity of species is highest in tropical regions and decreases as they approach the poles (French Society for the Protection and Study of Mammals, 2003). Nearly half of all bat species are listed as threatened or vulnerable by IUCN (International Union for the Conservation of Nature) [5]. The main causes of this situation are increased urbanization, the destruction of natural habitats and the fragmentation of what remains of them into relatively isolated islands of varying sizes [6, 7]. The degree of human 'improvement' of green spaces has led to a lack of 'natural' vegetation and the consequent reduction in insect fauna [8–11]. These changes in available habitat have resulted in bats exploiting "man-made structures" such as bridges [12], abandoned warehouses and mines and the attics and eaves of houses [13]; some of these animals benefit from the concentration of prey present under electric lighting [14, 15].

Chiroptera are the only flying mammals, representing a quarter of all known mammal species. Despite being the most diverse group of mammals after rodents, there is relatively limited published information available on this group. Bats were historically divided into 2 suborders: the Microchiroptera, which have about 800 species, are relatively small in size and capable of echolocation, and the Megachiroptera, which include about 170 species of relatively large and non-echolocating Old World fruit bats [16]. However, recent molecular studies [17, 18] suggest that this classification should be reviewed, as some families previously attributed to the microchiroptera are closely related to the Old World fruit bats. These include families of temperature insectivorous bats, such as the Rhinolophids. The suggested new classification places the Old World fruit bats and their relatives in a sub-order called the Yinpterochiroptera, with the remaining species attributed to the Yangochiroptera.

Bats are thought to have appeared in a warm climate, probably at the beginning of the Eocene; the earliest known fossil, *Icaronycteris index*, dates back to about 60 million years [12]. In the world, according to phylogenetic work, all existing research support the hypothesis that they appeared during the lower Eocene (52–50 million years) coinciding with a significant global rise in temperature, suggesting that they are from Laurasia, possibly from North America, and Gondwana [18]. In 2011, Ravel et al. found the oldest occurrence of bats in Africa (5.8 to 48.6 million years) in Algeria—El Kohol, in the Brezina region of the southeast the Atlas Mountains—demonstrating that the basal group of bats had a distribution worldwide at the beginning of the Paleogene [19].

Thanks to their longevity, a fairly high position in the food web and a very wide distribution, Chiroptera are a good candidate for being a biodiversity indicator [20]. The year 2012 was declared International Year of the Bat by the United Nations Environment Program (UNEP), to acknowledge the many services provided by bats and to make people overcome some of the prejudices that persist about these harmless animals.

According to Tuttle, Honorary Ambassador for this global event, this initiative was taken in light of the essential role of bats [21]. They provide invaluable services that humans cannot afford to lose, they play a role in maintaining the health of ecosystems and they have a very important impact on the human economy. The order of Chiroptera is the richest in mammal species, nevertheless, in recent decades, populations have declined alarmingly and many species are now endangered. For example, white-nose syndrome, which affects bat populations in most parts of the United States, has killed more than 1 million bats.

Because they are only active at night and difficult to observe and understand, bats are ranked among the most misunderstood and intensely persecuted mammals on our planet. The insectivorous species (Microchiroptera for the majority and the only ones present in Algeria) are the main predators of a large number of insects that fly at night. All over the planet, bats prey on mosquitoes and consume hundreds of other species of insects that humans consider detrimental to their health or economy as they cause losses estimated at billions of dollars a year. To some extent, bats thus participate in the prophylactic means of controlling the diseases mosquitoes carry, such as malaria or dengue fever. Whatever their geographical distribution, all authors agree that bats are one of the most powerful natural insecticides [22].

A decline in bats may therefore induce greater demands for insecticides, raising the cost of the production of many crops such as rice, maize and cotton because without them considerable additional volumes of insecticides would be used. Foresters have also realized that bats are a valuable ally of the forest ecosystem and are increasingly involved in protective approaches, with increasingly ecological management approach [23].

Bats also play a significant economic role: They allow biological discoveries that ensure the development and exploitation of many products and raw materials. Even their feces can be exploited by agriculture or help with research [22]. While the Executive Secretariat of the Agreement on the Conservation of Bat Populations of Europe (Eurobats) had launched 2012 as the year of the bat, a study published in the journal Science made the link between the decline of bats in the United States and the financial impact for agriculture. According to researchers, the disappearance of bats could cost farmers $ 3.7 billion a year as a result of increased pesticide use. This is a “conservative estimate” of environmental services rendered by bats, warn researchers. By studying their eating habits, they have also been able to establish the positive impact of these mammals on crops. In Texas, for example, bats eat up to 8 grams of caterpillars each night, while Midwest caterpillars eat *Chrysomeles*, including corn, and pentatomidae. Services provided range from $ 12 to 174 per acre (about 40 acres), depending on the nature of production and the type of cultural practice. Scientists hope that “some will disagree with this estimate in order to open a scientific debate on the subject.”

According to Tuttle, fruit bats (Megachiroptera) are just as important in maintaining entire plant life ecosystems; their contribution to seed dispersal and pollination is essential to the regeneration of tropical forests, which are the lungs of our planet [21].

Many of the plants that depend on these bats are also of great economic value; their products ranging from wood to fruit, spices, nuts and natural pesticides.

Chiroptera are useful for more than one reason and they have a very important ecological role. For 30 million years, bats have been helping entire ecosystems to live and regenerate. In island environments, endemic species often play a vital role in the survival of island ecosystems. On oceanic islands, fruit bats are often the only species capable of pollinating certain plant species or carrying fruit over great distances. Cox, an American biologist, says that 30% of trees in Samoa are directly dependent on bats. During the dry season, in these same territories, 80–100% of the seeds deposited on the ground are transported by bats. Today, this essential role of pollination and seed dispersal is known and recognized. An American study conducted in the 1990s has also shown that breeding of 300 tropical Old World plants depends totally or partially on bats [22].

In Texas, 1.5 million bats now live in crevices under the only bridge in the city center. When they started to colonize this bridge, the health authorities warned they were dangerous and could spread diseases. However, thanks to BCI’s (Bat Conservation International) outreach work, there was widespread public awareness of the situation. In 30 years, not one person has been attacked or contracted an illness. The fear has been replaced by the love of these animals who eat 15 tons of nocturnal insects and which bring in 12 million dollars each summer thanks to the tourism. Hence the deduction that it is now well-proved that people and bats can share even our cities to great mutual benefit.

It is determined that 450 products used by humans depend directly and indirectly on bats. This impressive list includes, among others, 110 foods or beverages, 72 medicines and 66 tree species used in cabinet making. Some pollinated fruits represent an important economic value for developing countries. This is the case of Durian fruit, *Durio zibhetinus* and Petai, *Parkia speciosa* and *P. javanica*, which are increasingly used as food for some Asian populations. In Africa, the Roussettes are the only species to disperse the seeds of Iroko, a rare species. In the Sonoran Desert, in the southwestern United States and in the arid areas of Mexico, the long-nosed bat plays a major role in the pollination of agaves and large cacti. An entire economy is directly dependent on them, because from these cacti are drawn Tequila and Mescal, two alcohols which represent important currency flows for the local economy [22].

Even the excrement of bats is important, like that of birds. The guano of bats represents a significant source of income for low-income countries. Natural and of very good quality, this fertilizer can, moreover, be exploited on the spot at very low costs [22]. As long as the bats remain present and the environment allows them to feed, this commodity will also be renewable. The guano harvest offers economic benefits to developing countries as it prevents them from importing phosphate fertilizers, often bought in hard currency, which increases their external debt. But bat droppings also have other interests. Millions of unknown bacteria live in the guano and contribute to its degradation. Discovered in the enormous piles of excrement in the southern caves of the United States, bacteria have been isolated and subjected to research programs [22]. The use of these new organisms could make it possible to optimize landfill waste disposal, to partially abandon certain fossil fuels and to produce even more efficient detergents. Only a small part of the microorganisms contained in bat guano has been studied so far and new applications may be discovered in the coming years. The destruction of a colony of bats may eliminate these millions of organisms at the same time even before they have been studied [22].

Pure guano is a good fertilizer for plants, it has a composition of 10-3-1 in NPK and it is also a soil conditioner because it improves its texture and richness. In addition, it contributes to the detoxification of the soil because it is a bio-corrector favoring the proliferation of micro-organisms that eliminate toxic residues and it plays at the same time the role of fungicide by eliminating phytopathogenic fungi and nematocide by promoting the development of decomposing micro-organisms that contribute to the control of nematodes, and it is also an activator of compost: decomposer micro-organisms accelerate the composting process [24, 25].

Bats are also given special attention due to some of their characteristics, which are either unique or important. One can quote their surprising morphology, with their aptitude to flight, as well as their echolocation system. The ecological value of the bats justifies that all their species be considered as "species of fauna strictly protected" by the Bern Convention, 1979, relative to the Conservation of the Wild Life and the Natural Environment. Bats are also listed in Appendix II of the Bonn Convention, 1979, on the Conservation of Migratory Species of Wildlife. Bats are studied and monitored by many international and national organizations, including BCI (Bat Conservation International), Batcon (Bats conservation) and Eurobats (European bats), and in 2013, Africa saw its organization created after the Naivasha summit in Kenya on February 15, 2013. This had the participation of 19 African countries, Algeria not having been present; the organization was created to contribute to the preservation of the bats of Africa and the Western Indian Ocean Islands and is known as BCA (Bat Conservation Africa). The causes of the reduction in the density of bats are many; the image of the bat in the popular culture can be beneficial or evil, according to culture. Because of their "strange" appearance and their nightlife and, as a result, the mystery surrounding their way of life, they are often victims of popular beliefs and have long been persecuted by humans [17, 18].

In addition to the concerns for its survival, a health warning has come in recent years threatening their rehabilitation with the general public, leaving the threat of zoonosis to be the most feared such as rabies and the fear of bats being the origin of emerging viruses in the Old and New World such as the Ebola virus. The causes of the disappearance of Chiroptera are multiple; it seems to be explained also by the strict ecological requirements of the species in terms of habitats. In fact, a population of bats can only sustainably live in a region if it offers a coherent network of hunting grounds rich in prey and wintering, breeding and transition sites connected by functional circulation corridors, that is to say without any physical interruption. The reproduction and wintering roosts, free from any pollution, are at most 20 km distant from each other [26], within a rich bocage landscape in diversified environments: mainly grazed meadows, wooded areas, wetlands and orchards [27–31]. The animals also hunt large insects, mainly Lepidoptera, Coleoptera (Aphodius, Melolontha, Geotrupes) and Diptera (Tipulidae), which are key prey for some species [27, 28, 32, 33].

2. Presentation of Algeria and its Chiroptera

Algeria is the largest country bordering the Mediterranean (2,381,741 km^2) and the largest country in Africa, and it offers a wide variety of biotopes that make the existence of a great diversity of species of bats possible. There are Mediterranean and desert regions, mountainous regions, highland areas and ancient volcanic regions. Each of these areas can host a particular bat fauna. Chiroptera are represented by 26 species in 7 families; most of these are considered vulnerable in many countries of the world and are listed on the IUCN Red List of Threatened Species (International Union for the Conservation of Nature).

Although much work has been done on mammal fauna, very little work has been done on the bats of Algeria, despite their major ecological role in the maintenance of ecosystems [34]. Indeed, the valuable ecological services provided by bats are still ignored by the majority of the population and even by the authorities in charge of the management of fauna and flora [35]. The main consequence of this state of affairs is that bats are not taken into account in the conservation and management projects of the fauna and flora of ecosystems in many countries where they are threatened or in decline [35].

This lack of basic data on the chiropterofauna of Algeria is a barrier to knowledge and understanding of their role in maintaining the stability of natural ecosystems [34, 36]. Bats do indeed present systematic interests [37] including ecological [34, 38–40], veterinarian [41, 42], medical [43], economic and pharmacological [39, 44] (**Table 1**).

Family	Number of species	Species
Rhinopomatidae	01	*Rhinopoma cystops* Thomas,1903
Emballonuridae	01	*Taphozous nudiventris* Cretzschmar, 1830
Rhinolophidae	06	*Rhinolophus blasii* Peters, 1866
		Rhinolophus clivosus Cretzschmar, 1828
		Rhinolophus euryale Blasius, 1853
		Rhinolophus ferrumequinum Schreber, 1774
		Rhinolophus hipposideros (Bechstein, 1800)
		Rhinolophus mehelyi (Matschie, 1901)
Vespertilionidae	13	*Eptesicus isabellinus*
		Myotis punicus (Felten, Spitzenberger and Storch, 1977)
		Myotis capaccinii (Bonaparte, 1837)
		Myotis emarginatus (É. Geoffroy, 1806)
		Myotis nattereri (Kuhl, 1817)
		Nyctalus leisleri (Kuhl, 1817)
		Nyctalus noctula (Schreber, 1774)
		*Otonycteris hemprichii (*Peters, 1859)
		Pipistrellus kuhlii (Kuhl, 1817)
		Pipistrellus pipistrellus (Schreber, 1774)
		Pipistrellus rueppellii (Fischer, 1829)
		Hypsugo savii (Bonaparte, 1837)
		Plecotus gaisleri (Benda, Kiefer, Hanak et Veith, 2004)
Molossidae	02	*Tadarida aegyptiaca* (É. Geoffroy, 1818)
		Tadarida teniotis (Rafinesque, 1814)
Miniopteridae	01	*Miniopterus schreibersii* (Kuhl, 1817)
Hipposideridae	01	*Asellia tridens* (É. Geoffroy, 1813)

Table 1. Algerian bat species.

To get a general idea about the distribution of bats in Algeria, Kowalski and Rzebick Kowalska established a division of the territory according to large biogeographic sets [45].

The country is divided into five distinct areas, on a North-South axis, characterized by their climate:

The Tell: Large area from 80 to 190 km the Tell includes the plains and the richest territories of the country. The climate is Mediterranean. Sometimes the sirocco brings the heat and sand of the Sahara to the cities of the coast. The eastern part formed by the mountains of Kabylie and Constantine has the most water.

The chains of the Tellian Atlas are located between the sea and the high plains and extend over almost 7000 km (highest point: Mount Lala Khadija: 2308 m). They have forests of olive trees and oaks on their slopes. These regions are very populated.

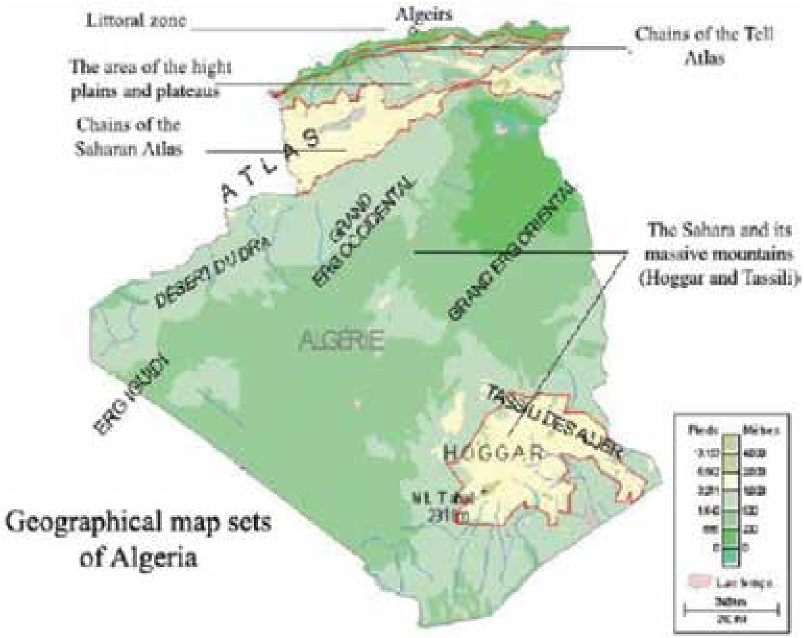

Figure 1. Geographical map sets of Algeria.

The High Plains and Highlands Domain: These immense steppe plateaus stretch from East to West, from 1000 to 600 m. The climate is semi-arid, allowing a cereal crop without irrigation thanks to certain depressions (called chott). Of semi-desert aspect, for a long time, these zones constituted places of Saharan transhumance.

The Saharan Atlas: The south of this succession of mountains marks the limit of the arid climate and limits of the Northern region with the Sahara. Mount Chelia in the Aurès rises to 2328 m.

The Sahara and its massifs (Hoggar and Tassili): covering a large part of southern Algeria, the vastness of the Algerian Sahara includes, with its 2 million km^2, a quarter of the entire desert. It is a dry and arid desert with varied landscapes: great ergs, dry valleys, arid plains and sand dunes. There are volcanic mountain massifs including the massif of Hoggar, which culminates in the highest mountain of Algeria, the Tahat, at 2918 m above sea level, and the Tassili massif. Temperatures range from an average of 36°C during the day to 5°C at night. Riches are found beneath the soil: not only oil and natural gas but also precious metals found during the recent survey of the Hoggar massif. This territory represents 97% of the country's exports (**Figure 1**).

3. History and data on the knowledge of Algerian bats

The first work done on bats in Algeria is represented by that of Dobson who received some bat specimens collected by Lataste [16]; they were individuals of eight species which are *Otonycteris hemprichii*, *Vesperugo* (Vesperus) *serotinus* sub-species *isabellinus*, *Vesperugo pipistrellus*, *Vesperugo kuhli*, *Vespertilio murinus*, *Vespertilio capaccinii*, *Miniopterus schreibersi* and *Rhinolophus euryale*.

In 1912, Weber undertook chiropterological exploration in different parts of the Algiers region and found individuals of *Rhinolophus euryale* and *Myotis murinus* (*M. punicus*) and in 1911 *Miniopterus schreibersii* in Birkhadem [46]. It was not until nearly 20 years later that Laurent cited a Saharan form of the genus *Plecotus*, a rare species of which only one individual was reported by Loche in 1867 in Blida [47]; he studied an individual collected in El Golea by Doctor Foley of the Pasteur Institute of Algiers and he came to the conclusion that there are two *Plecotus* species in the sub-Saharan regions of North Africa *Plecotus austriacus* and a new species *Plecotus auritus saharae*. He was followed by Heim de Balsac in 1936 who questioned the statement of Laurent concerning the genus *Plecotus* [47, 48] he stipulated that the Algerian species is none other than *Plecotus auritus christiei* of which there was another capture at Oumeche near of Biskra by Rotschild and Hartert [49]. In 1944, Laurent first banded bats in Algeria and North Africa in 1942 in a cave around Algiers [50].

In 1976, Anciaux de Favaux established the first complete study of Algerian bats [51]. He cites the presence of 23 species belonging to 5 families, many of which are rare and 2 remain problematic. Javrujan (1980) investigated Algerian bats, as well as border areas with Tunisia and Morocco, found 20 species and 660 individuals. In 1984, Hanak and Gaisler reported for the first time the presence of *Nyctalus leisleri* as a new species for the African continent, from Yakourene region to Tizi Ouzou [52], and they captured an individual of *Myotis nattereri* reported for the second time for Algeria [52]. In 1983 Gaisler completed this list [53], he worked with his collaborators mainly in the northeastern part of the country with the town of Setif as the central point, and it was he who for the first time signaled the presence of *Myotis nattereri* for Algeria, as well as the reappearance after a century-long absence of *Pipistrellus pipistrellus* and *Myotis capaccinii* [54]. They also report the presence of *Hypsugosavii* in three regions of the country at altitudes ranging between 1050 and 2004 m; they gave very important details about its ecology and he studied the distribution of 10 species namely *Rhinolophus ferrumequinum, R. hipposideros, R. euryale, R. mehelyi, R. blasii, Myotis blythii, M. emarginatus, Pipistrellus kuhlii, Plecotus austriacus* and *Miniopterus schreibersii*. Other work was done by Gaisler et al. [54] and Kowalski et al. [45].

Kowalski et al. and Gaisler and Kowalski studied the dynamics of bat populations in the caves of northern Algeria between 1978 and 1983 and worked on the annual cycle of cave-dwelling species in 26 localities of the country [54, 55], including the Ain Nouissy Cave near Mostaganem (35° 48′N, 0° 2′E), the Yebdar Cave located near Ain Fezza in the Tlemcen Mountains (34° 53′N, 1° 18′W), Cave of Mersa Agla in Honaine (35° 10′N, 1° 39′W), Sig (35° 32′N, 0° 12′W, the mountains of BeniChougrane, the hills of Mourdjadjo at 6 km S from the village of Misserghin near Oran (35° 38′N, 0° 43′W), At the seaside at Madagh (35° 40′N, 1° 0′W), the cave of Aokas (36°) 38′N, 5° 14′E), the cave of Tichy, the valley of Chabet lakhra (36° 39′N, 5° 17′E) there are several artificial galleries of 50–800 m of length carved in the rocks, cave at the foot of Mount Chelia in the Aurès (35° 19′N, 6° 40′E), Hot Cave near Tiddis (36 22′N, 6° 39′E), in the Saharan Atlas considered as the southern limit of the Mediterranean species, in the cave El Rhar in Ain Ouarka (32° 44′N, 0° 10′W) located in semi-desert and rocky, consisting of a single gallery about 800 m long [56], Brezina (33° 6′N, 1° 16′E) and several caves located between the desert. They noted that the hibernation period in Algeria is shorter than in Europe, but that the reproductive cycle was similar and copulation took place in autumn and fertilization in spring. Parturition was also seen taking place earlier than in Europe for the same species and they noted a tendency to form harems during the breeding season.

The above observations show that bats found in the caves of northern Algeria remain there throughout the year and are not migratory toward Europe as presumed by Heim de Balsac [48]. In 1912 Weber examined and studied the hibernation of bats in Algeria and found specimens belonging to several species in the state of torpor in winter [46]. When the weather is favorable, bats are observed to be active during the winter in northern Algeria [56]; previously, there was no information concerning the winter activity of cave-dwelling bats from Algeria. The caves of Algeria contain more bats in summer than in winter. The same observation has also been made in other areas of the Mediterranean, for example in Dalmatia [57], Provence [58], Sardinia [59] and Corsica [60]. This distinguishes them from Central European caves, which are used primarily as hibernacula while breeding and maternity colonies are exceptionally held in summer.

The hibernation period in northern Algeria is shorter than in European countries. In March in the cave of Misserghin fresh droppings began to accumulate under the bat colony, proving that they had started foraging for food, bat movements inside and between the bats' winter roosts seem to occur especially in Algeria; this was indicated by changes in the composition, number and distribution of bats during consecutive visits to the caves of Algeria. These movements between hibernacula have also been documented in Europe [61].

In the book Mammals of Algeria in 1991, Kowalski and Rzebick Kowalska reported the existence of 26 bat species, confirming the data of Gaisler in 1983 who undertook a variety of work on bats in 1979 and in 1984, and Kowalski and his collaborators had to analyze and study cave-dwelling bats of Algeria [45, 62].

4. Zoogeography of Algerian bats

The bats reported for Algeria belong to the Palearctic region, whose boundaries were delineated by Corbet [63]. This region is described as beginning in the north with the Spitsbergen Islands; the Azores, Madeira and the Canary Islands are included, unlike the Cape Verde Islands which are excluded. In Africa, the western boundaries start at 21°30′N (Between Western Sahara and Mauretania), and the countries that are included are Algeria, Libya and Egypt and excluded are Niger, Chad and Sudan. The Hoggar Mountains are included in contrast to Tibesti. The entire Arabian Peninsula is included. The Asian boundary begins between Pakistan and Iran and continues in Afghanistan to central China.

By working on five large areas resulting from a climatological division of the Algerian territory made by Ochando [64], In 1986 Gaisler and his collaborators stipulated that seven species are characteristic of northern Algeria [54], of which the first and second zones represent the Mediterranean zone, or the climate varies from sub-humid to semi-arid. The third and fourth zone or medulla zone corresponds to the zone with an arid climate, except for some mountainous regions where the climate is semi-arid and possibly the highlands and the Saharan Atlas. The fifth zone is the Sahara with its desert climate and the Saharan mountains.

Family	**Number of species**		**Districts**				
			The littoral zone	**Chains of the Tell Atlas**	**Height plains and plateaus**	**Chains of the Saharan Atlas**	**Sahara and massive mountains**
Rhinopomatidae	1	*Rhinopoma cystops*				X	X
Emballonuridae	1	*Taphozous nudiventris*					X
Rhinolophidae	6	*Rhinolophus blasii*	X	X	X	X	X
		Rhinolophus clivosus	X	X	X	X	X
		Rhinolophus euryale	X	X	X	X	
		Rhinolophus ferrumequinum	X	X		X	
		Rhinolophus hipposideros	X				
		Rhinolophus mehelyi					
Vespertilionidae	13	*Eptesicus isabellinus*	X	X	X	X	X
Miniopteridae		*Myotis punicus*	X	X	X	X	X
		Myotis capaccinii	X	X	X	X	X
		Myotis emarginatus	X	X	X	X	x
		Myotis nattereri	X	X	X	X	X
		Nyctalus leisleri	X	X	X		
		Nyctalus noctula	X	X			
		Otonycteris hemprichii	X	X			
		Pipistrellus kuhlii	X	X			
		Pipistrellus pipistrellus					
		Pipistrellus rueppellii					
		Hypsugo savii					
		Plecotus gaisleri					
Miniopteridae	01	*Miniopterus schreibersii*	x	x	X	x	
Molossidae	2	*Tadarida aegyptiaca*	X			X	X
		Tadarida teniotis					
Hipposideridae	1	*Asellia tridens*				X	X
			16	14	10	13	11

Table 2. Presence–absence of bat species according to the five Algerian geographical sets.

The principal species of northern Algeria, according to this division, are *Pipistrellus pipistrellus*, *Myotis punicus*, *Myotis schreibersii* and more-rarely *Myotis capaccinii*, *Myotis emarginatus*, *Myotis nattereri* and *Nyctalus leisleri*.

The results of this table are derived from the data of Gaisler [53], Hanak and Gaisler [52], Gaisler [56], Gaisler-Kowalski [54] and Kowalski and Rzebick Kowalska [45], and we have provided any necessary updates.

Table 2 shows that 16 of the 26 species (61.53%) of Algerian bats live in the littoral zone, which represents less than 10% of the total land area. This is followed by the two Atlas mountain ranges—the Sahara Atlas and the Tell Atlas which both have 56% of Algerian bat species. The areas with the least diversity of bats are in the high plains and plateaus and the Sahara and massif mountains respectively with 40 and 48%. These last two areas account for more than 70% of the land area of Algeria. These results may reflect the fact that the sampling effort is very biased, because according to the literature, the majority of studies and surveys have been carried out in the northern part of the country: the littoral zone and the Tell Atlas.

5. Habitat and distribution

According to Anciaux de Faveaux (1976) and some of our observations, the bats of Algeria can be divided, according to the habitat they occupy, into four main groups [51]. We found species that fit in two or more groups: troglophilic species, lithophilic species, phytophilic species and synanthropic species.

5.1. The troglophilic species

These are species that overwinter underground in caves and artificial cavities. During the summer breeding season, they seek warmer shelters such as attics, roofs of houses and mosques, ruins and rock crevices. They are represented by 14 species belonging to six families (**Table 3**).

Family	Species	Habitat
Hipposideridae	*Asellia tridens*	In man-made tunnels
Rhinolophidae	*Rhinolophus blasii*	In caves
	Rhinolophus clivosus	In caves
	Rhinolophus euryale	In caves
	Rhinolophus ferrumequinum	In caves
	Rhinolophus hipposideros	In caves
	Rhinolophus mehelyi	In caves
Rhinopomatidae	*Rhinopoma cystops*	In caves, basements of mosques
Vespertilionidae	*Myotis punicus*	In caves
	Myotis capaccinii	In caves, cracks in the pillars of bridges
	Myotis emarginatus	In caves
	Plecotus gaisleri	Winter in caves and was in attics of houses, cracks in trees and minarets
Emballonuridae	*Taphozous nudiventris*	In dry caves
Miniopteridae	*Miniopterus schreibersii*	Old aqueducts, caves

Table 3. Troglophilic species of bats.

5.2. The lithophilic species

These are species that usually roost in rocky crevices and cracks in walls. There are four species belonging to two families (**Table 4**).

5.3. The phytophilous species

These roost in the foliage of trees and under tree bark. All five species belong to the family Vespertilionidae (**Table 5**).

5.4. The synanthropic species

These species roost under the roofs and against the internal walls of human dwellings, under bridges in towns or cities, and hunt around electric street lights in the city (**Table 6**).

5.5. Distribution by roost type

Table 7, a same species can belong to one, two or more groups. The most represented family is Vespertilionidae because its 14 species occupy four roost types. It is also apparent that troglophilic species are the most numerous (14 species), belonging to six families with all the six species of the Rhinolophidae. One family (the Molossidae) has no troglophilic species. There are four lithophilic species, belonging to two families (Vespertilionidae and Molossidae). The latter family only contains lithophilic species. Four species of Vespertilionidae are phytophilic in Algeria, and two other species of this family are synanthropic. In conclusion, we note that

Family	**Species**	**Habitat**
Molossidae	*Tadarida aegyptiaca*	Unknown
	Tadarida teniotis	In old bridges, aqueducts, cracks of rocks
Vespertilionidae	*Otonycteris hemprichii*	Wall cracks in underground cavities especially in the Saharan oases
	Hypsugo savii	In rocks crevices and hollow trees in mountainous region

Table 4. Lithophilic species of bats.

Family	**Species**	**Habitat**
Vespertilionidae	*Eptesicus isabellinus*	In trees and between leaves and branches of trees
	Nyctalus noctula	In trees, hibernating in cracks of rocks
	Nyctalus leisleri	In Oases
	Myotis nattereri	Near water and trees
	Pipistrellus rueppellii	In Oases

Table 5. Phytophilous species of bats.

Family	Species	Habitat
Vespertilionidae	*Pipistrellus kuhlii*	Cracks, bridges and houses
	Pipistrellus pipistrellus	Cracks and houses

Table 6. Synanthropic species of bats.

Family/habitat	Troglophilic species	Lithophilic species	Phytophilous species	Synanthropic species
Vespertilionidae	4	2	5	2
Molossidae		2		
Rhinopomatidae	1			
Hipposideridae	1			
Emballonuridae	1			
Rhinolophidae	6			
Miniopteridae	1			
Total	14	4	5	2

Table 7. Distribution of the bats by roost type.

the family whose species occupy the four biotopes is the family Vespertilionidae. One family (Molossidae) is lithophilic and the rest of the other families (Rhinopomatidae, Hipposideridae, Emballonuridae, Miniopteridae and Rhinolophidae) are all troglophilic.

6. Biology of conservation

In terms of conservation biology, all species in our study area are protected in Algeria and have a heritage status on the IUCN Red List. The major threats to which they are subjected are mainly of an anthropogenic nature, all the roosts have been more or less affected, the caves are overcrowded in summer and they are subject to disturbance by the activities of the public works services and the widening of roadways. Some old cellars have been restored without taking into consideration the presence of bats and sometimes even demolished. Others are obstructed by buildings, the other roosts, the majority of which are forested, are spared by the direct action of man, but are threatened by repeated fires.

On the basis of this observation, we propose protection measures for sites of interest and, lastly, we propose a succinct action plan for Chiroptera that can be used as a management tool for the managers of the various departments concerned with the conservation of sites of interest and the environment. This action plan will have as a first action, the census of bat houses at a national level, then a follow-up of an inventory of the species, which will give us an overview of the Algerian chiropterological inheritance and will allow us to take adequate measures of protection. For this, a non-governmental organization was created to work on the protection of bats, its name is ALGERIAN BAT GROUP, and it works on the promotion of the knowledge of the beneficence of this species of mammal.

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Chapter 4

Bats in Bulgaria: Patterns of Species Distribution, Richness, Rarity, and Vulnerability Derived from Distribution Models

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Additional information is available at the end of the chapter

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Abstract

Bats are affected by a variety of anthropogenic pressures, and effective conservation measures require a complex approach by not only covering the roosts themselves but also the surrounding habitats and migration corridors. The development of concrete localized conservation measures requires detailed quantitative data to assess habitat status regarding the most crucial factors for concrete species. This chapter aims, by modeling using a Maxent based on many georeferenced locations and the state of ecologically relevant ecogeographic variables, to reveal the spatial trends in the habitat suitability of 29 bat species; to obtain meaningful biogeographical species groups; and to provide a countrywide quantitative assessment of bat richness, rarity, and vulnerability. The modeling results showed that altitude, karstic areas (presence of caves), topographic wetness index, and presence of deciduous forests were the most influential factors. In this respect, three well-defined groups were delineated. The species' richest areas were mostly located in semimountain karstic areas with a well-developed broadleaved forests, and the lowest in xerophilous, bare habitats, especially those of anthropogenic origin. Regarding rarity, more rare species were associated with caves and mountains. Vulnerability (in terms of IUCN criteria) was positively affected by the presence of caves showing the importance of protecting karstic areas.

Keywords: species distribution modeling, Chiroptera, distributional patterns, ecogeographical variables, satellite imagery, species richness, rarity, vulnerability

1. Introduction

Bulgaria has a uniquely high diversity of bats. Of the 35 species that are found in continental Europe, 33 species are found in Bulgaria. This is largely due to the transitional geographic location of the country, the diverse habitats, the significant elevation gradient from the sea level to the altitude above 2900 m, the preserved wildlife in many parts of the country, especially in the mountainous and semi-mountainous regions, and the presence of over 5900 caves. All the bat species are strictly protected by the National Biodiversity Act (Annex 3). Twelve species are listed in Annex 2 of the Habitat Directive. Despite the legal protection, many species have conservation problems. The main threats identified both for bats as a whole and for individual species, fall into two general categories such as anthropogenic influence on the roosts and habitat loss and degradation [1].

The first group of threats mainly concerns the cave-dwelling species. Many of them are vulnerable to human impacts because they are often more visible and found in higher numbers. Anthropogenic disturbance and vandalism, excessive caving visits, destruction, placing doors and bars that prevent or hinder the partial or full access to them, agricultural and animal breeding activities in caves, and underground water catchments are among the major potential threats. Measures to mitigate the impact of these threats are directed at identifying important underground roosts and their legal protection. Out of the 5900 caves in Bulgaria, there are about 125 caves and cave's complexes declared as Natural Monuments. Among them, 52 caves are known as Important Bat Underground Habitats of national and 13 of international importance [2]. Within the borders of 17 Protected Sites, there are at least 120 caves, many of them with importance to bats. Additionally, 817 caves fall within the borders of National and Nature Parks and 173 caves are part of Strict or Managed Nature Reserves. The most important bat underground sites according to Habitats Directive (92/43/EEC) are designed as Natura 2000 network sites. Some of the other Natura 2000 sites, particularly those covering large areas, also contain many bat caves [1].

Regardless of the formal legal protection of important bat caves and their immediate surroundings, it still affects only a small portion of the bat's diversity. In fact, the fate of the protected areas and the biological diversity they contain is influenced to a great degree by actions within the surrounding landscape. Effective conservation measures require a complex approach, covering the habitats around caves, including bats' foraging habitats and migration corridors.

Conservation of the habitat is also important for a large group of bats that are not directly related to caves and whose ecology is little known. Many human activities are potentially negative in this respect—destruction of natural vegetation especially forest, including clearing of the few remaining natural lowland forests for agricultural purposes and of older forests in the higher elevations for timber; widespread alternations of mid-elevation forests due to clearing, fires, heavy pressure from livestock grazing, and artificial planting and forestation (especially the replacement of broad-leaved forests with conifer plantations). Destruction of some habitat elements has a particularly negative impact on bats. Felling old tress and trees with hollows restrict the possibilities of finding appropriate roosts, especially for the nursery colonies; destruction of the natural open water areas (lakes, marshes, river arms); destruction of the hunting habitats and the flight corridors. Negative for bats are many activities associated with agricultural land uses: plowing of meadows, including formerly uncultivated lands; overgrazing; expansion of monocultures and input-intensive agriculture, especially the intensified use of fertilizers and pesticides; poorly planned construction and development projects, including wind turbine construction, tourist resorts and facilities, highways and other transportation projects, mines, and quarries, as well as urban expansion in general [1, 3].

The development of concrete measures for integrated bats conservation requires better insight into the environmental requirements of the species. It is necessary to identify locally specific measures. Given that there are differences in the ecological characteristics of the species in different regions, specific quantitative data are needed. The detection of distribution patterns along environmental gradients is an important task in conservation ecology. By knowing species-environment relationships, species and species assemblages can be used in understanding the conservation needs of poorly known species with a narrow niche breadth. Although such analyses and generalizations aimed at identifying groups of species with similar ecological requirements already exist [1, 4–6], such classifications were made by eye and were based entirely on expert judgment.

With the advent of increased interest in numerical classification, clustering of multivariate species data became very popular in such studies. To be effective, this approach needs to base on comprehensive quantitative data on the distribution of individual species. Such data, however, are not always available, especially for rare species and those with a hidden lifestyle such as most bat species. In recent years, habitat models relating habitat characteristics, in the form of digital coverage of ecogeographic variables, and species occurrences or abundances are increasingly used for estimating habitat suitability and forecasting species distribution. Moreover, this approach, based on niche theory, has proven useful in understanding the rules governing species assembly at various spatial scales. The search for causes determining patterns in species distributions in natural and disturbed landscapes is of primary importance in ecology, and establishing relationships between species distributions and environmental characteristics is a widely used approach. Modeling also plays an increasingly important role in conservation [7, 8], particularly for understanding impacts of global change on biological diversity, identifying gaps in protected area networks, and for planning and reserve design [9]. Furthermore, the model approach provides the opportunity to obtain high resolution maps that are particularly important for terrestrial conservation planning, where cell sizes of 1–100 km^2 are commonly required, depending on the organism and local habitat heterogeneity [10].

Recently, the author [1] modeled bat species listed in Annex 2 of the Habitat Directive across the country using a 0.63 km2 resolution. The study was based on location data with precise geographic coordinates available to date, mainly those published in the summary article of Benda et al. [4], using three modeling methods such as ecological niche factor analysis, generalized linear model, and discriminant analysis.

In recent years, more effective modeling methods based on presence-only data have become increasingly popular. Among these methods, Maximum Entropy, a recently developed modeling method, implemented as the free software 'Maxent' [11] is particularly popular. It attempts to find the distribution of maximum entropy (i.e., least constrained) that still agrees with all the observed data, and the value of the environmental variables at the locations where the species has been observed. Maxent performs well compared to other modeling methods [12], including when few presence data are available [13], making it especially attractive in data-poor regions. However, the method is vulnerable to bias in the input data [14]. It also shows a tendency to over fitting the presence data [15] and thus further enlarges the effect of sampling bias and spatial autocorrelation.

In recent decades, a growing number of research studies have shown that niche models developed by incorporating remotely sensed predictors are more robust; these data can improve the prediction accuracy and tend to refine mapped distribution of species and habitats, compared with climatic/topographical variables-only models [16].

Remote sensing data can play an important role in developing cost-effective tools for modeling, mapping, planning, and protecting biodiversity. This is especially true at the scale of specific landscapes where the detection of patterns of species distribution can be greatly improved by including this type of data [17].

In recent years, many new data on the distribution of bats in Bulgaria have been accumulated. Of particular importance in this respect was the project 'Mapping and Determining the Nature Conservation Status of Bats', activity 4, project DIR - 59,318-1-2 'Mapping and Determining the Nature Conservation Status of Natural Habitats and Species - Phase I', run between 2011 and 2013 by the Ministry of Environment and Waters. For complete project reports concerning bat species included in Annex 2 of the Habitat Directive see [18]. The abundant new data collected within the project, a result of intensive and extensive targeted studies for a brief period of time in context of the current state of nature, allow for a more in-depth analysis in the light of what has been known so far and the existing knowledge gaps.

This chapter aims to achieve the following: on the basis of presence-only modeling approach, combining current data on species distribution with a range of environmental layers, including satellite imagery, to reveal quantitatively the distributional patterns of bats in Bulgaria; to investigate potential ecological factors responsible for these patterns; to obtain meaningful biogeographical species groups; to document geographic patterns of species richness, rarity, and vulnerability; to analyze relationships between environmental factors, including anthropogenic changes of land cover and these biodiversity indices; and to highlight critical areas for bat conservation.

The result of the study can be useful for guiding further strategic conservation decisions, to assist the elaboration of management plans and to form a base for formulating restrictions and regimes to be included in future management plans of Natura 2000 sites, and to evaluate the impact of plans and projects on habitats and species listed in the Habitats Directive.

2. Material and methods

2.1. Species data

The data used in this study come from a database of georeferenced records developed as part of the project 'Mapping and Determining the Nature Conservation Status of Bats', activity 4, project DIR - 59,318-1-2 'Mapping and Determining the Nature Conservation Status of Natural Habitats and Species - Phase I', deposited in the Ministry of Environment and Waters and available under request. The data were collected during the period 2011–2012 within the Natura 2000 network. Bats were caught by hand from their roosts or by using mist-nets placed at entrances of caves, galleries, and at rivers and streams. All determinations were based on captured individuals, following the field guide of Dietz & Von Helversen [19]. Many of the captured individuals were photographed. Doubtful determinations were considered if their photographs and recorded standard measurements allowed the confirmation of the initial species identification. Exceptions were the determinations of the four species of the *M. mystacinus* morpho complex (*Myotis mystacinus*/*M. alcathoe* and *M. brandtii*/*M. aurascens*). Although the original determinations made by field experts were accepted, they should not be considered as certain, having in mind that 'further accumulation of genetic and morphologic data is needed to justify the variations and allow practical species identification' [20].

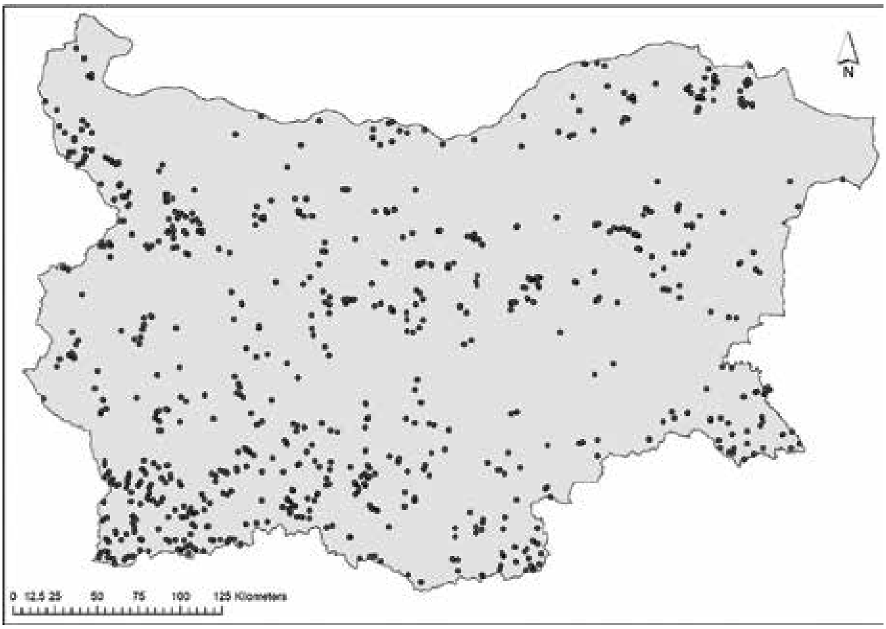

Figure 1. Spatial distribution of all georeferenced localities of 29 bat species used to model their habitat suitability. The number of points for each species is shown in **Table 1**.

In compiling the data set, the occurrence localities were screened to remove duplicate occurrences. In total, the final data set consisted of 1235 georeferenced point localities (**Figure 1**), which rendered 2766 unique species-locality combinations representing the distribution of 29 species. In Bulgaria, research efforts were mostly focused on bats roosting and swarming at caves and galleries. Relatively limited amount of records was available for the forest-dwelling species. The spatial coverage of the obtained data set clearly overcomes this discrepancy providing a balanced amount of data covering the bat's habitat diversity over the country.

2.2. Ecogeographical predictors

Two topographical variables were used as proxies for abiotic conditions are as follows: elevation above sea level and topographic wetness index (**Figure 2**). The first variable was based on 1-arcsecond (30 m) SRTM digital elevation model freely available at the United States Geological Survey's EarthExplorer site [21]. Preliminary analyses have shown that on the surveyed territory, the elevation is strongly negatively correlated with the mean annual temperature, maximum temperature warmest month and quarter, minimum temperature coldest month and quarter, mean temperature wettest and driest quarter, while rainfall is positively correlated along the altitudinal gradient.

The digital elevation model was used to calculate topographic wetness index (TWI) using, SAGA GIS [22], which represents areas with high water retention potential (higher scores). It describes the depressions of the relief, where water bodies and river beds most often occur, and the local humidity is higher. It can be supposed that it will be an important ecogeographical predictor of habitat suitability for many bat species, in particular, in lower parts of the country which are hot and dry during summer. It is also known that many species of bats prefer the proximity of water and/or riverine vegetation where insect abundance tends to be higher [23].

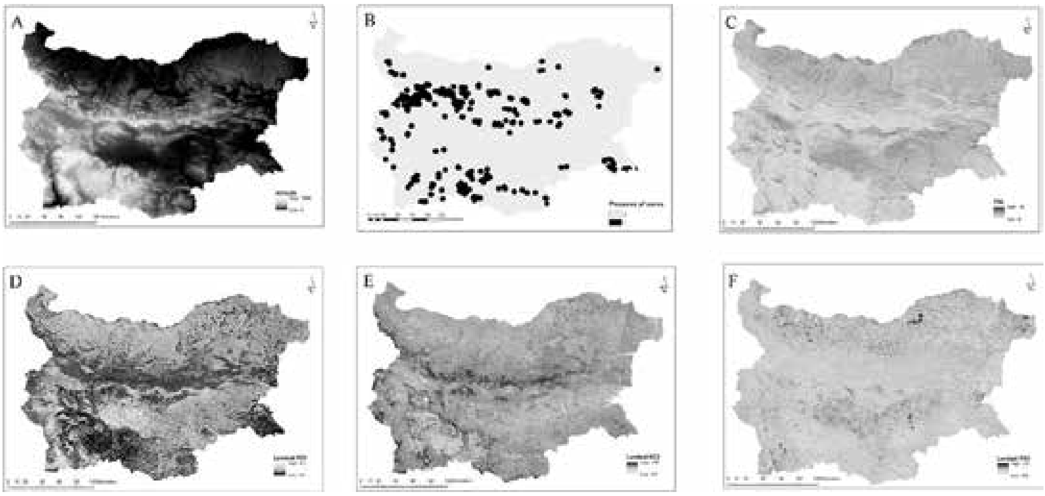

Figure 2. Environmental layers. (A) Altitude. (B) Presence of caves. (C) Topographic wetness index. (D) First principal component of Landsat spectral data (LPC1). (E) Second principal component of Landsat spectral data (LPC2). (F) Third principal component of Landsat spectral data (LPC3).

Considering the importance of caves as roosts for a large part of the bats in Bulgaria, a digital layer was compiled, showing the presence of caves in a radius of 5 km (**Figure 2**). It was based on the coordinates of the studied caves, available in the database.

Landsat imagery was used to present the peculiarities of the Earth's surface. In the selection of scenes, the aim was to represent the season of maximal vegetation development and to cover a period closest to the period during which the data were collected. However, in this regard, the author was struggling with some problems with the quality of the available images taken after 2003 due to a hardware failure and missing 22% of the pixels of Landsat 7 scenes [24]. For this reason, images taken before this date were selected. Ten scenes (georeferenced GeoTIFF files) from paths 181–185, rows 29–31 for the months of June–August of the years 1999–2000 from the Enhanced Thematic Mapper Plus (ETM+) sensor onboard Landsat 7 satellite were acquired from USGS [25] (for details see [26]). Despite the fact that the satellite images represent an earlier period, the peculiarities of the land cover showed the same general spatial patterns as during the study period. Correspondence between the state of the land cover presented by satellite imagery to that at the time of study is also because the data were collected within the Natura 2000 network, where the human impact on vegetation is poorly pronounced. This was also verified by comparing the land cover descriptions available in the field protocols with that shown on the satellite images and on Google Earth™.

Adjacent bands in multispectral satellite images were highly correlated, which implies redundancy in the data. To overcome this problem, spectral values for different bands have been summarized by principal components analysis (PCA), and three uncorrelated principal components were extracted (**Figure 2**), presenting over 95% of the variability of the initial spectral data. To facilitate the interpretation of the environmental information presented by the obtained PCs, an analysis of the relationship between the principal component scores and the CORINE land cover classes at the third level [27] was made. For this purpose, for each cover type, the mean values of the pixels representing the principal component scores for each of the three components were calculated [25]. For the first Landsat PC1 (LPC1), the comparisons showed that moist places and forest vegetation (water bodies, watercourses, coniferous forest, mixed forest, broad-leaved forest) had the lowest pixel scores (average values of 1–1.5). Moors and heat land, transitional woodland shrub, green urban areas, sport and leisure facilities were associated with the middle part of the gradient (average values of 1.5–2). The range of 2–2.5 presented moderately anthropogenically influenced habitats such as agricultures and natural vegetation, fruit tree plantations, natural grassland, complex cultivation patterns, pastures, road and rail networks, vineyards, urban fabric, and nonirrigated arable land. The highest scores on this gradient (average values in the range of 2.5–3) represented xerophilous bare surfaces—sparsely vegetated areas, most of which are highly anthropogenically influenced—industrial units, mineral extraction sites, dump sites, dunes at beaches, and bare rocks. These comparisons show that LPC1 represents the nature of the vegetation—from well-developed forest vegetation in relatively humid conditions through shrubs and open spaces to bare and anthropogenically disturbed places. In practice, it can be said that it largely reflects the type of vegetation mainly in the form of the degree of its anthropogenic disturbance. Comparisons with the second principal component of spectral data (LPC2) showed that it separates the coniferous forests (low mean scores) compared to other types of vegetation, mainly to deciduous forests (high mean scores). Open places and bushes occupy an intermediate position. In mountainous areas, it very well reflected the belts of forest vegetation. The range of scores on the third principal component (LPC3) was too narrow, which means that it reflected only slight differences in the nature of the land cover, which makes its interpretation difficult. Still, it can be said that it separated the sites covered with vegetation (lower mean scores) from those without vegetation, including most places of anthropogenic origin (higher mean scores). The environmental data set used in this study can be considered as sufficiently representative to characterize the ecological requirements of species. This provides a good basis for ecological modeling and it can be expected that the resulting models have the necessary ecological realism.

Since the grain of Landsat and topography images (30 × 30 m) was too fine with respect to the scale at which the bat species discriminate and utilize essential habitat resources, environmental layers were rescaled to pixel size of 200 m. Although this resolution is still too fine, at least for climatic features of given area, it ensures a closer link between the values of other important factors and the bat locations. It corresponds well to such microhabitat features as the presence of suitable roost sites and foraging habitat [28].

2.3. Statistical model

In order to reveal the patterns of distribution of the species in the context of the available locations and the environmental factors considered to be relevant in this respect, modeling has been done by using the software Maxent (version 3.2.1). Model calculations were made using logistic output. Five cross-validation replicates were run for each species model and averaged into a single model. Recommended default values were used [11]. For each species, presence points were randomly divided into calibration (training) and evaluation (test) sets (30% samples for evaluation), and ROC curves and AUC figures were obtained. The potential sampling bias was addressed by the inclusion of the so-called bias file that allows generating background data with the same bias as occurrence data [29, 30]. The bias file was constructed using a Maxent model built on the basis of all locations. Model performance was evaluated based on the area under the curve (AUC) of the receiver operator characteristics (ROC) value. The AUC value is an indicator of the predictive accuracy of a model, correctly ranking presence locations higher than random. The AUC value ranges between 0 and 1, with higher values indicating better model fit; a model with an AUC = 0.5 indicates that the model performed no better than random, and a value over 0.75 is considered to be a good model performance [12]. The difference between the AUC values based on training and test localities was regarded as a measure of the degree of model over fitting. The smaller the difference between the two, the lesser the overfitting present in the model, resulting from preferential sampling and spatial autocorrelation [31].

2.4. Postprocessing

Based on obtained species models, Levin's niche breadths were calculated by using ENTools package. The measure treats suitability scores as proportional to utilization and reflects species' relative spread across a niche and vary in terms of suitability scores across space [32].

To summarize the results from modeling, a principal component analysis (PCA) was carried out on the matrix of correlations calculated from the 29 species models, using the 'Principal components' feature in ArcGIS v10.1 (ESRI). PCA summarizes the species models into a few new axes that best explain the variation found in the initial data set. The pixel scores of the first three axes, explaining the maximum variation were presented as raster layers. In order to figure out what these axes represent, the correlations between each of the PCA axes and the species raster files used as input were calculated. Similar correlations were also calculated between principal components and the environmental layers. Band Collection Statistics tool of ArcGIS v10.1 (ESRI) was used. The results were presented graphically in the form of ordination diagrams. Furthermore, based on the matrix of Euclidean distances between species in the coordinate system of the first three ordination axes, a dendrogram reflecting the similarity between the models was built. Ward's method was used for this purpose.

Modeling data were further used to evaluate several synthetic parameters such as species richness, rarity, and vulnerability. For this purpose, the habitat suitability models were rescaled to a coarser resolution of 2.5 × 2.5 km. This grain can be considered close to the 'natural scale of resolution' for a species distribution model [33]. Various telemetry studies found home ranges of species to encompass 2–3 km^2 or less [34–36].

Two types of data were used for this purpose: quantitative, that is, the continuous Maxent habitat suitability values and qualitative, based on presence/absence values. In order to convert the continuous model predictions to discrete the presence/absence values, an arbitrary threshold of 50% was set. This threshold is too restrictive and probably lowered the actual number of species in a particular area. On the other hand, it corresponds to the recent recommendation to favor restrictive thresholds when stacking binary models to compute species richness [37]. Additionally, bearing in mind that the data were collected over all seasons, this threshold may help the regular presence of a species in an area (in summer, related to reproduction and in winter, related to hibernation) to be distinguished from accidental occurrence of vagrant or migrating individuals during spring and autumn [38]. Thus, it can be considered as representing the geographical locations of the excellent and optimal species habitats. Once the thresholds were set, the richness map was produced by combining/stacking binary species maps, using the Raster Calculator feature in ArcGIS v10.1.

To develop the rarity pattern, we used the Index of Relative Rarity (IRR) normalized between 0 and 1 [39]. This index weighs species richness or total suitability according to the range sizes of the species present. Weights (W) were calculated as

$$W = \exp\left(-\frac{Q_i - Q_{min}}{r_i \times Q_{max} - Q_{min}} \times 0.97 + 1.05\right)^2 \tag{1}$$

where Q_i is the occurrence of species i, Q_{min} and Q_{max} are, respectively, the minimum and maximum occurrences in the species pool, and r is the chosen rarity cut-off point (as percentage occurrence).

Occurrence-based index of relative rarity (OIRR) was calculated as

$$OIRR = \frac{\frac{\sum w_i}{S} - w_{\min}}{w_{\max} - w_{\min}} \tag{2}$$

where w_i is the weight of the i-th species in the assemblage, S is the assemblage species richness, $w_{\min}$ and $w_{\max}$ are the minimum and maximum weight, respectively.

Abundance-based IRR (AIRR) was calculated as

$$AIRR = \frac{\frac{\sum a_i w_i}{N} - w_{\min}}{w_{\max} - w_{\min}} \tag{3}$$

where a_i and w_i are, respectively, the habitat suitability and weight of the i-th species in the grid cell, N is total habitat suitability of all species for the cell, and w_{min} and w_{max} are the minimum and maximum weights, respectively. The package 'rarity' was used [40].

For calculation of vulnerability index (V), species were ranked according to the five threat categories defined by the International Union for Nature Conservation (IUCN 2017) as: (1) insufficiently known (data deficient), (2) least concern (3) near threatened, (4) vulnerable, and (5) endangered. The formula was

$$V = \frac{\sum_{i=1}^{S} v_{ri}}{S_r} \tag{4}$$

where v_n is vulnerability rank of species i and S_r is the richness of cell r.

In order to investigate which environmental factors best explained these synthetic indices, multiple regression analysis was used. It can be expected that this approach violates the assumption that residuals should be independent and identically distributed, resulting in inflated type-I errors due to residual spatial autocorrelation [41]. However, recently, it has been shown that short-distance residual spatial autocorrelation and the associated inflated type-I errors have no significant influence on the interpretation of regression coefficients [42, 43]. Regression analyses were performed by using Statistica 7.0 software (StatSoft, Inc. Statistica for Windows, Tulsa, OK).

3. Results

3.1. Distribution models

All models had a high level of predictive accuracy (**Table 1**), with AUC-training values between 0.7 and 0.97. AUC-test values ranged between 0.65 and 0.9. The mean difference across species between AUC-training and AUC-test was 0.054 indicating some over fitting, that is, that some models fit too tightly to calibration data, limiting to some extent their ability to predict

Species	N-locs	Niche breath	Training AUC	Test AUC	Alt	Cave	TWI	LPC2	LPC1	LPC3
Barbastella barbastellus	68	0.74	0.71	0.66	35.99	16.87	1.76	21.78	23.11	0.48
Eptesicus serotinus	86	0.87	0.78	0.69	25.06	44.38	4.61	14.09	10.25	1.62
Hypsugo savii	87	0.84	0.75	0.70	55.37	13.90	10.22	6.80	7.05	6.67
Miniopterus schreibersii	145	0.69	0.80	0.71	15.62	63.36	11.36	0.82	5.44	3.41
Myotis alcathoe	30	0.42	0.79	0.71	56.94	2.98	13.09	19.20	6.80	0.99
Myotis aurascens	13	0.98	0.83	0.72	11.70	39.23	15.17	24.49	5.09	4.33
Myotis bechsteinii	65	0.89	0.80	0.73	6.75	14.01	11.73	22.75	32.59	12.17
Myotis blythii	108	0.90	0.79	0.74	34.87	36.80	10.68	5.00	8.45	4.20
Myotis brandtii	18	0.50	0.78	0.71	68.94	4.57	1.39	19.21	5.80	0.09
Myotis capaccinii	83	0.72	0.78	0.74	22.76	66.85	1.21	0.66	3.36	5.17
Myotis daubentonii	61	0.95	0.76	0.74	23.94	11.42	21.74	10.03	31.71	1.16
Myotis emarginatus	86	0.90	0.82	0.74	13.90	56.43	8.09	3.78	15.08	2.71
Myotis myotis	79	0.86	0.81	0.75	8.00	71.39	7.71	4.16	6.14	2.61
Myotis mystacinus	30	0.56	0.82	0.75	58.81	2.82	15.31	6.52	16.15	0.40
Myotis nattereri	50	0.80	0.85	0.77	12.92	58.98	1.74	8.41	9.55	8.41
Nyctalus leisleri	53	0.80	0.83	0.78	12.25	2.72	28.36	47.74	4.90	4.03
Nyctalus noctula	62	0.90	0.80	0.78	14.95	2.63	52.38	25.90	3.78	0.37
Pipistrellus kuhlii	6	0.70	0.85	0.79	72.84	17.58	1.82	0.00	5.50	2.27
Pipistrellus nathusii	6	0.89	0.88	0.79	11.96	17.22	40.12	1.80	0.07	12.17
Pipistrellus pipistrellus	72	0.95	0.86	0.82	20.20	1.48	22.11	34.09	19.70	2.42
Pipistrellus pygmaeus	17	0.92	0.87	0.82	0.00	4.98	2.13	65.63	18.97	8.29
Plecotus auritus	56	0.49	0.87	0.83	83.81	1.12	2.77	0.97	6.13	5.21
Plecotus austriacus	130	0.93	0.93	0.84	45.18	11.37	14.22	6.02	13.45	9.77
Rhinolophus blasii	28	0.61	0.87	0.85	44.52	36.87	12.98	0.18	3.48	1.98
Rhinolophus euryale	95	0.79	0.90	0.86	28.89	51.08	9.74	1.66	7.16	1.48
Rhinolophus ferrumequinum	464	0.94	0.88	0.86	16.73	47.76	8.22	2.67	22.69	1.92
Rhinolophus hipposideros	439	0.90	0.86	0.86	19.00	62.91	10.03	0.80	6.34	0.93
Rhinolophus mehelyi	12	0.67	0.90	0.87	48.83	30.86	5.66	8.33	4.94	1.39
Vespertilio murinus	32	0.64	0.88	0.88	63.81	1.52	11.25	1.04	16.13	6.24
Mean	—				31.76	28.23	12.33	12.32	10.98	3.83

Table 1. Mean training and test AUC's for the replicate runs and estimates of the relative contributions of the ecogeographic variables to the Maxent model.

independent evaluation data. However, it should be mentioned that when the models were run without bias file (results not shown), the mean value of the differences in species models was 0.09.

Contrary to expectations, there was no correlation between the niche breadths and the AUC-test statistics. The same was valid for the number of points for each species. This contradicts to the existing opinions that the generalist species have lower AUC scores [12]. This result shows that even species with large niches, broadly distributed in the territory of the country are closely dependent on specific ecogeographic factors.

Nyctalus noctula, Myotis emarginatus, M. blythii, Rhinolophus hipposideros, Pipistrellus pygmaeus, Plecotus austriacus, Rhinolophus ferrumequinum, Pipistrellus pipistrellus, Myotis daubentonii, and *M. aurascens* had the widest niche. These are the species that are widespread throughout the country. With the narrowest niche were such species *as Myotis alcathoe, Plecotus auritus, Myotis brandtii, Myotis mystacinus,* confined to higher elevations.

The altitude and the presence of caves were the two ecogeographic variables that determine to the greatest extent the habitat suitability on the territory of the country. The altitude had the greatest impact on some mountain species, such as *Hypsugo savii, Myotis alcathoe, Myotis mystacinus, Vespertilio murinus, Myotis brandtii, Pipistrellus kuhlii, Plecotus auritus,* showing their strong commitment to the climatic peculiarities of the mountain regions in Bulgaria. The altitude hardly affected such species as *Pipistrellus pygmaeus, Myotis bechsteinii, Myotis myotis, Myotis aurascens, Pipistrellus nathusii, Nyctalus leisleri, Myotis nattereri, Myotis emarginatus, Nyctalus noctula*, which indicates that the climatic variables are of less significance compared to other factors.

The presence of caves determines to a large extent the suitability of the habitat and the distribution of some species such as *Eptesicus serotinus, Rhinolophus ferrumequinum, Rhinolophus euryale, Myotis emarginatus, Myotis nattereri, Rhinolophus hipposideros*, and *Myotis myotis*. The proximity of caves did not affect the habitat suitability of *Plecotus auritus, Pipistrellus pipistrellus, Vespertilio murinus, Nyctalus noctula, Nyctalus leisleri, Myotis mystacinus, Myotis alcathoe, Myotis brandtii, Pipistrellus pygmaeus*, and *Plecotus austriacus*.

The topographic wetness index reflecting the presence of water bodies in the lower parts of the country had the greatest impact on *Pipistrellus nathusii* and *Nyctalus noctula*.

The appearance of vegetation (coniferous vs. deciduous forests) as represented by LPC2 had a strong influence on dendrophilous species such as *Barbastella barbastellus, Myotis bechsteinii, Myotis aurascens, Nyctalus noctula, Pipistrellus pipistrellus, Nyctalus leisleri*, and *Pipistrellus pygmaeus*.

The effect of LPC1, representing the more general features of the land cover (wet places covered with predominantly dense forest vegetation vs. dry and bare sites) was less pronounced. This gradient had a strong influence on *Pipistrellus pygmaeus, Pipistrellus pipistrellus, Rhinolophus ferrumequinum, Barbastella barbastellus, Myotis daubentonii*, and *Myotis bechsteinii*. Most of them are dendrophilous species.

The effect of LPC3 was negligible—there were no species strongly affected by it.

3.2. Species groups

More information on the direction of impact of the ecogeographic variables used in modeling can be obtained from the results of the PCA based on the correlation matrix of the layers showing the habitat suitability of the species. The PCA correlation biplots showed distinct patterns in the distribution of bat species and ecogeographic variables (**Figure 3**). The first axis (spPC 1) was mainly described by altitude and explained 37% of total variation, whereas the second axis (spPC 2) was related to the presence of caves, contributing another 25.5% of total variation. The most important environmental descriptor for the third axis (spPC3) was LPC2 and to a lesser extent TWI. This axis explained 11.41% of the variability of the species models and represented the positive association of some species with the broad-leaved forests and the associations of some species with water bodies in lowlands. The three species axes explained 74.24% of the total variance.

The first principal component (spPC1), representing the influence of the altitude, and hence, the effect of the main climatic parameters, temperature and humidity, separated cold-lowing mountain species (high positive correlations) from some Mediterranean species occurring mainly in lowlands (high negative correlations with this axis) (**Figure 4**). The other species, albeit showing lower correlations with this axis, also demonstrated well-defined pattern with respect to altitude. Positive correlations on this axis exhibited species whose optima are in the mountain foothills and in the middle mountain belt (**Figures 3**, **4**). Poor correlations with this axis showed the species closely related to caves (**Figure 4**). However, their position on the ordination diagram indicated that they prefer the middle part of the elevation gradient (**Figure 3**). This is largely because most of the caves in Bulgaria are located in the foothills and lower parts of the mountains. Moderate negative correlations with the first axis showed species occurring mainly at the lower part of the elevation gradient (**Figures 3**, **4**). Regarding the second axis, cave-dwelling species formed a well-defined group in the uppermost part of the plot. Correlations to the third axis showed clearly the environmental preferences of species that are not closely confined to caves (**Figures 3**, **4**). They had positive correlations with this axis. These were the mesophilous species that form two groups on the ordination diagram (**Figure 3**)—those inhabiting the middle mountain belt, preferring deciduous forests (high positive correlations with LPC2) and those attached to the more open but humid habitats in the lower parts of the country. Species with negative correlations on this axis prefer dryer habitats with sparse vegetation. In this group, species associated with higher altitudes prefer rock cliffs, and those associated with the lower part of the elevation gradient prefer sites with degraded vegetation.

The dendrogram derived from the Euclidean distances between species within the coordinate system of the first three principal components showed the presence of several well-defined ecological groups (**Figure 5**).

Group 1 comprised relatively rare species with markedly discontinuous distribution pattern in Bulgaria occurring mainly in mountainous regions. With respect to habitat type, the majority of them are confined to moist and deciduous forests. *H. savii* is a petrophilous Mediterranean species.

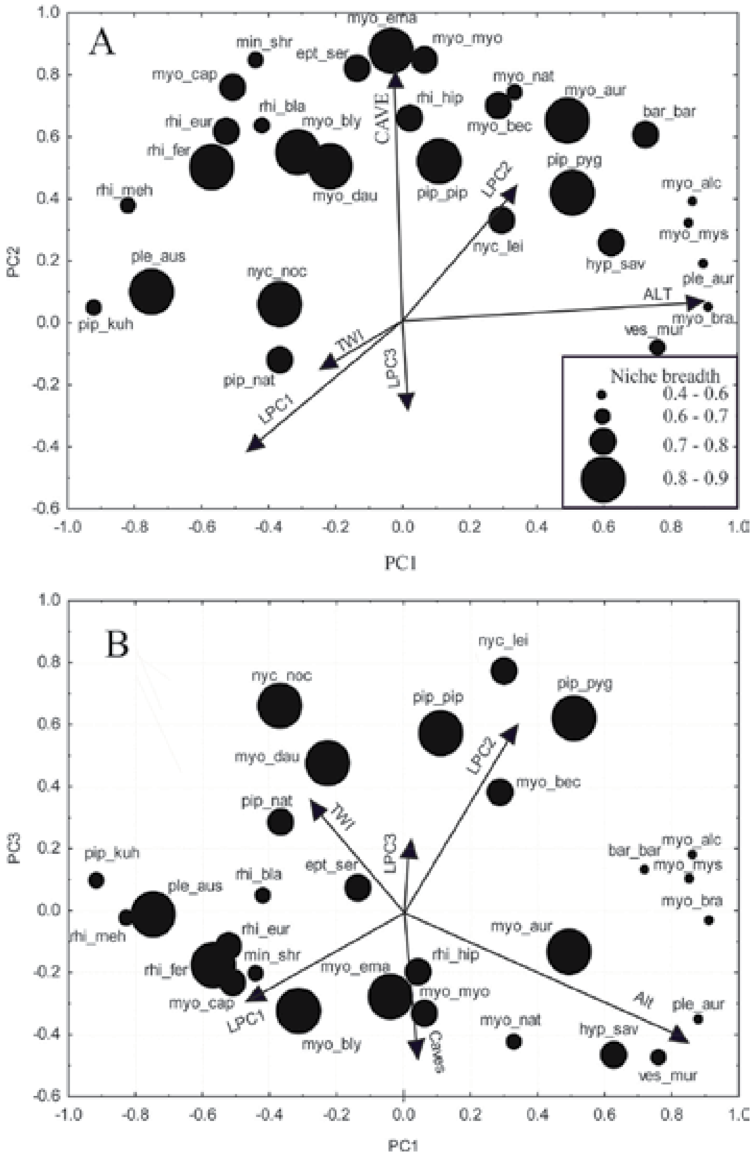

Figure 3. Graphical representation of Pearson's correlation coefficients for the 29 bat species (circles) and ecogeographic variables (arrows) with the first three species PCA axes. (A) PC1 vs PC2. (B) PC1 vs PC3. The size of circles corresponds to the species niche breadth. ALT – Altitude, caves – Presence of caves within radius of 5 km, TWI – Topographic wetness index, LPC1–LPC3 – Landsat principal components. The species names are represented by three-letter abbreviations of the generic and species names.

Group 2. Two subgroups can be distinguished. Group 2a consisted of species with wide niches occurring at low, medium, and medium-high altitudes; although preferring caves, they also inhabit non-karstic areas where they use a variety of other roost types such as mine galleries, buildings, rock crevices, and hibernating in underground spaces. Group 2b comprised species more closely confined to caves, preferring karstic territories at the lower range of the altitudinal gradient.

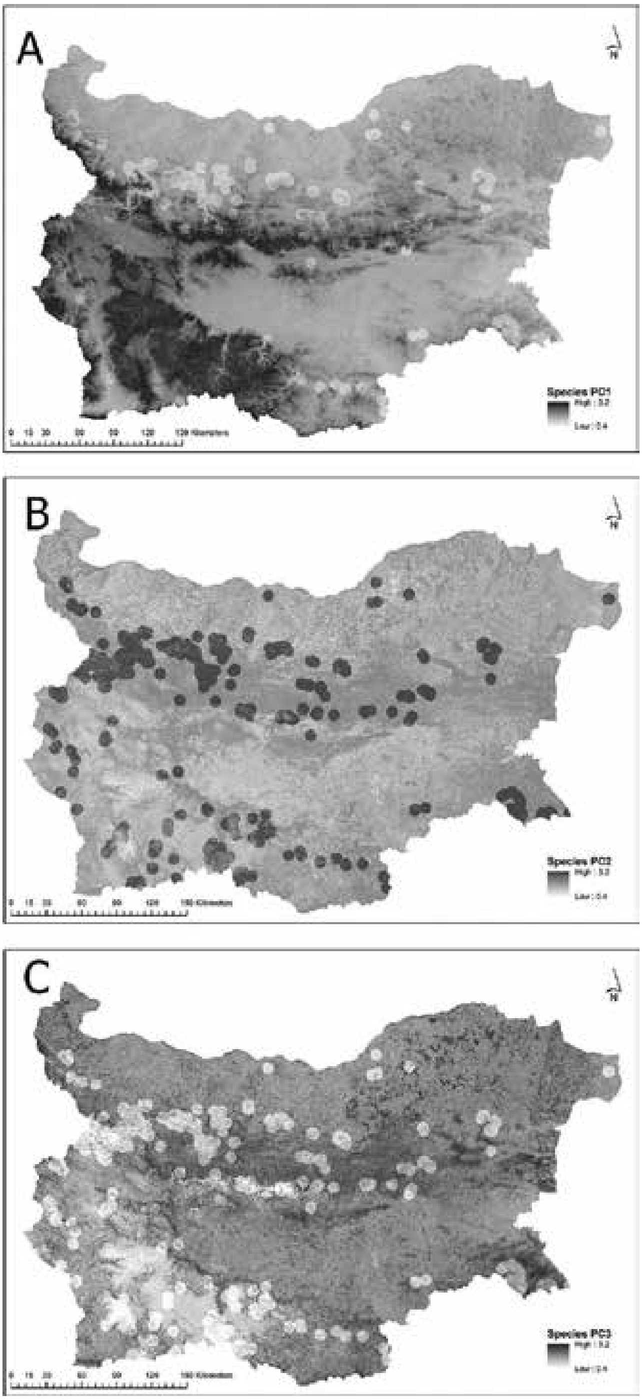

Figure 4. Results of principal component analysis of species models. (A) Principal component scores on the first PC (sppPC1)—High scores suggest the habitat suitability for higher altitude species; the low ones represent the habitat suitability for warm-loving species in the lower parts of the country. (B) Principal component scores on the second PC (sppPC2)—High scores represent distribution of cave-dwelling bats. (C) Principal component scores on the third PC (sppPC3)—High scores suggest high habitat suitability for forest mesophilous species.

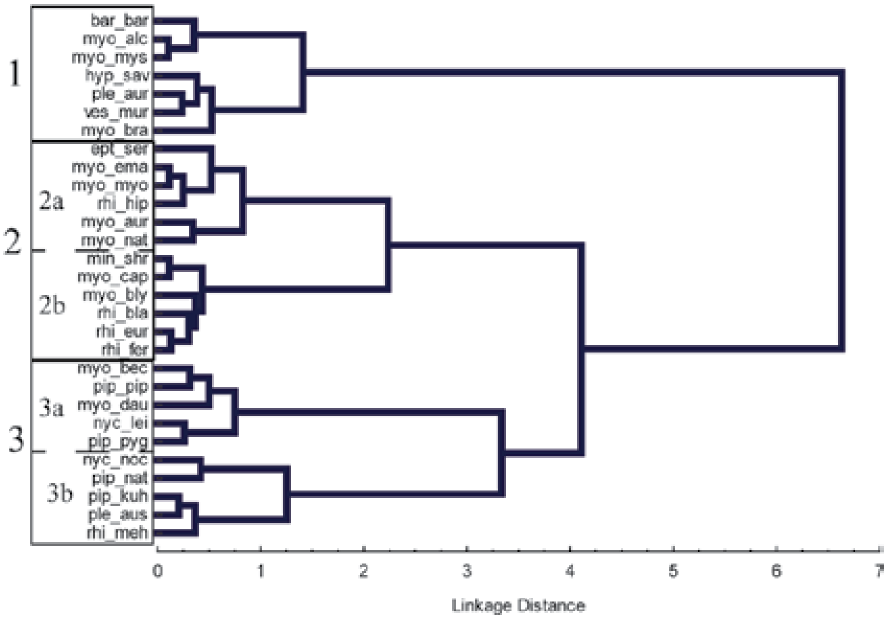

Figure 5. Dendrogram showing the similarity between bat species based on their correlations with the first three principal components.

Group 3. Two subgroups were evident here. Group 3a comprised dendrophilous species, inhabiting wooded and humid areas in low and medium elevation. Group 3b embraced species restricted to lower altitudes, often associated with open areas, xerophilous sparsely vegetated rocky places or water basins.

3.3. Species richness, rarity, and vulnerability

Superimposing the Maxent species models and derived weighted values according to rarity and vulnerability, resulted in the species maps of richness, rarity, and vulnerability, presented in **Figure 6**.

Correlation coefficients between these indices showed that the number of species was moderately positively correlated with rarity (0.67) and relatively less correlated with vulnerability (0.43), while the last two metrics were not correlated with each other. The beta coefficients of individual environmental factors as well as their overall contribution in the prediction of vulnerability (VU), species richness (SR), and rarity (RA) are presented in **Table 2**. The species richness was strongly affected by the presence of caves and moderately negatively influenced by LPC1. In total, the model explained 82% of the variance in species richness. Rarity, presenting the concentration of rare species was moderately positively affected by the altitude and to some extent by the presence of caves. Vulnerability was positively affected by presence of caves and negatively by TWI, altitude, and LPC3.

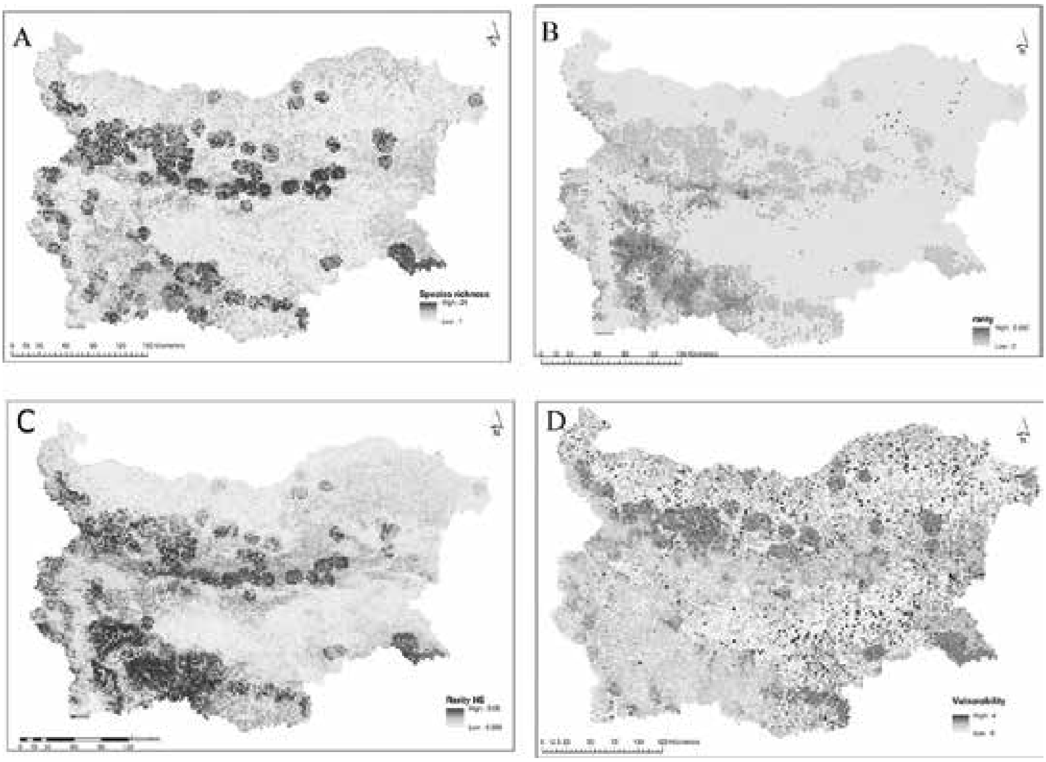

Figure 6. Geographical patterns of bat species richness (A), rarity (B) presence/absence data, (C)-quantitative data, and vulnerability (D).

Environmental predictors	SR	Ra	Vu
Cave PA	0.69	0.38	0.39
WI	−0.12	0.17	−0.449
lpc3	0.06	0.02	−0.299
lpc2	0.22	−0.09	0.079
lpc1	−0.35	−0.18	−0.10
Alt	0.018	0.56	−0.40
Adjusted R^2	0.82	0.59	0.46

Table 2. Standardized regression coefficient of multiple regression showing the relative contribution of each environmental variable in the prediction of species richness (SR), rarity (RA), and vulnerability (VU). All models are highly significant at $P < 0.0001$.

4. Discussion

The results obtained from the modeling show that they correspond well to the knowledge about the ecology and the distribution of the species. The obtained result agrees with the prevailing opinions that, compared with less mobile species, the realized distributions of bats correspond closely with their potential distributions [44, 45]. This makes it clear that this approach is reliable and useful in two respects. On the one hand, it allows to identify the influence of individual environmental factors and to quantify their relative effect on species. Thus, modeling is also a realistic method for studying the ecology of individual species. On the other hand, on the basis of the statistical relations, it allows a reliable forecasting of species distribution.

The obtained results show that species form clusters that can be clearly explained in terms of analyzed ecogeographic variables. Generally, altitude is the key factor responsible for the largest differentiation between the species, especially between species in group 1 versus those in group 3b. The species placed in the center of PCA plots, belonging to group 2, tend to occur in environments characterized by the intermediate values of the investigated factors and hence explaining their wide distribution. The influence of altitude is not unexpected given that, in Bulgaria, it determines the spatial differentiation of the main climatic parameters such as temperature and rainfall [6]. Both parameters are known to impose limits on the ability of bats to forage for food [44, 45] and to survive prolonged hibernation periods or seasonal heat [46]. These climatic factors may also act indirectly by limiting the availability of essential resources.

Two factors related to geomorphology (presence of caves and topographic wetness index) are also considered to be important factors shaping bats distribution patterns. The presence of caves is important for the majority of the species. Although the topographical wetness index does not have a strong influence on most species, it largely determines the distribution of *Pipistrellus nathusii, Myotis daubentonii,* and *Nyctalus noctula* (**Figure 3**). The obtained result agrees well with the available knowledge that these species prefer the proximity of water and/or riverine vegetation where insect abundance tends to be higher [4, 5].

Surprisingly, the effect of vegetation-related variables, LPC1 and LPC2, was relatively weak. Nevertheless, it should be mentioned that, LPC2, presenting the influence of deciduous forests, appears to be an important factor determining the habitat suitability of a large number of species, especially those that are not closely confined to caves. The relatively weak influence of this factor is largely a consequence of its correlation with the altitude and indirectly with the degree of anthropogenic disturbance of the forest cover, having in mind that most of the forests in Bulgaria are preserved mainly in mountains. Regardless of this correlation, the independent influence of this factor is very well demonstrated with respect to some species and allows outlining the distribution of some poorly known dendrophilous species. For some rare species, such as *M. bechsteinii* and *Nyctalus leisleri,* the positive influence of deciduous forests is much more pronounced than that of altitude. They also have large niche breadths, indicating that the rarity of these species is mainly due to the destruction of forests on large areas of the country. The modeling results also show that in the lower parts of the country, the few available favorable habitats are too fragmented. This confirms the need to protect the connecting landscape elements in the lower part of the country.

The correlation of environmental predictors with species richness indicates that it is greatest in karstic areas and decreases in the direction of xerophilous, bare, and anthropogenically disturbed habitats, which is not a surprise. It is interesting to note, however, that species richness is not influenced by altitude (**Table 2**). It is often claimed that elevation gradient mirrors the latitudinal one, and species richness is assumed to decrease monotonically because of reduced temperature and consequent decrease in productivity. This is an indisputable fact on a larger geographic scale across continents. In fact, as it can be seen on the map (**Figure 6**), species richness appears to be higher in the middle mountain range. This is to a certain extent contradicts to the existing view that the species richness in Bulgaria is highest at the lower part of the elevational gradient, between 100 and 300 m, reaching 17–20 species [47]. This pattern can be explained by the fact that the role of changes in factors other than temperature is also significant. In the lower parts of the country, the forest is heavily destroyed, and the habitats of the bats are disturbed on large areas. Conversely, in the middle mountain belt, because of the rugged terrain, the anthropogenic disturbance of natural vegetation is weaker. Furthermore, elevation gradients have a more or less stable condensation zone at middle altitudes causing favorable conditions for many taxa, including invertebrates during the entire vegetation season (summer drought act in an opposite direction in lower elevations). On the variable terrain, local climate can vary considerably over short distances allowing small areas to present climatic optima for many bat species. Thus, middle mountain belt, being a transient zone, allows the co-occurrence of cold-loving species, preferring mountainous areas and some southern species, with wider ecological tolerance. In the highest parts of the mountains, species richness really decline. Thus, the change of the species richness of bats with altitude in this country is hump-shaped with a maximum at the lower part of the altitudinal gradient. This is one of the four common patterns noted in the literature, resulting from optimal combination between water availability and temperature [48, 49]. For bats in Bulgaria, however, the anthropogenic factor is also likely to be of significant importance for the observed trend.

Rarity primarily provides an insight into the facet of species biodiversity that is most at risk of extinction [50], also with respect to the maintenance of vulnerable ecosystem functions [51]. Different axes of rarity are usually considered: restricted abundance, restricted geographic distribution, and narrow niche breadth. In this study, the metric mainly reflects the spatial aspect. The obtained results suggest that, on the territory of Bulgaria, rare species occur predominantly in the karstic and mountain regions. In most cases, these are obviously species with limited tolerance with respect to the environmental conditions in the country. Of particular interest are the rare species confined to the mountains. It can be supposed that they will be most vulnerable to the climate change. It can be expected that the ecological amplitude for these species will continue to shrink, and their abundance will decrease during climate warming. Rare species associated with caves will obviously be vulnerable to human disturbances in caves and their surroundings.

The beta coefficients for vulnerability (**Table 2**) show that in the lower and drier parts of the country, as well as near caves, there is a higher relative share of vulnerable species. As has already been mentioned, the anthropogenic negative impact on habitat characteristics important to bats is most pronounced in the lower parts of the country. The negative relation of LPC3 to species richness (**Table 2**) can be interpreted in this direction. The relative share of rare species is higher in sites covered with vegetation (lower mean scores of LPC3) and low in most places of anthropogenic origin (higher mean scores). Overall, the relative share of vulnerable species is greatest in the lower parts of the country, near caves, and in drier places with a relatively well-preserved natural vegetation.

In this study, we quantitatively analyzed the Bulgaria-wide, high-resolution patterns in distribution of 29 bat species, species richness, rarity, and vulnerability. It was shown that species distribution models can effectively be used to reveal these patterns, covering areas that never have been sampled. The analyses revealed the individual role of important ecogeographic factors such as altitude, presence of caves, topographic wetness index, and various land cover features derived from satellite imagery. The results quantitatively confirmed the previously recognized types of distributional patterns, which were based on informal expert opinions. For the first time, high-resolution maps of species richness, rarity, and vulnerability were made.

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Bat Conservation Management in Exploited European Temperate Forests

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Abstract

Forests offer important refuge to bats by providing attractive roosting and foraging habitats. Their conservation is a major responsibility of forest managers. The use of tree cavities by bats in forests depends on the specific demands of each species, with a large range of different types of microhabitats utilised, from degraded cavities such as peeling bark to healthy hollows in live trees ensuring the temporal stability of the habitat. The conservation of tree-dwelling bats should not be dissociated from their fission-fusion behaviour which involves the use of many different roosts. Conservation measures must therefore take into account forest habitats suitable for feeding and in particular, forest parameters such as structure, composition, vegetation and foliage, among other elements such as deadwood, all upon which the forest manager can intervene. Acting in favour of bats requires close consideration of their complex individual responses concerning roost selection and foraging habitat selection, which is largely dictated by the reproductive status of individuals. Thereafter it is possible to evaluate the impact of wood harvesting on bats and to infer silvicultural conservation measures. The implementation of recommendations must then subsequently be based on a strong involvement on the part of the forest manager.

Keywords: Chiroptera, tree cavities, roost network, foraging habitat, deadwood, forest management

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1. Introduction

In Europe, forests cover an area of approximately 4.5 million km^2, from the boreal forests of Scandinavia and Russia to the forests of the Mediterranean, including natural forests, plantations and intensive production forest systems [1]. They constitute a habitat particularly attractive to bats by providing the potential for roosting and foraging. Since the 1990s, conservation biologists have considered the forest as one of the most important refuges for biodiversity, in particular for a number of terrestrial mammals and bats [1–3]. Moreover, forests probably represent one of the least altered habitats across the continental landscape. Thus, forest managers must engage in implementing favourable management strategies for these species [2, 4]. Our knowledge about bats was still largely considered fragmentary at the beginning of the twenty-first century, outlined in a review on the relationships between bats and forests in North America [5]. In Europe, studies have multiplied in recent years promoting a greater understanding of the impacts of forest management on bats. This path to knowledge has revealed the relationships between bats, roosting sites, and foraging habitats across a number of settings, from natural forests, to intensive production forests, and to plantations with exotic species [6]. Unsurprisingly, bat species abundance and richness is considerably higher in forests that resemble a natural state [2, 7], which is probably in response to a greater presence of certain habitats related to the abandonment of logging practices, such as deadwood and tree cavities [8–10]. However, provided society's demand for wood products persists, the sometimes intensive exploitation of forests will continue to have a strong impact on biodiversity. In Europe, some sites already have high-quality favourable habitats at the landscape scale, principally in forests, and contribute markedly to the concentration of bats, especially the most specialised species [8]. These sites have consequently been included in the Natura 2000 network and are subject to contractual or regulatory management measures favouring biodiversity at the landscape scale. However, recent studies on certain forest habitats within the Natura 2000 network, notably beech (*Fagus sylvatica*) forests show that the measures implemented are slow to produce significant positive results for bats [9]. This can be explained by the slow evolution of forests with tree microhabitats taking considerable time to form, particularly in beech stands [10]. Hence, the integration of biodiversity issues should not wait until results are convincing before engaging in concrete conservation management actions as, in any case, they are typically slow at being implemented without strong regulatory measures. In forests primarily destined for logging, two key questions arise: towards which conservation strategy it is necessary to direct managers? And, is the setting aside of certain areas a sufficient response for bats? Thus, reconciling the issues related to both the exploitation of wood and the conservation of bats, accounting as much for roosts as for their foraging habitats is a true challenge for society [11].

2. Bat use of tree cavities

2.1. Types of roosts

In forests exploited for timber production, the number of available trees with cavities that can be used by bats are generally low, as young vigorous trees are favoured for wood production

[12, 13]. The formation of cavities is very slow. Less than 1% of *Quercus robur* trees of 100 years old or less formed a cavity, compared to 50% of trees aged between 200 and 300 years old and all trees older than 400 years [14]. In forests, time is therefore an essential component to consider. Among cavities, only 9% were used by bats in a lowland temperate forest [15], corresponding to only 1% of trees sufficient in size to possess a cavity [16]. Because bats are incapable of creating their own roosts, they must rely on cavities created by wind, frost, the natural degradation of wood [17, 18], or by other organisms such as saproxylic insects and birds [19, 20]. The selected cavities must provide effective protection against predators and adverse weather conditions (wind, rain, and extreme temperatures) while also supporting social exchanges between individuals [17, 21, 22]. Cavities are generally more numerous on broadleaved trees than on conifers, and are not only favoured by the vitality and diameter of trees but also by the time elapsed since the last harvest at the forest stand level [23, 24]. In Mediterranean hardwoods such as *Quercus ilex*, tree diameter is the best predictor for the formation of microhabitats such as woodpecker hollows, insect holes and peeling bark [24]. Given that cavity-bearing trees are generally scarce in timber production forests, microhabitat density including bat-usable cavities is thus favoured in exclusion areas/set-asides, irrespective of the silviculture stage [23–26].

Bat colonies use tree cavities. As a result, their reproduction is all the more favoured if the forest area they occupy has a high density of potential roosting sites [27]. However, the majority of European forests are subject to the effects of timber harvest, presenting a considerable constraint to the biodiversity associated with tree microhabitats. This therefore constitutes the first major pressure facing bats in forests [2, 12, 13]. Any conservation strategy at the regional scale must therefore take into account the bat species present and the available cavities. Furthermore, the type of cavity selected indeed varies according to the species, *Barbastella barbastellus* preferentially selects cavities such as peeling bark on deadwood, in particular snags [13, 28], that are well exposed to sunlight. This prerequisite contributes to maintaining the necessary heat inside the roost especially when rearing young, consequently reducing the physiological demands linked to thermoregulation [27]. Other species, notably *Nyctalus leisleri* and *Myotis brandtii,* also show preferences for relatively degraded cavities, rather ephemeral and sometimes even distinctly exposed, despite the potential risk of predation [29, 30]. However, most tree-dwelling bat species across different genera select roost types other than defoliating bark, principally woodpecker hollows and narrow fissures/cracks which represent more sustainable cavities, and which are generally protected from terrestrial predators. Maternity colonies target a large available volume in the cavity, situated on a healthy part of the tree and as high as possible; over time a preference for live trees is evident since they ensure better thermal regulation within the roost during periods of extreme weather [15]. Most bat species, for instance, *Myotis bechsteinii*, *M. brandtii*, *Plecotus auritus*, *Vespertilio murinus* and *Pipistrellus* sp. select healthy large diameter trees [16, 30, 31]. Furthermore, whatever the selected roost, the closure of the forest environment allows individuals to take advantage of the foliage and the decline in luminosity to begin foraging earlier and return later all the while sheltered from potential predators [32]. This emergence behaviour has been demonstrated notably for *Barbastella barbastellus* [33], *Myotis nattereri* and *Plecotus auritus* [31]. In contrast, *Nyctalus noctula* and *N. leisleri* have a less manoeuvrable flight not allowing for cluttered areas at the entrance/exit of roosts. They seek out a compromise between the need to avoid predators and the need to take maximum advantage of available solar radiation during the day to minimise energy expenditure concerning the warming of breeding roosts. The cavities selected are thus situated high in trees in order to limit the predation risk where the canopy foliage is sparser favouring the insulation of roosts [34].

With increasing pressure for timber products in European forests, tree-dwelling bats must demonstrate sufficient plasticity in their behaviour in order to adapt to the challenge of a fluctuating availability of suitable roosts. *Nyctalus noctula* and *N. leisleri,* which preferentially use old trees of large diameters [29], can adapt to using young trees [12]. *Myotis nattereri* may target woodpecker hollows but is also known to utilise narrow fissures in small diameter trees such as Birch, *Betula* sp. However, this capacity to adapt can have its limits. In New Zealand, certain colonies of *Chalinolobus tuberculatus* appear no longer able to produce enough young to maintain colony numbers when usable cavities are lacking and food resources are reduced following forest exploitation [35]. Hence, management can affect the capacity of forests to produce the required roosts for maternity colonies. As a result roosts clearly become a limiting factor for bats.

2.2. Fission-fusion behaviour

Bat colonies select cavities of which the size and the type govern the structure and the numbers of the group occupying them. Consequently, pregnant females of *Myotis bechsteinii* may target small cavities high in trees limiting the risk of predation, and then select large cavities with a significant volume that can shelter larger groups at lower sites when they are lactating. In contrast, pregnant females of *Plecotus auritus* select a diversity of cavities in order to use smaller roosts after the birth of young (therefore limiting the size of the group) [31]. Most available cavities in forests have a reduced internal volume. Indeed, cavities of large volume take longer to form and are mainly found on old trees of large diameters [36, 37]. In order to respond to such ecological constraints, i.e. the limited number of tree microhabitats of suitable volume, forest-dwelling bat populations split into subgroups, demonstrating an exchange of individuals on a daily basis [38, 39]. Thus, groups divide and disperse each night (fission) then form new groups the following day, reorganised in accordance to the specific rules of each species, often selecting a new roost (fusion) [38].

Fission-fusion may limit the risk of parasitism [38, 40, 41], as tree cavities being confined spaces are conducive to the development of micro-organisms linked to wood degradation [19] and maintain an increase in humidity and heat favouring the development of bat parasites. In mammals, parasite density decreases with the frequent changing of rest sites [42]. For bats, this phenomenon outlines the importance of using a large number and diversity of cavities. The changing of roosts also allows bats to limit the risk of predation, as predators would no longer know which cavity exit to prowl [41]. Though, the frequency in which bats switch roosts is more dependent on meteorological conditions and the individuals' reproductive status [31, 43]. A disadvantage is that over time, these repeated fissions can lead to a loss of familiarity among individuals as life in a fission-fusion society imposes constant regroupings of different individuals [17, 22, 44, 45]. *Myotis bechsteinii* counteracts this problem with the oldest females organising the colonies around a few lineages or familiar groups that have maintained social links for more than 5 years [45]. In every example, fission-fusion behaviour involves the presence of a close network of primary roosts surrounded by "satellite" roosts, with the gradual and regular establishment of new roosts, especially when the oldest ones begin to degrade [46].

2.3. Roost networks

The turnover of roosts in relation to fission-fusion dynamics occurs, on average, every 2 or 3 days (**Table 1**). As a result, a substantial quantity of available cavities within the home range of a given bat colony is essential. The frequency in which bats change roost is largely influenced by the individuals' reproductive status, as outlined above. Females often change roosts when pregnant and tend to stay longer in the same cavity when lactating because maintaining higher temperatures, which is crucial, is energy-intensive for animals [22]. Accordingly, *Nyctalus lasiopterus* changed the cavity every 2.52 ± 0.74 days before the birth of young but stayed 4.88 ± 1.91 days in a cavity after birth [47]. Similarly, pregnant *Barbastella barbastellus* switched roosts every 2.6 ± 1.6 days, whereas lactating females stayed in the same cavity for up to 9.4 ± 1.8 days [27]. Conformably, reproductive females of the species *Myotis bechsteinii*, *M. nattereri* and *Plecotus auritus* stayed longer in their roosts than non-reproductive females [31].

Myotis bechsteinii may exploit more than 300 different cavities in the same year [31] and is able to use more than 15 different zones for roosting purposes [48]. This is in line with other species such as *Myotis nattereri*, *Barbastella barbastellus* and *Plecotus auritus* [13, 28, 31]. In New Zealand a colony of *Chalinolobus tuberculatus* used more than 300 cavities and re-used only 48% over the course of a year [49]. Conversely, *Mystacina tuberculata* selected a small number of roosts but was likely to stay for longer periods of time [50], demonstrating a much higher loyalty to its chosen cavities. Roosts should be voluminous in order to accommodate a large number of individuals (310 ± 88.1 on average) [51]. However, for the majority of species, colonies do not

Species	**Duration in number of days**	**Reference**
Chalinolobus tuberculatus (1)	1.7 ± 2.0	[51]
Mystacina tuberculata (1)	5.6 ± 6.9	[52]
Eptesicus fuscus (2)	1.7 ± 0.7	[53]
Myotis septentrionalis(2)	1.6 ± 0.5	[54]
	1.26 ± 0.40 to 1.20 ± 0.49	[55]
Myotis bechsteinii (3)	2.1 ± 1.1	[56]
	1.3 ± 0.8	[31]
Myotis nattereri (3)	1.2 ± 0.6	[31]
Barbastella barbastellus (3)	2.6 ± 1.6	[27]
	2.0 ± 1.8	[28]
Nyctalus lasiopterus (3)	2.68 ± 0.82	[50]
Plecotus auritus (3)	1.4 ± 0.8	[31]

Table 1. Average duration of presence (± standard deviation) in one roost by a number of forest-dwelling bat species demonstrating a fission-fusion society, in New Zealand (1), North America (2) and in Europe (3).

exceed more than a few dozen individuals in one roost. This pattern was observed in the small European tree-dwelling bat species such as *Myotis bechsteinii, Myotis nattereri, Barbastella barbastellus* and *Plecotus auritus* [31]. On the other hand, *Nyctalus noctula* composes larger groups that occupy large cavities for greater periods of time (unpublished). These diverse behaviours thus imply the need for different conservation strategies. Bat colonies that exploit many cavities are less sensitive to the disappearance of roosts but species that occupy a tree cavity for longer lengths of time are obviously more affected by their disappearance [32, 50]. Thus, the forest manager is faced with the challenge of maintaining a high capacity to accommodate all species throughout his territory. In addition, depending on the forest, the number of cavities can vary considerably. If we consider only woodpecker hollows and fissures on live trees, the number of microhabitats per hectare in a production forest may be greater than 10, while other forests may offer only a very limited or even zero carrying capacity [2, 6, 17, 32]. In the latter, a loss or alteration of roosts constitutes a major limiting factor for bats.

3. Foraging habitats in forests

3.1. The importance of forests as feeding opportunities

The literature is rich in identifying the main forest characteristics utilised by most European bat species [2, 6], as forests undoubtedly remain complex environments offering foraging habitats for these species, even when insect populations fluctuate. Studying forest habitats rather than prey abundance can thus contribute to a greater understanding of foraging behaviours [52, 53]. Regardless of the species, certain forest habitats are more attractive than others, broadleaved forests above all [50, 54–59]. It is therefore difficult for a forest manager to apply bat-friendly practices without a precise description of the factors determining habitat selection. According to the numerous studies, forest management causes changes (in terms of the composition and the structure of a forest stand) that are either acceptable or not for bats, as foraging behaviour may be jeopardised [60]. Logging forests for timber production may therefore reduce a colony's ability to sustain itself due to a lack of feeding resources [60, 61].

3.2. Favourable forest stands

At the bat community level, the silvicultural parameters that best explain the selection of certain forest habitats are that of structure, composition, and the quantity of foliage among other elements beyond the stand itself.

The maximal diameter of trees, different from stand age (but related) generally translates to a forest stand of overmature trees with the presence of microhabitats [10]. Microhabitats can even serve occasionally as refuge for bats that forage several kilometres from their roosting site, when weather conditions dramatically change [31]. Indeed, old forest stands are the most important habitats for bats as they offer a great potential for roosting [31, 60]. In a diverse forest landscape, bats will predominantly select broadleaved tree stands dominated by oaks and tend to avoid conifers [31]. This is in direct response to the entomological richness associated with these tree species [62]. Native *Quercus* spp. have the highest number of dependent insect species including various orders of saproxylics as well as defoliators (*Coleoptera, Lepidoptera, Heteroptera*, etc.). They are followed by *Betula* spp. which can sometimes have a greater number of individuals present but have less taxonomic groups associated with *Salix* spp., *Crataegus* spp., *Prunus* spp., and *Populus* spp. The first conifer species is *Pinus sylvestris* before *Fagus* spp. and *Picea abies* [63]. Moreover, the more the forest habitat is diversified, the more the insects' emergence is spread over time. For example, defoliators commonly emerge at different times in accordance with shade-tolerant and shade-intolerant trees [19]. In addition, a diversification of accompanying tree species and a strong presence of forest gaps in mature conifer plantations can have a positive impact on bat activity [64, 65], with bats contributing significantly to the control of insect pests in forests [66]. Furthermore, a higher density of vegetation and a greater heterogeneity from the ground to the canopy appear to increase bat species richness. *Myotis bechsteinii* principally forages within the dense canopy [31, 67] whereas *Myotis myotis* is a specialist of bare ground-dwelling prey [68]. Indeed, a complex structure of the forest with dense foliage, depressions, protuberances, and other ecotones is favourable to the development of different thermal and hygrometric conditions, the source of high entomological production [23, 69]. This can result in a higher activity of hawkers and gleaners [59, 70–72]. The latter forage for prey by gleaning insects from the substrate in dense foliage, while the former requires open spaces, such as forest clearings, paths, corridors, and edges even though they mainly hunt insects dependent on foliage [59, 70, 71]. Hence, the more diverse a forest is in composition, structure, and stratification, the higher bat species abundance and species richness will be [2]. Finally, additional forest environments such as streams and ponds, which present drinking sites for all individuals, also favour the occurrence of forest-dwelling bats [6, 7].

4. The role of deadwood

In Europe few bat species roost in dead trees. *Nyctalus leisleri* and *N. lasiopterus* are known to roost from time to time in cavities found on dead or dying trees [29, 73], and *Barbastella barbastellus* roosts regularly behind peeling bark, especially on snags [27, 28, 74] just like some *Myotis* and *Pipistrellus* species. The use of these ephemeral roosts is usually only part of a network of trees surrounding optimal roosting sites [13].

Deadwood constitutes an important support for the development of wood decaying insects with nearly a third of all forest insects directly depending on it [19, 26, 75]. Foraging bats can indeed take advantage of the presence of fresh deadwood by targeting any emerging *Coleoptera* insects. It is often the case with conifer stands that have been cut and stacked which favour the rapid concentrations of bark beetles (*Scolytidae*), subsequently attracting opportunistic species of *Nyctalus*, *Eptesicus* and *Pipistrellus* (**Figure 1**) [76, 77]. More widely, the richness of bat species has been found to be positively correlated to the volume of deadwood, either lying or standing, greatly increasing when deadwood quantity exceeded 25 m^3/ha [78]. This relation can be explained by deadwood-dwelling preys or by changes in the forest structure, due to openings created by dead trees that are favourable for edge-hawkers such as *Pipistrellus* spp., *Eptesicus*

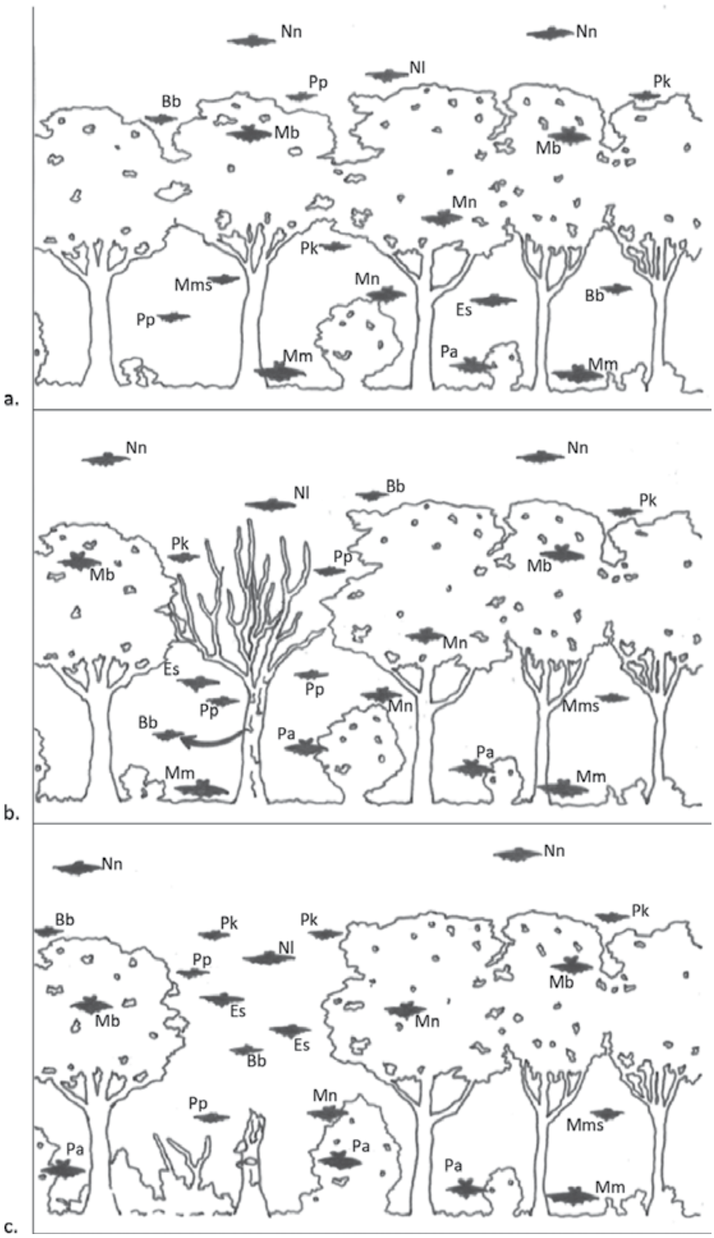

Figure 1. The spatial distribution of foraging bats in a forest stand. Gleaners (*Myotis* and *Plecotus*) forage within the foliage of the trees and around shrubs and bushes in the understory, whereas hawkers (*Nyctalus*, *Eptesicus*, *Barbastella* and *Pipistrellus*) are distributed above and under the canopy (a). When a tree dies, (b) a space free of vegetation forms. This clearing is generally avoided by gleaners and possibly exploited by hawkers where the space is not too cluttered by dead branches. *Barbastella barbastellus* may take advantage of any peeling bark for potential diurnal roosts. Once the dead tree has fallen, (c) hawkers distribute at the top of the clearing. The forest gap allows light to penetrate to the ground level, favouring the development of low vegetation. Certain gleaners (*Myotis nattereri* and *Plecotus auritus*) take advantage of this opportunity by foraging in the understory while others (*Myotis myotis*) require bare ground, and *Myotis bechsteinii* continues to exploit the foliage of the canopy. Bb: *Barbastella barbastellus*; Es: *Eptesicus serotinus*; Mb: *Myotis bechsteinii*, mm: *Myotis myotis*; Mms: *Myotis mystacinus*; Mn; *Myotis nattereri*; Nl: *Nyctalus leisleri*; Nn: *Nyctalus noctula*; Pa: *Plecotus auritus*; Pk: *Pipistrellus kuhlii*; Pp: *Pipistrellus pipistrellus*.

serotinus and *Nyctalus leisleri*. On the other hand, gleaners that pick up insects from the substrate e.g. leaves (most of *Myotis* and *Plecotus*) prefer to forage within the foliage [59, 70, 79–81] and do not dwell in areas with large quantities of deadwood, selecting above all forest habitats that are cluttered by vegetation [78].

5. Individual responses of bats to habitat selection

Bats respond differently to roosts as well as foraging habitats (or home ranges) according to their reproductive state. The energy needs of reproductive females are such that they become a lot more demanding than the other individuals [82]. *Myotis bechsteinii* and *Plecotus auritus* which are two ecologically and morphologically similar species illustrate this different use of available resources influenced by their reproductive status. Pregnant females of *M. bechsteinii* have smaller home ranges than non-reproductive females, change roost frequently often selecting roosts high in the trees and entering into a torpor when meteorological conditions deteriorate [31, 82]. Then, lactating females and young forage over high-quality habitats while non-reproductive females forage in lower-quality habitats such as conifer or young broadleaved stands. Social exchanges take precedence when selecting roosts, with colonies settling in large cavities without much vegetation clutter at the entrance allowing for several individuals to leave and enter the roost at a time [32]. On the contrary, pregnant females of *P. auritus* use large home ranges and can roost alone in a tree far from the main colony for several days. Lactating females systematically stay within the colony, foraging in good-quality habitats close to the cavity. Non-reproductive females use the same types of habitats but forage further from the colony [31]. Thus, the conservation of a network of cavities is clearly crucial for both species, including the preservation of woodpecker hollows at elevated positions on trees for *M. bechsteinii*. The same advice applies to other species with behavioural differences in the utilisation of tree cavities and habitat selection in Europe such as *Myotis daubentonii* [64] and *Myotis nattereri* [31], and on other continents, such as *Myotis septentrionalis* [65], *Eptesicus fuscus* [74], *Chalinolobus tuberculatus* [70, 83] and *Mystacina tuberculata* [84].

6. Bat conservation in the context of forest management

6.1. The impacts of silviculture

Regardless of the type of silvicultural practice undertaken in forests around the world, biodiversity will be affected. Harvest exclusion areas or setting aside reserves within production forests constitute sites that are richer in terms of species present, whereas timber plantations with more economically profitable methods employed, notably short rotation forestry, are the most impacting of approaches [1, 26, 71]. For bats, silvicultural logging reduces food resources, destroys breeding sites, and can kill individuals or colonies when trees are felled [2, 5, 6, 71]. Females of *Plecotus auritus* have been shown to entirely avoid forests recently logged during lactation periods even if mature trees have been preserved [32]. The same avoidance has also been observed in juveniles of *Myotis bechsteinii* and *Myotis nattereri* probably due to the decrease in the volume of foliage, which is an important source of insect production for these species [31]. More generally, logging forests for timber induces a net loss of prey-bearing mature broadleaves causing an immediate reduction in food resource. Therefore, bats are forced to move to new habitats next to their previous foraging grounds that are already occupied by other individuals, reducing the carrying capacity of the milieu. The silvicultural harvesting of mature trees that possess cavities inevitably leads to a reduction of the total number of roosts available to bats. Even if the natural ageing of trees continues and is accompanied by the gradual formation of new cavities, principally by woodpeckers, the setting aside of areas of unlogged mature forest to protect habitat diversity must still be maintained in order to ensure the temporal and spatial continuity of bat colonies [2, 6, 31]. Indeed, only harvest exclusion areas where the natural forest cycle is allowed to continue without the intervention of man represent truly ideal habitats for bats [80]. However, strict protection obviously remains an unrealistic measure across the European forest scale, implying a need for other forest management strategies.

6.2. Forest management orientations in favour of bats

Given the major differences in the ecological functioning of forest habitats, i.e. different compositions and structures, combined with a diverse range of silvicultural techniques employed to manipulate growth conditions, it becomes difficult for the conservation biologists to propose bat-friendly management measures [2, 81]. The growing literature comparing managed and non-managed forests demonstrates that bats do have the ability to occupy exploited forest systems, which gives hope for improving the conservation status of many species throughout European forests [1]. However, so as to implement effective conservation measures for bats, it is vital to know what habitat parameters to conserve and balance this with appropriate silvicultural treatments that ensure the continuing exploitation of wood while assuring the safety of the loggers themselves and the public who use the forests for recreational purposes. Although it is necessary to further improve knowledge on the relationship between bats and forest management [2], some recommendations can already be put forward. In order to conserve both roosts and foraging habitats, it is imperative that the manager ensures the temporal and spatial continuity of mature broadleaved stands composed of native species by maintaining at least 35% of the surface area of each forest (about 1000 ha). One way of maintaining suitable habitats for bats in forests would be by setting aside a number of small sites of no more than a few hectares in size, leaving the forest within each site to complete its natural cycle. By doing so, this would assure the presence of tree cavities, deadwood, and certain heterogeneity to naturally occur across an entire forest mosaic. In addition, within production forest plots, maintaining a small number of live or dead trees possessing cavities even after felling treatments have been carried out can ensure a minimum continuation of usable roosts. This can be of particular ecological interest: live trees possessing cavities surrounding a dead tree form a group of trees representing a particularly attractive habitat for bats. Also, a tree possessing a large voluminous cavity at a high position can accommodate certain species for an extended period of time such as *Nyctalus noctula*. Because isolated trees are at a greater risk of falling (due to abiotic factors) it is possible and recommended to maintain a group of trees, ensuring a forest ambience, around a cavity while, again, limiting the potential risk of injury to forestry workers or public. Maintaining quantities of deadwood, where possible both snags and ground-lying, should target the minimal threshold of 25m^3/ha. Finally, diversity in tree species, a diversity in the vertical stratification and structure of a forest stand can only further support a diversity and abundance of food resources for the various species of bats.

7. The involvement of forest managers in France

In Europe, the accumulation of knowledge over the last decade on the relationships between bats and forests has orientated programmes geared towards a greater consideration for bats. In addition, the Natura 2000 network has been adopted in the European Community making it possible to designate numerous sites considered as fundamental for these animals [2, 13]. Forests being a key issue for the conservation of bats need to be taken into account as part of regional planning and forest management policies [2]. However, even though the number of appropriate management recommendations has increased in recent years the implementation of concrete conservation strategies is challenging, and unfortunately slow. Furthermore, forest managers must meet society's growing demand for wood products among other objectives such as reducing fossil fuel consumption, curtailing the impacts of climate change.

Of the 15 million hectares of forests in France (including overseas territories), 4.5 million hectares are managed by the French Forest Office who are mainly financed by timber production. This management body has integrated key conservation issues for biodiversity at various spatial scales within production forest systems. First, a number of harvest exclusion areas, whereby no silvicultural intervention occurs, have been created, each area ranging in size from ten to hundreds of hectares, totalling nearly 50,000 ha. Second, 3% of managed forests are "habitat islands" (generally ranging from 1 to 10 ha in size) where a true naturalness approach allows the natural cycle of forests to ensue ageing and decomposition of trees. Third, three microhabitat-bearing trees or dead trees are systematically protected per hectare. Fourth, at least one-third of a mature broadleaved forest's area is maintained in each forest canton as often as possible. The exploitation by clearcutting cannot exceed a few dozen hectares for any single block and the natural regeneration of the ecosystem is favoured, which is thus less degrading to biodiversity than plantations. Lastly, a team of 45 conscientious forest engineers, technicians and ecologists set up in 2004 carry out forest inventories and studies to improve knowledge on the relations between bats and forests and to evaluate the impact of forestry in this Office. They convert the collected information into management guidelines that favour bat conservation. These people are trained in forestry and have years of experience in managing forest plots, and can use the technical terminology required when communicating appropriate strategies to silviculture. The internalisation of these issues by teams dedicated to the preservation of bats within forest management organisations is the best assurance of successful bat conservation within exploited forest systems worldwide.

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Chapter 6

Bats in Northern Mountain Region of Khyber Pakhtunkhwa, Pakistan

Mohammad Salim

Additional information is available at the end of the chapter

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Abstract

Khyber Pakhtunkhwa (KP) is the North Western Province of Pakistan lying between 31° 15′ and 36°57′ North latitude and 69° 5′ and 74° 7′ East longitude. It covers a land area of 74,521 Km^2. Great altitudinal range (174–7690 m) diverse temperatures (sub zero to 51°C) and varied rainfall (100–1200 mm) have given rise to a great diversity in habitat with an equally diverse fauna. The Province inhabits 100 species of mammals, 456 species of birds, 48 species of reptiles and 4500 species of plants. Chiroptera is one of the least studied mammalian order in KP. Tall hollow trees, old haunted buildings, inhospitable rock crevices and deep dark caves comprising critical bat habitat are perhaps a valid reason for limited research and studies on bats. Myths and bad omens associated with the nocturnal behavior of bats play an important role in keeping away the non-serious researchers. Literature search reveals that Chiroptera fauna of KP comprises of 4 families, 13 genera, and 29 species. These bats recorded in KP include fruit bats, mouse-tailed bats, vampire bats, horseshoe bats, leaf nosed bats, house bats, serotine bats and pipistrelle bats. This species diversity is a result of diversified habitat and the overlap of Oriental and Palearctic zoogeographic regions in the province. Conservation status of bats in KP is highly unsatisfying. A number of threats loom around bats. These include habitat loss, scarcity of food, slow rate of reproduction, and depredation by animals and birds, killing for medicine, high tension electric transmission lines, killing by fruit farmers, lack of awareness and absence of conducive conservation policy at Government level. The study recommends comprehensive bat research and surveys, habitat analysis, reconfirmation of bat taxonomy, development of bat call library and conservation awareness campaign. The Government of KP should conduct an analysis of the bat distribution, status and adapt a conservation and management policy for bats. The bats should accordingly be listed in the KP Wildlife Law 2015.

Keywords: Chiroptera, diversity, distribution, conservation, Khyber Pakhtunkhwa, Pakistan

1. Introduction to area

The northwestern part of Pakistan that has recently been named by the provincial government as "Khyber Pakhtunkhwa (KP)" possesses a unique physiographic diversity. It lies between 31°15′ and 36° 57′ North latitude and 69° 5′ and 74° 7′ East longitude. Afghanistan lies in the North West of the Province. Punjab and Balochistan provinces lie in the south and Gilgit Baltistan, Kashmir and parts of the Punjab Province bound the eastern parts of the Province. KP covers a land area of 74,521 Km^2 with a population of 30.52 million.

The Province is highly diverse in topography. It comprises of big plains, extensive deserts, low hills and high mountains. The province shares vast stretches of the world-known Karakoram, the Hindu kush and Himalayan Mountain ranges. The altitude ranges from 300 m at Dera Ismail Khan (DI Khan) in the south to 7690 m at Tirich Mir, the highest peak in the Hindu kush Mountain range in the north.

Flora of KP is equally diverse. About nine distinct vegetation types exist in the province. These include Riverain forest, Tropical thorn forest, Mazri palm scrub, and subtropical sub humid forest, subtropical humid Chir pine forest, moist temperate conifer forest, temperate Conifer forest, sub alpine scrubs and alpine meadows [1].

Owing to extraordinary physio-climatic features, the province is rich in wildlife resources. Its broad altitudinal (174–7690 m asl) and climatic range (temperature: −5 to 50°C; average annual precipitation: 1000–1200 mm; rainfall: 230–250 mm; annual average snowfall: 3 ft. (at only Lowari Top)) make it an excellent refuge for country's most prominent wild animal species. The province provides refuge to five out of six wild pheasant species, i.e., the western horned tragopan (*Tragopan melanocephalus*), the Himalayan monal (*Lophophorus impejanus*), the white-crested kalij (*Lophura leucomelanos hamiltonii*), the cheer pheasant (*Catreus wallichi*) and the koklas (*Pucrasia macrolopha*). It is also a home for four sub-species of markhor, i.e., the Kashmir markhor (*Capra falconeri cashmiriensis*), the Astor markhor (*C. f. falconeri*), the Kabul markhor (*C. f. megaceros*), and the Suleiman markhor (*C. f. jerdoni*). Two species of urial, the Punjab urial (*Ovis orientalis punjabiensis*) and the Ladakh urial (*O. v. vignei*), two species of bear, i.e., the Himalayan brown bear (*Ursus arctos*) and the Asiatic black bear (*Selenarctos thibetanus*) and one sub-species of the Balochistan black bear (*S. t. gedrosianus*) are also present here. In addition, five species of partridges, i.e., the chukar partridge (*Alectoris chukar*), the snow partridge (*Lerwa lerwa*), the see-see partridge (*Ammoperdix griseogularis*), the gray partridge (*Francolinus pondicerianus*), and the black partridge (*F. francolinus*) are also found in this province [2–4]. Owing to its ornithological importance, the Plass Valley has been designated as one of the global hot spot of biodiversity [5].

In spite of the presence of a rich and diverse wildlife, little attention has been paid to explore bat fauna of the north-western part of the country. Most of the available literature on bat fauna of this region has been contributed by foreigners, before partition of India and Pakistan, during the British reign. Since no comprehensive and updated field study is available, bat biologists still rely on [2, 6–13] for authenticity of their findings.

Literature survey has revealed that bat fauna of the KP consists of four families, 13 genera and 29 species representing more than a half of the bats of the country. These bat families include

Pteropodidae (the fulvous fruit bat *Rousettus leshenaultii*), Rhinopomatidae (the greater mouse-tailed bat *Rhinopoma microphyllum* and the lesser mouse-tailed bat *R. hardwickii*), Rhinolophidae (the greater horseshoe bat *Rhinolophus ferrumequinum*, the lesser horseshoe bat *R. hipposideros*, the Blyth's horseshoe bat *R. lepidus* and the big-eared horseshoe bat *R. macrotis*) and Vespertilionidae (the lesser mouse-eared bat *Myotis blythii*, the whiskered bat *M. mystacinus*, the dark whiskered bat *M. muricola*, the brown long-eared bat *Plecotus auritus*, the gray long-eared bat *P. austriacus*, the Asian barbastelle *Barbastella leucomelas*, the desert long-eared bat *Otonyctris hemprichii*, the Asiatic greater yellow house bat *Scotophilus heathii*, the Botta's serotine *Eptesicus bottae*, the northern serotine *E. gobiensis*, the common serotine *E. serotinus*, the particolored bat *Vespertilio murinus*, the common pipistrelle *Pipistrellus pipistrellus*, the javan pipistrelle *P. javanicus*, the Thomas's pipistrelle *P. paterculus*, the least pipistrelle *P. tenius*, the coromandel pipistrelle *P. coromandra*, the Leisler's noctule *Nyctalus leisleri*, the mountain noctule *N. montanus*, the common noctule *N. noctula*, the Hutton's tube-nosed bat *Murina huttoni* and the Scully's tube-nosed bat *M. tubinaris*) [2, 13–15]. This diversity of Chiropteran species is a result of the immense diversity of habitat, comprising of old buildings, old trees, mountain caves and cliffs. As far as the status of these bats is concerned, one species is Endangered, two are Vulnerable, six are Near Threatened, 15 are Least Concern and five were Data Deficient [16, 17].

Distribution ranges of most mammals in Pakistan have changed over the past few decades. However, no worthwhile studies documenting these changes except [2, 18–21] are available in the country to show such changes. New mammal species are being explored throughout the world. These discoveries are made especially in those areas which are either poorly surveyed or their mammal fauna is a combination of two or more zoogeographical realms. The north-western part of Pakistan fulfills both these conditions.

It is not only a poorly surveyed, climatically diverse, and habitat rich area, but is also uniquely located on the globe. It forms a buffer zone between Oriental and Palearctic regions and is also connected to Russia and China through land connections. Keeping in mind all these facts, this chapter gives authentic and up-to-date information of bats in the Northern Mountain Region of KP.

2. Diversity, distribution, and conservation status

2.1. Family Pteropodidae

Three species of fruit bats were recorded from Malakand division. These included the Indian flying fox *Pteropus giganteus* Brünnich 1782, the fulvous fruit bat *Rousettus leschenaultii* Desmarest, 1820, and the short-nosed fruit bat *Cynopterus sphinx* Vahl, 1797.

2.1.1. The Indian Flying Fox Pteropus giganteus (Brünnich 1782)

The genus *Pteropus* Brisson, 1962, has 65 species and consists of medium to large fruit bats [14]. It is distributed from Mafia and Pemba Islands (off the Tanzania), Madagascar, the Islands of the Indian Ocean, the Indian subcontinent, Southeast Asia, the Philippines, and Australia [13]. Of the 65, five species of the flying foxes are reported from the Indian subcontinent which include the Indian flying fox *P. g. giganteus* (Brünnich, 1782), *P. g. ariel* (Allen, 1908), *P. g. leucocephalus* Hodgson, 1835, the large flying fox *P. vampyrus* (Linnaeus, 1758), the Nicobar flying fox *P. faunulus* (Miller, 1902), the Island flying fox *P. hypomelanus* (Temminck, 1853), *P. h. satyrus* (K. Andersen, 1908), and the Blyth's flying fox *P. melanotus melanotus* (Blyth, 1863) and *P. m. tytleri* (Dobson, 1874) [13]. The status and geographical limits of this taxon are still uncertain [13]. *Pteropus giganteus* is included in Appendix II in IUCN SSC Action Plan (1992)-Not Threatened and is Lower Risk-IUCN 2003 [16, 22].

In Pakistan, this species has been reported from Rawal Lake, Saidpur and the Margalla Hills in Islamabad, Sialkot, Lahore, Changa Manga and Renala Khurd in Punjab, and from Jacobabad, Shahpur and Clifton Railway Bridge in Karachi [2, 13, 23]. It has recently been reported from Peshawar and Charsadda districts [20]. The species is widely distributed across India, tMaldives, Nepal, Bangladesh, and Sri Lanka [13].

More than 300 bats were recorded roosting in Jrandy (N34° 24.808′ E71° 48.202′) tehsil Dargai in Malakand district. A single roost of the Indian flying fox was located at Agritech Limited Hazara Phosphate Fertilizer Plant (N33° 58 21.30′ and E72° 53 46.04′), Hattar Road, Haripur, during present survey, i.e., May–August 2014. Fifty specimens of the Indian flying fox (*Pteropus giganteus*) were collected from this roost. Ten of them were males while the remaining were females.

2.1.2. The greater short-nosed fruit bat Cynopterus sphinx (Vahl, 1797)

The genus *Cynopterus* F. Cuvier, 1824, has seven species [14]. It consists of those species which possess having shorter and broader muzzle with a deep margination between the nostrils. It is distributed from India to Malaysia, Indonesia, Thailand, and the Philippines [13, 24]. Of the 7 species, two species of the short-nosed fruit bats are reported from the Indian subcontinent which include the short-nosed fruit bats *C. sphinx* (Vahl, 1797) and the lesser dog-faced fruit bat *C. brachyotis* (Müller, 1838) [13]. *Cynopterus sphinx* is included in Appendix II in IUCN SSC Action Plan (1992)-Not Threatened, Lower Risk-IUCN 2003 and is Least Concerned-CAMP 2003; CAMP 2002 [15–17, 22].

Typically, this is an Oriental faunal zone species and is confined to warmer sub-tropical areas where there are large numbers of flowering and fruiting trees. This short-nosed fruit bat has been reported from Karachi and Malir by Eates and Murray [23, 25]. No specimen has been collected either by the Zoological Survey of Pakistan or by the Bombay Natural History Society during its mammal survey of Southern Sindh. According to farmers in the Malir area, a small fruit bat does occur which attacks the "chiku" fruit (*Achras sapota*) as well as the custard apple (*Annona squamosa*) hovering near the ground and it seems probable that this is *Cynopterus*. With the spread of banana cultivation in recent decades up to Hyderabad, it is however, likely that this bat is followed as far north as that city [2]. Colonies of up to 25 individuals have been recorded in India by Vasishta and Badwaik [26]. It has been suggested that this species may be beneficial as an agent in seed dispersal (feeding on ripe dates and dropping the pits some distance from the food tree) [27], and in pollinating flowers which produce nectar at night. It is probably not numerous enough in Pakistan to do any considerable damage to the fruit crops.

A skeleton of the greater short-nosed fruit bat was collected from the floor of "Kashmir Smasta" (N34° 25.780′ E72° 13.727′), a cave from which 22 *Rousettus leschenaulti* were also captured. Initially, this skeleton was also thought to be of a *Rousettus* bat, but the dental formula and cranio-morphological measurements confirmed it to be the greater short-nosed bat.

2.1.3. The fulvous fruit bat Rousettus leschenaultii (Desmarest, 1820)

The genus *Rousettus* Gray, 1821, includes medium-sized fruit bats that are distributed from sub-Saharan Africa, Arabia and Madagascar to the Indian subcontinent and Southeast Asia [13]. Of the 10 species belonging to this genus, two are reported from the Indian subcontinent which include the fulvous fruit bat *R. leschenaultii* (Desmarest, 1820) and *R. l. leschenaultii* (Desmarest, 1820) and the Egyptian fruit bat *R. aegyptiacus* (E. Geoffroy, 1810) and *R. a. arabicus* (Anderson and de Winton, 1902), [13, 28]. Both are seasonally migratory and colonize Himalayan valleys in summer in the fruit growing districts up to 1200 mm (4000 ft.) elevation [2]. *Rousettus leschenaultii* is included in Appendix II in IUCN SSC Action Plan (1992)-Not Threatened, Lower Risk-IUCN 2003 and is Least Concerned-C.A.M.P. 2003 [16, 22].

It is a highly gregarious species and colonies vaulted roves, natural rock caves and open wells. These roosts were in the more wooded regions in the Himalayan foothill zone and adjacent plains. Being partly migratory, the fulvous fruit bat is mainly a summer visitor to Pakistan with the exception of known Lahore and Malir colonies. It has been recorded near Muzaffarabad in the Jhelum valley of Azad Kashmir, Malakand, the Vale of Peshawar, Sialkot, Lahore, and Karachi [2, 8, 29]. The population of this bat does not seem large enough to have a much effect on the fruit industry in such regions of Peshawar and Mardan. Mirza discovered a colony numbering several 1000 in a rock cave at 1060 m elevation in the Malakand. This was only a summer colony [29] which corroborates their seasonally migratory movements.

A total of 22 specimens of *R. leschenaulti* were captured from Malakand division. Of these 22, seven were captured from Tura Gata (N34° 26.818′ E71° 48.973′), five from Cupni (N34° 27.691′ E71° 48.220′), seven from Brah (N34° 29.915′ E71° 46.822′), and 4 from Daim (N34° 36.647′ E71° 47.704′).

2.2. Family Rhinopomatidae

Two species of this family were recorded from Malakand division. These included the greater mouse-tailed bat *Rhinopoma microphyllum* Brünnich, 1782, and the lesser mouse-tailed bat *Rhinopoma hardwickii* Gray, 1831. Although both these species have a small dermal ridge on their muzzle, they are distinguishable based on forearm length relative to their tail length. Forearm in *R. microphyllum* is longer than *R. hardwickii*, but tail in *R. microphyllum* is generally smaller than the forearm as compared to *R. hardwickii* which have a longer tail than their forearm.

2.2.1. Greater mouse-tailed bat Rhinopoma microphyllum (Brünnich, 1782)

The genus *Rhinopoma* (E. Geoffroy, 1818) has four species worldwide and three of them occur in the Indian subcontinent which include the lesser mouse-tailed bat *R. hardwickii* Gray, 1831, the greater mouse-tailed bat *R. microphyllum* (Brünnich, 1782), and the small mouse-tailed bat *R. muscatellum* Thomas, 1903 [14]. The greater mouse-tailed bat is distributed from Mauritania, Nigeria, Senegal, Arabia, Iran, Afghanistan, Pakistan, India, Sumatra, and Cameroon to Egypt [14]. The species is relatively abundant in the Indian subcontinent with one endemic subspecies (*R. m. kinneari*) and is Least Concerned (South Asian Chiroptera C.A.M.P. Report, 2002; [16, 17].

In Pakistan, the species has been reported from Ara [30], Sakesar, Rohtas [31], Gujrat, Multan, Mailsi, and near Jhelum in Punjab [2]. In Sindh, colonies have been found in Sukkur, Gambat [33]; Hyderabad, Karchat Hills, Karachi [2], and Lasbela (South Balochistan) [7]. The species has also been reported from Sadiqabad and Qutabpur. Mirza found a large summer colony inhabiting a natural rock cave in the Malakand Hills [2]. It is also found in Amb in Khyber Pakhtunkhwa [32].

A total of 58 greater mouse-tailed bats were recorded co-roosting with *R. leschenaultii* in a cave at Tura Gata (N34° 26.783′ E71° 49.070′) tehsil Dargai.

2.2.2. Lesser mouse-tailed bat Rhinopoma hardwickii (Gray, 1831)

R. hardwickii has an average forearm length of 59.2 mm (52.9–64.0 mm) and rarely exceeds 60–67 mm. According to Roberts [2], this is much less common species than *R. microphyllum* in Pakistan. The species has been reported from Amb in Khyber Pakhtunkhwa [34]. It has also been reported from Ara [30], Sakesar, Rohtas in Salt Range and Chitti Dil [31] in Punjab, around Karachi and Karchat Hills near Hyderabad [2] and Landi in southern Sindh [33].

According to Bates and Harrison [13], *R. hardwickii* is widespread and believed to be common in the Indian Subcontinent. Both the species *R. hardwickii* and *R. microphyllum* use the same type of diurnal roosts. The species is considered to be "Least Concerned" (South Asian Chiroptera C.A.M.P. Report, 2002; [16, 17]).

More than 25 bats were recorded roosting in a cave of Tura Gata (N34° 26.818′ E71° 48.973′) tehsil Dargai in Malakand district.

2.3. Family Megadermatidae

The greater false vampire bat *Megaderma lyra* E. Geoffroy, 1810, is the only species of this family found in Pakistan. One colony of these bats was recorded from the study area.

2.3.1. The greater false vampire Megaderma lyra (E. Geoffroy, 1810)

The genus *Megaderma*, E. Geoffroy, 1810, has two species which consists of the greater false vampire *M. lyra* Geoffroy, 1810, and the lesser false vampire *M. spasma* Linnaeus, 1758 [14]. They are large bats without any tail and extensively developed interfemoral membrane. The genus *Megaderma* consists of those species having large oval ears, fold of skin across the crown and have an elongated bifurcated tragus [2, 13]. Megadermatidae consists of four genera and five species, two of which occur in the Oriental Region and one genus and one species in Pakistan [12, 14, 24]. *Megaderma lyra* Geoffroy, 1810, differs from *M. spasma* by its longer forearm, broad and short tragus, smaller postorbital process, and deep prenasal notch. Because of these differences [35], *M. lyra* has been in a separate subgenus, *Lyroderma*. According to Ref. [36], the species (under the generic name *Eucheira*) can be divided into two subspecies, *E. l. lyra* and *E. l. caurina*, both of which are found in and near the Indian Peninsula, and the specimens derived from South China (characterized by larger skull and narrower prenasal notch) belong to a different species, *E. sinensis*. Since the differences are very slight between *E. l. lyra* and *E. l. caurina*, we agree with [37] and [38, 39] who recognized only the nominate subspecies *M. l. lyra* in India, Pakistan, Bangladesh, and Sri Lanka. *E. sinensis* is generally accepted as a subspecies of *M. lyra* [6] and is distributed in South China, Burma, Thailand, Cambodia, Laos, and Malaysia. The area of *M. lyra* was figured by [35], but with some inaccuracy, since the species is living in Pakistan [40], Afghanistan [7], and Vietnam [41]. The species is "Lower Risk" IUCN, 2003 and IUCN/SSC Action Plan 2001 [13, 14].

The false vampire bat *M. lyra* Geoffroy 1810, is an old world tropical gleaning bat. It detects its prey both via echolocation [42] and based on prey generated rustling noises [43]. *M. lyra* is a large bat with ugly appearance because of their big head, prominent muzzle, huge naked ears, and peculiar nose leaf. The skin of the nose leaf is pink and naked and roughly lozenge-shaped with a narrow vertical ride running down its center. Ears are bluntly rounded at their tips, sparsely covered with hairs, and pinkish gray color when the animal is alive. The tragus is pinkish brown, long, and slender, being divided into two lanceolate but unequal lobes. The outer lobe is much longer up to 13 mm, and slenderer than the inner lobe which is blunter at its tip. The pelage is fine, soft, and moderately long. The upper surface of the body is a uniform mouse gray faintly washed with brown. The ventral surface is paler, with the hair tips on the throat and belly white; the hair bases are gray. Dorsally the body fur is blue gray and consists of long silky hair. The belly fur is a paler, more yellowish gray. Whitish hairs extend around the posterior ears bases and on to the wing membrane from the axillae to the groin. The upper lip tends to be rather sparsely haired with a fleshy furrow dividing the middle of the lower lip. Female have two pectoral mammae with two more false teats in the pubic region. Juvenile have a comparatively dark pelage. The wings are broad due to the last or fifth digit being relatively long. There is no trace of a tail in this species, but the interfemoral membrane is well developed, stretching from heel to heel and being supported by long but weakly developed calcars. The hind feet that are comparatively large is in the development of the first digit which consists of only two joints while the remaining digits have three joints [2, 13].

In India, the colonies of this species have been observed in man-made structures such as temples, caves, forts, dilapidated old buildings, underground tunnels, old cow sheds, grain go downs, cellars, open walls, and shallow soap stone mines [37, 44, 45]. According to Hill [31], the species has been reported from Murree foothills at Lehtarar at 920 m, while Roberts [2] recorded it from Lahore in old ruined Mughal cellars at Shalimar gardens and from Sialkot. At Sukkur in Sindh, it has been found occupying the hillside caves (these are shallow man-made caves in limestone conglomerate) [2]. The species has been observed entering the verandah of an occupied house in Karachi to devour its prey [23]. The British Museum has one specimen, marked Balochistan and it seems likely that this specimen comes from Lasbela. It has not definitely been recorded anywhere else in Pakistan. In Pakistan, it appears that this bat is rather rare and decidedly local in distribution except in the northern sub-montane zone where it may be more widespread than is presently known. Further collecting will undoubtedly reveal its presence in the valley of Peshawar and possibly Mardan [2].

Twenty bats were recorded in a cave (N34° 26.762′ E71° 49.064′) at Tura Gata tehsil Dargai in Malakand district along with *R. leschenaultii* and *Hipposideros fulvus*.

2.4. Family Rhinolophidae

The family Rhinolophidae is characterized by a horseshoe-shaped nose leaf on the muzzle which consists of an erect posterior lancet, a lower horizontal horseshoe that surrounds the nostrils, and a perpendicular median sella. The genus *Rhinolophus* Lacepede, 1799, has 76 species worldwide of which 16 species exist in the Indian subcontinent and five have been recorded in Pakistan. These five species include the greater horseshoe bat *R. ferrumequinum* Schreber, 1774, the lesser horseshoe bat *R. hipposideros* Bechstein, 1800, the Blasius horseshoe bat *R. blasii* Peters, 1866, the Blyth's horseshoe bat *R. lepidus* Blyth, 1844, and the big-eared horseshoe bat *R. macrotis* Blyth, 1844 [2, 13, 14]. This family is distributed from southern England to Caucasus, Iran, Pakistan, India, China, Japan, Morocco, Algeria, and Tunisia. It is considered to be a monogeneric group [12]. The reater horseshoe bat is Least Concerned worldwide [15, 17] and Near Threatened in South Asia (South Asian Chiroptera C.A.M.P. Report, 2002; [16, 17].

Rhinolophidae bats are easily distinguished from the rest of bat families based on a prominent horseshoe-shaped nose leaf apparatus. Two species of this family were recorded from Malakand division. These included the greater horseshoe bat *Rhinolophus ferrumequinum* (Schreber, 1774) and Blyth's horseshoe bat *Rhinolophus lepidus* (Blyth, 1844).

2.4.1. The greater horseshoe bat Rhinolophus ferrumequinum (Schreber, 1774)

R. ferrumequinum is widely distributed in northern Himalayan region and extends southwards through the mountains of Waziristan and northern Balochistan. This bat seems to be rare in southern Balochistan because of the lesser supply of suitable insect prey and very dry climate which is unfavorable to the family Rhinolophidae [2]. Specimens have been collected from around Dir town (USNM), Abbotabad (HZM), Karakar pass (FMNH), Gilgit (type loc. of *proximus*) [13], and Kululai in Swat [2]. These larger greyer specimens have been assigned to the subspecies *R. f. proximus* [2]. Small colonies found in Balochistan near Kalat, Nushki, and Quetta have been assigned to *R. f. irani* [13, 46].

A total of 46 bats were recorded roosting in a cave at Loya Agra (N34° 34.868′ E71° 43.114′) tehsil Batkhela in Malakand district.

2.4.2. Blyth's horseshoe bat Rhinolophus lepidus (Blyth, 1844)

This species is a new record for Pakistan. The first specimen was captured by Mrs. Nora Pendleton from a phosphate mine near Abbottabad [2, 13]. The species has also been collected from Afghanistan [12] and in the dryer parts of Rajasthan, India [9], so the status of this species is unknown in Pakistan [2]. IUCN 2003 and IUCN/SSC Action Plan (2001) declare this species to be Data Deficient. It was in the lower risk (LR/lC) category according to IUCN 2007 report and is a chiropteran of Least Concern according to IUCN [17] Red List of Threatened Animals and C.A.M.P. Report, 2002.

Rhinolophus lepidus shortridgei found in South Asia differs from *R. l. lepidus* in having a longer hind foot (55–63% of the tibia, against 45.8–47.5%) and longer mandible [47].

Bates [13] collected specimens of *R. lepidus* from Nepal, India, and Pakistan. Three bats were captured through mist net in Malakand University (N34° 40.054′ E72° 03.653′) in Malakand district. Fifty specimens of the Blyth's horseshoe bat (*Rhinolophus lepidus*) were collected from Fizaghat Kaan (N34° 47′ 24.42″ E 72° 22′22.16″) elevation 3105 ft., Nalai Kaan

(N34° 46′59.17″ E72° 22′204.19″) elevation 3324 ft., and Gull Dara Kaan (N34° 47′19.66″ E72° 22′11.55″) elevation 3106 ft. district Swat. Fifteen of them were captured from Fizaghat Kaan (4 male and 11 female), 19 from Nalai Kaan (1 male, 18 female), and 16 from Gull Dara Kaan (5 male, 11 female).

2.5. Family Hipposideridae

2.5.1. Fulvous leaf-nosed bat Hipposideros fulvus (Gray, 1838)

Hipposideridae is a family of bats commonly known as the "Old World Leaf-nosed Bats." This large family is characterized by elaborate modifications of the nose and muzzle, forming leaf-like projections that are thought to help focus echolocation signals emitted through the nose. It comprises 80 species in 11 genera throughout the world. In Pakistan, it is represented by three genera and four species. It is a medium small species of *Hipposideros* with characteristically very large ears, the tip of which is broadly rounded off; the feet are small. The nose leaf has a greatest width of about 5 mm; its general morphology is like that of *H. ater* [13]. Adult weigh between 8 and 9 g [48].

The baculum is small and comparable to that of *H. ater*. It has a straight shaft with a simple base and tip [13]. It is closely similar in appearance to *Hipposideros cineraceus* from which it can mainly be distinguished by its slightly greater size and more rufescent dorsal pelage with very pale basal portion to the hairs. The dorsal fur of this species can vary widely in color in parts of western India [37], but in Pakistan, all specimens from the Punjab have long soft fur with the hairs pinkish white basally terminating in dark reddish brown or chestnut tips. Some individuals have more yellowish white fur close to the body with the tips of the hairs gray brown or even golden yellow in specimens from Sindh according to Murray, 1874.

This species seems well adapted to arid regions in the areas having a scattered growth of tropical thorn scrub or dry sub-tropical scrub. It particularly favors the open burrows of Porcupines and Hyenas for its diurnal roost as well as utilizing underground cellars, railway tunnels, and open wells "Kharezes" in Balochistan. They are very susceptible to predation from crows and kites if flying abroad in daylight [49]. Specimens have been collected in the northern Punjab from around Rawalpindi [9] and Chaklala [30] in the salt range. It apparently does not penetrate the foothills in the north and is absent from most of the Indus plain, occurring again in Southern Sindh around Sukkur [33], the Mausoleum of Amir Khan Mono and in Gholam and Gharo, all in Thatta district [50] and Shujawal [34]. In southern Balochistan, it has been collected from Panjgur and Hoshab [2]. The species is least concerned in South Asia [16, 17, 15]; South Asia Bat CAMP, 2002, and is lower risk: Least Concern in Microchiroptera Action Plan [51].

Among the four recorded bat species of this family from Pakistan, only the fulvous leaf-nosed bat *Hipposideros fulvus* Gray, 1838, was recorded from Malakand division.

More than 66 bats were recorded roosting in a cave of Tura Gata (N34° 26.770′ E71° 49.090′) tehsil Dargai in Malakand district.

2.6. Family Vespertilionidae

Thirteen bat species belonging to seven genera were recorded from Malakand division. These included Hodgson's bat *Myotis formosus* (Hodgson, 1835), Eastern barbastelle *Barbastella leucomelas* (Cretzschmar, 1830/1831), Asiatic greater yellow house bat *Scotophilus heathii* (Horsfield, 1831), Asiatic lesser yellow house bat *Scotophilus kuhlii* (Leach, 1821, Serotine *Eptesicus serotinus* (Schreber, 1774), Botta's Serotine *Eptesicus bottae* (Peters, 1869), common pipistrelle *Pipistrellus pipistrellus* (Schreber, 1774), Javan pipistrelle *Pipistrellus javanicus* (Gray, 1838), Coromandel pipistrelle *Pipistrellus coromandra* (Gray, 1838), Least pipistrelle *Pipistrellus tenuis* (Temminck, 1840), Dormer's bat *Pipistrellus dormeri* (Dobson, 1875), Desert yellow bat *Scotoecus pallidus* (Dobson, 1876), and Schreibers' long-fingered bat *Miniopterus fuliginosus* (Kuhl, 1819).

2.6.1. Hodgson's bat Myotis formosus (Hodgson, 1835)

This is geo-graphically widespread but little-known bat [13]. It is apparently common in South Korea [52]. *Myotis formosus* ranges from Afghanistan to China, Taiwan, Korea, Japan, Philippines and Indonesia. Bates and Harrison [13] collected specimens of *M. formosus* from India and Tibet. Five bats were captured through mist net in Wach Khwar (N34° 58.104′ E72° 28.270′), Barcharai Daim (N34° 33.737′ E71° 44.872′), Chinai Ghaz (N35° 00.850′ E72° 03.439′), and Mattak (N34° 59.066′ E72° 02.907′) in Malakand division.

2.6.2. Asian barbastelle Barbastella leucomelas (Cretzschmar, 1830/31)

This is rather a small and delicately built bat with a very striking body color. The dorsal fur is long and silky and of a blackish gray color basally, with the extreme tips of hairs a pale golden brown giving it a hoary appearance. The belly fur is paler grayish brown. The ears are large and conspicuous being rather a squarish in outline and forward slanting.

Present limited evidences indicate that this bat is associated with forests in the northern mountain regions, either Himalayan moist or dry coniferous forest. Since this species is not gregarious in its diurnal roosts, it is never very plentiful throughout its range and the paucity of Pakistan specimens indicates that it is uncommon if not rare [6] include Gilgit and the Punjab within its range based on reports by Blanford, but there are no specimens in the British Museum or Bombay Natural History museum collections from Gilgit. However, a specimen was collected at Dunga Gali in 1907 at 2350 m (7800 ft.) and a second mummified specimen in the same location by the author on 2 May 1980. A third specimen was collected in 1965 by the University of Maryland expedition from Naltar, Gilgit, in spruce forests (*Picea smithiana*), at about 2450 m (8000 ft.) elevation. Siddique does not include this specimen in either of his checklists (1961, 1970). It was collected from Afghanistan in Paktia Province [53] and from several localities in northern Iran [54]. Elsewhere it occurs in Russian Turkestan, Chinese Xinjiang, Transcaucasia [55], southern China, and north to Japan [12]. In India, it occurs in Darjeeling, Nepal, Sikkim, and the Bhutan Duars.

Only one bat was captured through mist net in Lamin Bala (N35° 27.802′ E72° 14.310′) in Upper Dir district.

2.6.3. Asiatic greater yellow house bat Scotophilus heathii (Horsfield, 1831)

Scotophilus heathii is geographically distributed in Afghanistan to South China, including Hainan Island, south to Sri Lanka, Vietnam, Cambodia, Thailand, and Burma. In Pakistan, the species is common and widespread throughout the Indus plains. It has been collected from Kohat (NWFP), Islamabad city, Multan, Lahore and Sialkot districts (Punjab), Kashmoor, Sakkur, Jacobabad, Mirpur Sakro, Dadu, Landi, Malir, Karachi (Sindh) [2, 8, 18, 33, 50]. IUCN categorizes the species as "Least Concern" [17].

Twenty-two bats were captured through mist net in Head Koper (N34°24.454′ E71°50.061′), Bazdara Bala (N34° 30.355′ E72°04.692′), Malakand Top (N34°34.007′ E71°55.736′), Batkhela (N34°36.903′ E71°57.768′), and Daim (N34°36.647′ E71°47.704′) in Malakand district.

2.6.4. Asiatic lesser yellow house bat Scotophilus kuhlii (Leach, 1821)

It is uncommon in Pakistan with a very restricted distribution. The species is present only in southern Sindh [2]. Geographically, this species is distributed in Bangladesh, Pakistan to Taiwan, south to Sri Lanka, Burma, Cambodia, W Malaysia, Java, Bali, Nusa Tenggara (Indonesia), southeast to Philippines and Aru Islands (Indonesia) [15]. The species is categorized as "Least Concern" [17].

Two bats were captured through mist net in Head Koper (N34° 24.454′ E71° 50.061′) and Kot (N34° 29.778′ E71° 43.501′) in Malakand district.

2.6.5. Serotine Eptesicus serotinus (Schreber, 1774)

This species is rare in Pakistan. The only male specimen was collected by Roberts [2] from Dunga gali in Murree Hills. Walker and Molur [16] declare this species to be Data Deficient, Near Threatened (C.A.M.P. Report, 2002), and Least Concern according to IUCN [17] Red List of Threatened Animals.

E. s. pashtomus was described as a new subspecies by Gaisler [7] in his account of bats collected in Afghanistan from Jalalabad district. The zygomatic width of *pashtomus* being 14.5 mm while Felten [56] in describing a further collection of bats from Afghanistan also assigned *E. serotinus* to the subspecies *pashtomus* which was collected from eastern Afghanistan close to the border with Chitral [56].

Fifteen bats were captured through mist net in Head Koper (N34° 24.454′ E71° 50.061′), Bakrai (N34° 23.939′ E71° 52.202′), Astanadaro Kalay (N34° 24.913′ E71° 49.466′), Barcharai Daim (N34° 33.737′ E71° 44.872′), Amlok Dara (N34° 43.773′ E71° 52.502′), and Pull Saokai (N34° 38.553′ E72° 01.749′) in Malakand division.

2.6.6. Common pipistrelle Pipistrellus pipistrellus (Schreber, 1774)

The taxonomic status of this bat species is unknown from Pakistan. The species is distributed in British Isles, S Denmark, W Europe to the Volga and Caucasus, Morocco; Greece, Turkey, Israel and Lebanon to Afghanistan, Kashmir, Kazakhstan, Pakistan, Burma, Sinkiang (China), perhaps Korea, Japan, and Taiwan. The British Museum has one specimen that was collected from Kashmir in the beginning of nineteenth century. Two other specimens were collected from Gilgit by an expedition carried out by University of Maryland in 1965 [2]. The species has a restricted range in the Indian subcontinent [13] and seems to be common in Pakistan as there has been no further field studies on bats in Kashmir or Gilgit [2]. The species is "Least Concerned" [17]. Pipistrelles in Europe have recently been shown to comprise two cryptic species *P. pipistrellus* which echolocates with most energy around 45 kHz, and *P. pygmaeus*, with most energy at 55 kHz [57, 58].

Only a single specimen was captured through mist net in Lamin Bala (N35° 27.802′ E72° 14.310′) in Upper Dir district.

2.6.7. Javan pipistrelle Pipistrellus javanicus (Gray, 1838)

Pipistrellus javanicus distributed in East Afghanistan, North Pakistan, North and Central India, South and East Tibet (China), Burma, Thailand, Vietnam, through SE Asia to Lesser Sunda Isles and Philippines; perhaps Australia. No literature is available on the distribution of this species in Pakistan; however, a single specimen was collected from Gharial, Murree Hills [15]. The species falls in "Least Concern" category [17].

Only one bat was captured through mist net in Malakand University (N34° 40.054′ E72° 03.653′) in Malakand district.

2.6.8. Coromandel Pipistrelle Pipistrellus coromandra (Gray, 1838)

Ten specimens of *Pipistrellus coromandra* has been collected from Chitral and 17 specimens from Saidu Sharif in Swat; the mean head and body length was 43 mm. The mean tail length was 35 mm. The mean hind foot and ear length were 7 mm and 11 mm, respectively. The mean forearm length was 32 mm. The Swat specimens averaged 6 g in weight [2]. These Pakistan specimens and also those from Afghanistan (Jalalabad) [7] appear to average slightly larger than the population from central India [59]. The species also has been collected from Dir, Yakh Tangai in Khyber Pakhtunkhwa and from Chakri in Punjab [13]. This is a widely distributed and apparently common species in southern Asia. This species is categorized as "Least Concern" [17].

A total of eight specimens were captured through mist net in Barcharai Daim (N34° 33.737′ E71° 44.872′), University of Malakand (N34° 40.054′ E72° 03.653′), Koza Agra (N34° 35.171′ E71° 41.802′) in Malakand district and from Shaheed Benazir Bhutto University, Sheringal (N35° 16.204′ E72° 00.172′), Thal (N35° 28.812′ E72° 14.588′), Dir (N35° 12.327′ E71° 52.540′), and Mian Banda (N34° 50.378′ E71° 51.984′) in Dir district.

2.6.9. Least pipistrelle Pipistrellus tenuis (Temminck, 1840)

Pipistrellus tenuis is the smallest pipistrelle found within the subcontinent with an average forearm length of 27.7 mm. The species is hard to differentiate from smaller individuals of *P. coromandra* based on forearm length. Its body weight averages about 2 g [60]. The species is distributed in

Afghanistan to the Moluccas; S China, Laos, Vietnam, Cocos Keeling, and Christmas Islands (the Indian Ocean). The species has been recorded from Malakand [2], Chitral [9], Multan and Chaklala [30], Chakri, Gambat, Sukkur [34], Karachi, and Malir [8]. The species is considered as "Least Concerned."

Thirty-five bats were captured through mist net in Bakrai (N34° 23.939′ E71° 52.202′), Timergara (N34° 49.471′ E71° 50.396′), Koz Koper (N34° 24.399′ E71° 50.171′), Matkani (N34° 37.380′ E71° 51.055′), Head Koper (N34° 24.454′ E71° 50.061′), Malakand Tunnel (N34° 33.158′ E71° 54.168′), Maina (N34° 29.765′ E71° 44.585′), Kot (N34° 29.778′ E71° 43.501′), Manzaray Baba (N34° 29.480′ E71° 42.353′), Qadar Kalay (N34° 24.076′ E71° 50.723′), Shaheed Benazir Bhutto University Sheringal (N35° 16.204′ E72° 00.172′), Astanadaro Kalay (N34° 24.913′ E71° 49.466′), Thana (N34° 38.334′ E72° 04.233′), Daim (N34° 36.647′ E71° 47.704′), Tutakan (N34° 36.978′ E71° 49.511′), Community Game Reserve Brah (N34° 29.820′ E71° 46.327′), Ziarat Kalay (N34° 37.213′ E71° 48.715′), Kas kalay (N34° 24.573′ E71° 48.978′), Fishing Hut (N34° 38.900′ E72° 01.941′), Faqeer Abad (N34° 23.323′ E71° 53.324′), Haryan Kot (N34° 29.382′ E71° 47.871′), and Mola Misray (N34° 25.251′ E71° 49.085′) in Malakand division.

2.6.10. Dormer's bat Pipistrellus dormeri (Dobson, 1875)

Pipistrellus dormeri is confined to India and Pakistan [13]. It is restricted to the Indian subcontinent where it is an abundant species in areas such as Rajasthan [61]. The species has been collected from Sialkot in Punjab and Shikarpur in Sindh [9]. This species is categorized as "Least Concern" (CAMP, 2002).

Only eight bats were captured through mist net in Dir (N35° 12.327′ E71° 52.540′), Fishing Hut (N34° 38.900′ E72° 01.941′), Head Koper (N34° 24.454′ E71° 50.061′), and Malakand Top (N34° 34.007′ E71° 55.736′).

2.6.11. Desert yellow bat Scotoecus pallidus (Dobson, 1876)

Scotoecus pallidus is endemic to the Indian subcontinent and has a local and restricted distribution in Pakistan. It was first described by Dobson in 1876, from a specimen collected from Mian Mir (Lahore). Further collections were made from different regions of northern Sindh (Kashmore and Mirpur in Jacobabad, Larkana, Sukker and Dadu Districts) and Punjab (Muzaffargarh and Sialkot). Its population status is uncertain and deserves further study [15].

Twenty-two bats were captured through mist net in Manzaray Baba, Dir (N35° 12.327′ E71° 52.540′), Jrandy (N34° 24.808′ E71° 48.202′), Koz Koper (N34° 24.399′ E71° 50.171′), Mola Misray (N34° 25.251′ E71° 49.085′), Astanadaro Kalay (N34° 24.913′ E71° 49.466′), Malakand Top (N34° 34.007′ E71° 55.736′), Badraga (N34° 23.314′ E71° 50.295′), Head Koper (N34° 24.454′ E71° 50.061′), Pull Saokai (N34° 38.553′ E72° 01.749′), Qadar Kalay (N34° 24.076′ E71° 50.723′), Kot (N34° 29.778′ E71° 43.501′), Fishing Hut (N34° 38.900′ E72° 01.941′), and Matkani (N34° 37.380′ E71° 51.055′) in Malakand division.

2.6.12. Schreiber's long-fingered bat Miniopterus fuliginosus (Kuhl, 1819)

It has not been collected from Pakistan up till now, but Gaisler [7] asserts that it is likely to occur in the country as it is present in Afghanistan and Iran, close to the western borders, and in India, close to the eastern borders of Pakistan [2]. The status of this species is unknown in Pakistan, IUCN 2008-NT.

Six bats were captured through mist net in Barcharai Daim (N34° 33.737′ E71° 44.872′), Fatehpur (N35° 04.345′ E72° 29.502′), Bahrain Pull (N35° 12.418′ E72° 32.963′), Fizagat (N34° 47.586′ E72° 23.672′), Fish Hatchery (N35° 08.439′ E72° 32.917′), and Baidara (N34° 57.494′ E72° 26.635′) in Malakand division.

3. Problems of conservation

Bats in the study area are confronted with numerous threats. Some of these threats are highlighted below.

1. Low rate of reproduction

   Bats have a low rate of production. Most of the Chiropteran give birth to only one or two pups. Numerous threats to bats' survival compiled with slow rate of reproduction make their survival precarious.

2. Habitat loss

   Mountain caves, rocky crevices, old abandoned buildings, and old trees act as favorite roosting places for bats. These places and objects are critically endangered in the study area and are being rapidly destroyed. Caves and rock crevices face destruction on account of use of explosives and dynamites for mining of marble, gem stone, and other minerals. The caves are also excavated for finding archeological artifacts, thus disturbing the bat roost. Tall, old trees are being cut for fuel or for reclamation of land for agriculture and housing. Old dilapidated historic places are being renovated for tourism and the culture of building houses with hollow wooden roofs is being replaced by reinforced cement concrete (RCC) roofs. All these practices lead to destruction of bat habitat, ultimately threatening their survival.

3. Food scarcity

   Farmers do not like frugivorous bats because of the damage they do to their fruit orchards. Consequently, the farmers either kill these bats or they change the fruit species composition in the orchards, thus considerably reducing the amount of food available to bats. Reduction in the quantity of food ultimately affects the bat population.

4. Environmental pollution

   Every increasing use of pesticides, chemical toxins, air water pollution through industrial wastes and exhausts affects bats as adversely as they do the human beings. Contaminated food and water take a heavy toll on bats and threaten their long-term survival.

5. Natural disasters

   Natural disasters such as earthquakes, floods, and fire cause devastation of habitat of bats. Mountain areas of KP, including the study area, are prone to frequent natural disasters.

Earthquakes and landslides result in caving in or closure of cave entrances, thus killing large number of bats inhabiting them.

6. Depredation by birds and animals

   Certain birds such as owls and eagles and mammals, including jungle cats, civets, and flying squirrels prey upon bats for food. An abundance of these predators in habitat may result in rapid decline in bat population.

7. Killing for food and medicine

   A tribe in Nepal is reported to hunt bats for food. Although, this is not the case in KP, yet people kill bats for use in medicine for curing baldness, rheumatism as aphrodisiacs. Some people also consider bats as a bad omen; therefore, they kill them.

8. Lack of awareness

   The bats live in lonely and hidden corner of crevices and they are not known to the common man. Those who know them are not aware of the role they play in the ecosystem. These ugly looking nocturnal creatures play an important role in the ecosystem. They are not only a valuable component of the biodiversity, but also represent a unique mammalian order, Chiroptera. Bats are biological controllers of insects, pests, and some rodents, are crop pollinators, and a source of highly valuable guano.

   Being unaware of these values and roles of bats, people do not show any concern about their conservation. The wildlife laws of the country are also silent about bats and no penalties have been prescribed for their illegal hunting, killing or trading. Conservation of bats demands that people, particularly farmers are made fully aware of the importance and role of bats in the country. Besides implementation of an awareness campaign about bats, the bat conservation lessons need to be included in the primary and middle school curriculum.

4. Recommendations for future research guidelines

1. **Bat surveys:** this is the first extensive exploration of that small portion of the KP which comprises of only three districts of Malakand division, i.e., Malakand, Dir, and Swat. Although more focus remained toward Malakand district, 6 families, 14 genera, and 21 species were identified. Moreover, two new country records (*Myotis formosus* and *Miniopterus fuliginosis*) were also made. Further bat surveys in poorly surveyed parts of the country especially in KP and Balochistan may result in identification of some other new bat taxa. More bat surveys involving greater field efforts may also confirm the presence or absence of those already described species from the country.

2. **Distribution ranges and species-specific habitat analysis:** the presence of 13 new locality records **(***Pteropus giganteus, Cynopterus sphinx, Rhinopoma hardwickii, Megaderma lyra, Rhinolophus lepidus, Hipposideros fulvus, Barbastella leucomelas, Scotophilus heathii, Scotophilus kuhlii, Eptesicus serotinus, Pipistrellus javanicus, Pipistrellus dormer* and *Scotoecus pallidus*) and two new country records (*Myotis formosus* and *Miniopterus fuliginosis*) gives credence to

the idea that distribution ranges of most of the bat species have changed over the past 60 years. Thus, serious scientific studies are needed to redefine distribution ranges and identify species-specific habitats using global positioning system and radio-telemetric studies.

3. **Reconfirmation of bat taxonomy:** genetic analysis of none of the bat species of the country has been made using molecular markers thus leaving behind a chance to doubt identification of cryptic bat species. Thus, molecular genetic studies of all the bat species of the country are highly recommended. These could even lead to the discovery of such bat taxa which are new to science.

4. **Bat call library:** There was only one bat detector with my supervisor and he was the only professor in the whole country which was working on bats at that time. He has bought this equipment in his project funded by HEC Pakistan. Under his supervision there were only four students which were working on bats at that time. So, none of the bats could be recorded. Bat call analysis has boosted bat identification throughout the world, but the lack of such sophisticated equipment in the country has become a major bottleneck in the establishment of a bat call library.

5. **Awareness campaigns:** a majority of the countrymen are unaware of the ecological services rendered by bats. Khyber Pakhtunkhwa is the major fruit growing region of the country. Based on misperceptions, the locals consider all bats as vermin and kill them ruthlessly. Conservation education to highlight the significance of bats must be included in the curriculum of children at primary school level so that they may adopt a pro-conservation attitude in the first few years of their personality building.

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The Daubenton's Bat (*Myotis daubentonii*, Kuhl, 1817) and Its Role as a Reservoir for Europe Bat Lyssavirus Type-2

Nicholas Johnson

Additional information is available at the end of the chapter

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Abstract

The Daubenton's bat is found on a geographical cline from Western Europe, including the British Isles, across Central Europe and Asia, and as far east as Japan. The species is insectivorous and uses echolocation to detect and catch prey, with the distinct behaviour of hunting over water bodies such as lakes and rivers. The other distinctive feature of Daubenton's bats is that they appear to be the principal species of bat that harbours European bat lyssavirus type-2 (EBLV-2). The lyssaviruses, a group of viruses that includes the rabies lyssavirus, are generally associated with bats. Many are zoonotic with EBLV-2 being responsible for two human deaths. Reports of EBLV-2 in Daubenton's bats have been made from countries across Europe although the majority have been from England. This chapter will consider the biology of the Daubenton's bat, the association of EBLV-2 with this particular species and discuss the interaction between bat and virus.

Keywords: Daubenton's bat, European bat lyssavirus type-2, Europe, virus transmission

1. Introduction

Europe has 45 bat species considered indigenous to the continent (http://www.batlife-europe.info/about-batlife-europe/european-bats/, accessed 8 November 2017). This number is being constantly revised as new and cryptic species are identified. All are small- to medium-sized insectivorous bat species although colonies of the Egyptian fruit bat (*Rousettus aegyptiacus*) are known to colonise islands of the Mediterranean Sea [1]. The role of bats as a source of zoonotic viruses has been recognised over the past three decades with the emergence of viruses such as Hendra virus, Nipah virus and SARS-coronavirus [2]. However, European bats are nocturnal so contact with humans is minimal making them both an elusive species to study and a rare source of zoonotic pathogens [3]. Key amongst these is the European bat lyssaviruses (EBLVs), members of the genus *Lyssavirus*, family *Rhabdoviridae*. The type species of the genus is rabies lyssavirus (RABV), the virus responsible for virtually all cases of rabies in the world. The genus contains a growing number of viruses, the majority associated with bat species [4] (**Table 1**).

All can cause encephalitis in mouse models of infection and it is suspected that all are capable of causing rabies in humans. Of these, five have been reported from Europe. European bat lyssavirus type-1 (EBLV-1), EBLV-2, West Caucasian bat lyssavirus (WCBV), Bokeloh bat lyssavirus (BBLV) and Lleida bat lyssavirus (LLEBV). Despite the close association with bats, the first recognised isolation of EBLV-2 was derived from a human case of rabies. The patient was a bat ecologist working in Finland when he developed rabies [5]. Shortly afterward, a related virus was isolated from the brain of a pond bat (*Myotis dasycneme*). Since then there has been one further case of EBLV-2 infection in a human [6] and continual reports of the virus infection of Daubenton's bats (*Myotis daubentonii*).

The ability to discriminate between different lyssaviruses was only achieved with the advent of monoclonal antibody panels that show different binding patterns to particular viruses. This first alerted researchers that the viruses present in European bats were distinct from RABV found in North American bats [7]. Antigenic typing has now been superseded by genetic

Virus species	Bat reservoir	Human infection
Rabies lyssavirus	Numerous insectivorous, frugivorous and hematophagous bat species	Yes
Lagos bat lyssavirus	Various species including *Eidolon helvum* and *Rousettus aegyptiacus*	No
Mokola lyssavirus	Not known	Yes
Duvenhage lyssavirus	*Nycteris thebaica*	Yes
European bat lyssavirus type-1	*Eptesicus serotinus*	Yes
European bat lyssavirus type-2	*Myotis daubentonii*	Yes
Bokeloh bat lyssavirus	*Myotis nattereri*	No
Aravan lyssavirus	*Myotis blythii*	No
Irkut lyssavirus	*Murina leucogaster*	Yes
Khujand lyssavirus	*Myotis mystacinus*	No
West Caucasian bat lyssavirus	*Miniopterus schreibersii*	No
Australian bat lyssavirus	Various species including *Pteropus alecto* and *Saccolaimus flaviventris*	Yes
Shimoni bat lyssavirus	*Hipposideros commersoni*	No
Gannoruwa bat lyssavirus	*Pteropus medius*	No
Taiwan bat lyssavirus	*Pipistrellus abramus*	No
Lleida bat Lyssavirus	*Miniopterus schreibersii*	No

Table 1. Known lyssaviruses and their association with particular bat species.

discrimination based on genome sequencing [8] and the first complete genome sequence for EBLV-2 was reported in 2007 [9]. Of the other lyssaviruses detected in European bats, WCBV and LLEBV represent single isolations of virus so little is known about the epidemiology of these viruses. The most commonly encountered lyssavirus in European bats is EBLV-1 and almost all detections of this virus are from serotine bats (*Eptesicus serotinus*) [10]. A more recent addition is Bokeloh bat lyssavirus that is predominantly associated with Natterers bats (*Myotis nattereri*) from Germany and France [11].

The first report of EBLV-2 in the UK resulted from the discovery of an adult female bat in the cellar of a public house in Newhaven, Sussex in 1996 [12]. Virus was isolated from brain tissue removed from the bat. Subsequently, reverse transcription polymerase chain reaction (RT-PCR) and sequencing confirmed the virus species by comparison with sequences derived from lyssaviruses known at the time. It was speculated that the bat may have flown across the English Channel but subsequent isolations of virus from other locations in England suggested that the virus was actually endemic long before cases were detected [13]. All detections of EBLV-2 in bats in the UK (isolation of virus or detection of virus in a salivary swab) have been from Daubenton's bats. This pattern has been reflected across Europe with occasional bat-associated cases reported in The Netherlands [14], Germany [15], Switzerland [16], Finland [17] and Norway [18].

The following sections discuss the biology and ecology of the Daubenton's bat, research on the relationship between EBLV-2 and its reservoir host and a discussion on the transmission of the virus between conspecifics that might explain the persistence of this virus in European bat populations.

2. The Daubenton's bat

The Daubenton's bat was first described by the German naturalist and zoologist, Heinrich Kuhl [1797–1821] in his monograph, Die deutschen Fledermäuse, published in 1817. The name selected for the species was derived from the French naturalist Louis Jean-Marie Daubenton [1716–1800]. Kuhl went on to take part in an expedition to Java to study the islands fauna but developed a fever that subsequently killed him. He was buried in the Botanical Gardens of Bogor to the south of Jakarta where his gravestone can still be located.

Daubenton's bats are considered a medium-sized insectivorous bat with an adult wingspan of up to 27.5 cm and a body length up to 5.5 cm. Adults weigh between 7 and 12 g and have a reddish brown pelt. The common name of the species is the 'water bat' due to its feeding habit. This involves flying low across the surface of water bodies such as lakes, rivers and canals, feeding on a range of water-associated flies. These include chironomid midges, caddisflies and mayflies. Daubenton's bats echolocate in a call range between 35 and 85 kHz, and generally feed within 6 km of their roost. Roost sites range from natural sites such as tree holes to man-made structures, including houses [19]. During the summer, there is a degree of segregation between maternity colonies, dominated by a single male and bachelor roosts [20]. Hibernation takes place over the winter months, usually in caves, tunnels and mines.

Daubenton's bats are found from Ireland in the west, across Europe, Asia and the islands that form the Japanese archipelago. In Europe, the species can be found in the Iberian Peninsula and north of the Alps. Populations are also reported as far north as southern Sweden and Finland, almost as far as the Arctic Circle. Mating occurs in late autumn and is preceded by a behaviour termed swarming where bats congregate and fly near the entrance to a hibernation site. Daubenton's bats are not the only species that demonstrate this behaviour but they are commonly found early in the swarming season. In Britain, this is typically between August and October [21]. The behaviour is thought to be a form of lecking due to the male bias observed during trapping at swarming sites and may proceed mating.

Investigation into the population structure of the Daubenton's bat, based on genetic data, between UK bats and those on the European mainland suggests that there is regular movement of bats across the English Channel [22]. This suggests panmixia between the two populations with no barriers to the spread of genetic haplotypes, and in theory to the transmission of EBLV-2. A similar situation has been proposed for the straw-coloured fruit bat, *Eidolon helvum*, and its association with certain zoonotic viruses across its range in Africa [23].

The first report of EBLV-2 in a Daubenton's bat occurred in Denmark in 1986 [24, 25]. The virus from this account was not isolated. Subsequently, EBLV-2 was isolated from pond bats from the Netherlands in 1987 [8] and Daubenton's bats from Switzerland in 1992 [16]. Descriptions of initial encounters with EBLV-2 infected bats typically report grounding, particularly near rivers or canals, although occasionally bats are reported to fly in daylight. Live bats vocalise, show signs of distress and can bite aggressively although this may in part be a result of distress caused by captivity. Infected bats often appear emaciated and dehydrated despite attempts at rehabilitation [26].

3. European bat lyssavirus type-2 and its relationship with the Daubenton's bat

Phylogenetic analysis on early isolations of EBLV-2 confirmed that the virus was a lyssavirus related to rabies lyssavirus [27]. However, many questions remained about the transmission of the virus between bats and the pathogenesis in its reservoir host. Early reports indicated that infected bats exhibited signs suggestive of rabies including aggression, inability to fly and vocalisation. One of the earliest questions was the distribution of virus in an infected bat. Rabies lyssavirus is neurotropic, meaning that it targets neurons within the peripheral and central nervous system. The application of sensitive RT-PCR and virus isolation detected virus predominantly in the brain but also in other organs of an EBLV-2 infected Daubenton's bat [13]. However, quantitative RT-PCR demonstrated that the virus was most abundant in the brain and spinal cord of the bat [28] in a pattern like that observed for RABV. Virus detected in other tissue was likely to be derived from innervating nerves. The presence of virus in salivary glands and tongue suggested that this was likely the point of virus egress and that biting was the means of transmission between bats. A similar conclusion was made for the transmission of RABV in North American bats [29]. Experiments in a mouse model attempting to demonstrate aerosol transmission were unsuccessful for EBLV-2 [30]. However, once in the brain, EBLV-2 shows similar characteristics to rabies lyssavirus, infecting neurons, stimulating innate immune responses [31] and triggering signs of viral encephalitis [32, 33]. In order to confirm some of these observations, a series of experimental studies were established to investigate the methods of EBLV transmission in bats and characterised EBLV-induced disease in the natural host [34–36]. These studies demonstrated that subcutaneous inoculation was the most efficient means of infecting insectivorous bats with EBLVs. Clinical signs exhibited by infected bats ranged from sudden death with no apparent disease to a spectrum including weight loss and rapid progression to paralysis [35].

Field studies in the UK in response to the human case of EBLV-2 in 2002 provided evidence of virus circulation within the Scottish Daubenton's bat population [37]. Seroprevalence levels ranging from 0.05 to 3.8% were detected in colonies from across the country although oral swabs taken coincident with blood samples were all negative for EBLV-2. Subsequent surveillance in Daubenton's bat colonies in England found similar seroprevalence levels [38] suggesting that the virus affects bat populations across the country. This is supported by population genetic analysis of English Daubenton's bats [22] and the detection of EBLV-2 infected bats from locations across England, Scotland and Wales [39]. One location where EBLV-2 infected bats have been repeatedly detected is Stokesay Castle in Shropshire [40]. The tower of the castle (**Figure 1**) is known to host a summer maternity roost and there have been three bats found in the castle that have been infected with EBLV-2. Another infected bat was submitted from the nearby location of Newtown. A further practical question, bearing in mind the zoonotic potential of EBLV-2, was whether current vaccines developed against rabies lyssavirus would be protective against exposure following a bat bite. Cross-neutralisation and cross-protection studies in mice indicated that rabies vaccines would be protective [41].

Figure 1. A photograph of Stokesay Castle where EBLV-2 infected bats have been repeatedly detected. The site offers a number of features attractive to bats including the main tower where bats were roosting, a large pond in the foreground that could provide a feeding site and extensive woodland that would provide alternative roosts.
]

This lead to the public health recommendation that individuals that are in close contact with bats should be vaccinated, in addition to simple measures such as wearing gloves whilst handling bats. Furthermore, post-exposure vaccination could be offered to those that were bitten or had inadvertently been in contact with bats. This could also be extended to domestic animals, particularly cats that catch bats.

4. Discussion

All evidence to date suggests that the Daubenton's bat is the wildlife reservoir for EBLV-2. However, many questions remain concerning the persistence of EBLV-2 within the Daubenton's bat population in Europe. The virus is only detected sporadically. In the UK, this equates to a single isolation a year but this meagre number is presumably the tip of the iceberg of what must be constant virus transmission events occurring whilst the bats are active. With the exception of two bats submitted in May, the majority of submissions in the UK occur in late summer and early autumn (**Figure 2**). The incubation period, the time from exposure to the development of disease or death, for lyssaviruses in bats is highly variable. By their nature, this cannot be established in wildlife populations as the timing of the transmission event is not known. In a unique case, EBLV-2 was detected in a bat that had been held in captivity for 9 months [42]. Captive studies in Daubenton's bats reported an incubation period of 33 days [35] after infection by the sub-dermal route. The later study involving EBLV-1 infection of serotine bats gave incubation periods between 17 and 26 days following sub-dermal or intramuscular infection [36]. This suggests that the incubation period varies from just over 2 weeks to over 9 months, with factors such as virus dose and route of exposure influencing the time to development of disease. The presence of virus in the salivary glands and taste buds of infected bats implicates biting as the main means of transmission. This could presumably occur at a number of points in the Daubenton's bat life cycle including swarming and mating just prior to hibernation, to the formation of colonies during the summer months. The composition of UK

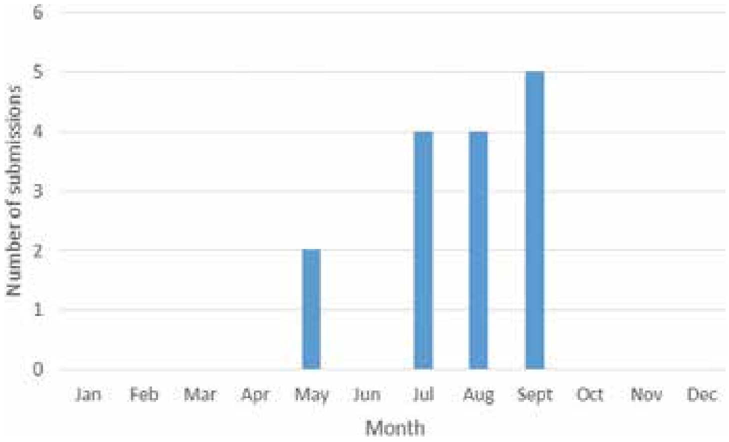

Figure 2. Seasonal distribution of EBLV-2 infected Daubenton's bats submitted for rabies testing in the UK (1996–2017).

submissions of EBLV-2 bats gives little help in resolving this. Although based on low numbers, 15 cases, there is no gender bias (7 males versus 8 females). There does appear to be a relatively higher proportion of juveniles submitted (8 versus 6 adults, where data is known), perhaps favouring transmission in maternity colonies and shorter incubation periods of 2–3 months. This would be supported by the repeated submission of EBLV-2 infected bats from the colony at Stokesay Castle. However, the means by which the virus persists through hibernation is not known and may rely on long incubation events in a proportion of cases. Modelling of rabies infection in North American bat populations suggests that this is critical for long-term persistence of rabies lyssavirus [43].

The geographical spread of EBLV-2 infected bats in the UK is also a mystery with cases submitted from disparate locations with no obvious link in time or space. A virus such as EBLV-2, which kills its host, should struggle to persist in small populations of bats. It is possible that a virus could persist in areas where Daubenton's bats are abundant and there is movement of individuals between colonies [44]. Alternatively, the virus could move across the wider landscape moving between populations as observed for rabies lyssavirus in common vampire bat (*Desmodus rotundus*) populations in Latin America [45]. In continental Europe, similar challenges have been encountered due to the uneven distribution of EBLV-1 in the serotine bat population [10, 46] and the sporadic nature of BBLV in Natterers bats [11]. A better understanding of Daubenton's bat behaviour, particularly how populations interact and move across the landscape may help in formulating hypotheses that could explain this distribution. Migration and dispersal, particularly by males may be a key feature driving virus persistence within bat populations. This is also considered to be critical for the spread of rabies in European red fox (*Vulpes vulpes*) populations. Bats may use rivers and valleys to provide corridors for long distance migration [47]. This would seem highly appropriate for a bat species that uses water bodies for feeding.

5. Conclusions

When the second case of EBLV-2 infection occurred in a human in 2002, very little was known about the biology of the virus and its relationship with its bat reservoir leading some authors to describe the relationship as an ecological enigma [48]. Since then advances have been made in the detection of more lyssavirus species in bat populations, the virus distribution in the bat host, the derivation of the complete EBLV-2 genome and the establishment of clear public health measures aimed at protecting those that handle bats. This includes the wearing of gloves to prevent exposure to virus and the knowledge that current vaccines against rabies will prevent infection with EBLV-2. However, much is not known, in part due to the difficulties in studying a protected, nocturnal, flying mammal. Lyssaviruses form intimate relationships with particular bat species that maintain the virus in the environment [49]. This could imply adaptation to the host that favours continued transmission in that host but limiting the viruses' ability to infect another species. Alternatively, host behaviour such as roosting, dispersal and mating could be drivers for conspecific transmission. Indeed, both may function to restrict particular viruses to a single bat species. It is clear that further multidisciplinary research will be needed to answer fundamental questions on the maintenance of EBLV-2 in the Daubenton's bat.

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Bats, Bat-Borne Viruses, and Environmental Changes

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Additional information is available at the end of the chapter

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Abstract

During the past decade, bats were shown to a major source for new viruses. Among them are well known coronaviruses such as SRAS or MERS but also Ebola. At the same time, no direct infection from bat to human has been demonstrated. The dynamic of transmission of bat-borne viruses is therefore a complex process involving both sylvatic and urban cycles, and intermediate hosts not always identified. The threat potentially exists, and drivers must be sought for man-made environmental changes. Anthropized environments are mosaic landscapes attracting at the same place different bat species usually not found together. Anthropized landscape is also characterized by a higher density of bat-borne viruses. The threat of new bat-borne virus outbreaks has greatly increased in the recent years along with media anthropization and the extremely rapid deforestation process. Deforestation could be a major contributing factor to new viral emergences due to more frequent contacts of livestock and humans with bats possibly containing infectious viruses.

Keywords: bats, bat-borne viruses, environment, landscape change, anthropization, emergence

1. Introduction

Emerging infectious diseases (EIDs) remain a major threat to public health. Most EIDs described in humans have been shown to be of zoonotic origin. During the past decades, growing evidence that viruses causing EIDs in humans share identity or strong sequence homologies with viruses circulating in bats were reported; this result pushed the epidemiologist to focus their attention on these wild mammals in order to determine whether bats play a particular role as virus diversity reservoirs worldwide and to understand the state of the threat in a context of ecosystem change.

Taxonomically, bats are grouped in the order *Chiroptera* (Gr. *cheir*, hand; *pteron*, wing) and they are the only mammals with adaptation for powered flight on long distance. Although bats are outnumbered by rodents in species richness, they represent the second species richness in the mammal world with 1230 species—more than 20% of all mammals on earth—inhabiting a multitude of ecological niches [1]. Bats are currently known as important reservoirs of zoonotic viruses worldwide [2] and factors underlying high viral diversity remain the subject of speculation. Bats have sometimes been considered as enigmatic mammals having a particularly effective immune system or antiviral activity [2, 3]. Obviously, bats are not very different from other mammals, and several bat viruses can cause disease and death of bats; in example, a study performed on 486 deceased bats of 19 European Vespertilionidae species showed that two thirds of mortality were due to trauma or disease and that at least 12% of these mammals had succumbed to infectious diseases (19 died from bacterial infections; 5 died from viral infections caused by bat adenovirus AdV-2 or bat lyssavirus EBLV-1; 2 died from parasitic infections) [4]. Yet, numerous viruses apparently remain non-pathogenic in bats, likely due to a long process of co-evolution; although most of these viruses apparently do not affect bats health, some of them have been shown to severely affect wild and domestic mammals, as well as humans.

2. History

The fact that bats play a role as reservoir of human viruses was recognized during the first half of the twentieth century, when rabies was found in South and Central America [5]. The hypothesis that bat may act as a reservoir of viruses causing EIDs in humans was next acknowledge several decades later, during the second half of the twentieth century. Most genotypes of rabies or rabies-related virus within the *Lyssavirus* genus of the Rhabdoviridae family have been documented in bats [6]. In the recent years, bats have gained notoriety after being implicated in numerous EIDs. Bat-borne viruses that can affect humans and have caused EIDs in humans fall into different families: paramyxoviruses including Hendra viruses [7] and Nipah viruses [8]; Ebola hemorrhagic fever filoviruses [9]; Marburg hemorrhagic fever filoviruses [10] and sudden acute respiratory syndrome-like coronaviruses (SARS-CoV) [11]. Their list is probably far from complete. Interestingly, the powerful retroviral hosting ability of bats had likely contributed to shape mammalian retroviruses [12]. Furthermore, sialic acid receptors for avian and human influenza virus are found in the North American little brown bats, which could potentially facilitate the emergence of novel zoonotic strains [13].

In this context, it becomes urgent to resolve, as soon as possible, three essential questions, namely: Will bats help to serve as a source of pathogenic viruses for animals and humans with regard to pathogens that have already caused EIDs in humans? Are bats reservoirs for viruses that have not yet infected humans but could be at the origin of EIDs in the future? Could bats be considered as "living test tubes" in which new viruses could be developed through genomic exchanges and genetic drift? To answer these questions, it is essential to monitor bat populations and to analyze the diversity of viruses circulating in these populations. Although informative, the study of circulating viruses in a few specimens and a particular ecosystem cannot account for the global dynamics of viral populations present in the different families of bats on the planet. The isolation and sequencing of viruses was an important step, but not enough performing to capture the extent of the phenomenon. Polymerase chain reaction (PCR), when primers were available, have also contributed to a better characterization of bat-borne viruses being related to viruses that have already produced EIDs in humans. More recently, high-throughput sequencing and metagenomic approaches have led to a quantum leap in surveillance and the quest for knowledge [14–17]. However, a global vision remains indispensable and the initiatives, which make it possible to compile the data of the various laboratories and to catalog them as comprehensively as possible, are welcome [18] (http://www.mgc.ac.cn/cgi-bin/DBatVir/main.cgi), in addition to other virus database such as the Virus-Host DB (http://www.genome.jp/virushostdb/; this database currently select 134/10028 items under "bat" query), the NCBI viral genome resources (https://www.ncbi.nlm.nih.gov/genome/viruses/; this database currently select 84 items under "bat" query) or Virus Pathogen resource, VIPR (https://www.viprbrc.org/brc/home.spg?decorator=vipr). It is worth noting that although bats are found on all continents except Antarctica [19], the accumulation of results is very variable from one continent to another. As shown in **Figure 1**, Asia is largely in the lead for data accumulation ahead of North America and Africa and next Europe and South America (**Figure 1A**). The preponderance of Chinese results for Asia's contribution is even more impressive (**Figure 1B**). Almost 60% (58.9%) of Asian articles originate from China, followed by Vietnam at 16.8%. All other contributing countries are below 7%, i.e. 6.5% for both Thailand and Cambodia. It is quite interesting to highlight the correlation between the number of publications and the geographical origin of scientific teams who publish them, because Asia/Southeast Asia is considered as one of the hotspot on the planet for the emergence of new viruses.

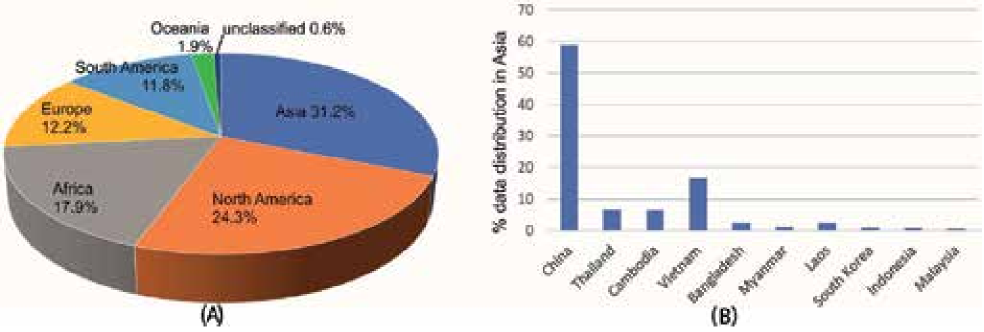

Figure 1. Data distribution. (A) Overall data distribution of bat-associated viruses by geographic region (Asia: 2274 publications; North America: 1772 publications; Africa: 1307 publications; Europe 891 publications; South America: 858 publications; Oceania: 142 publications; and unclassified: 47 publications). Adapted from the database of bat-associated viruses (http://www.mgc.ac.cn/cgi-bin/DBatVir/main.cgi). (B) Data distribution in Asia. China comes first with 1723 publications (58.9%), followed by Vietnam with 491 articles (16.8%), Thailand with 190 articles (6.5%) and Cambodia with 189 articles (6.5%) (http://www.mgc.ac.cn/cgi-bin/DBatVir/main.cgi, updated February 18, 2018).

3. Etiology and associated diseases

Globally, a small proportion of the approximately 55,000 annual human deaths caused by rabies virus are the result of infection by variants or virus associated with bats [19]. Human rabies caused by bat *lyssavirus* (genotype 1: rabies virus; genotype 2: Lagos bat virus; genotype 4: Duvenhage virus; genotype 5: European bat lyssavirus type 1, EBLV-1; genotype 6: European bat lyssavirus type 2, EBLV-2; genotype 7: Australian bat lyssavirus) was regularly reported in South and North America, Africa, Europe and Australia [20–22].

In 1994, an outbreak of an acute respiratory illness occurred in a human and 14 horses in Hendra, a suburb of Brisbane, Australia. These EIDs finally affected 2 humans and 22 horses [23]. Four additional outbreaks were observed during years 1994, 1999, and 2004, infecting two humans and five horses and killing all but one human. A virus of the *Paramyxoviridae* family, genus *Henipavirus*, carried by *Pteropus* bats, and named Hendra virus was shown to be the etiologic agent of this disease. Nipah virus (NiV), another member of the *Paramyxoviridae* family found in *Pteropus* bats, associated with encephalitis in humans, was discovered in an outbreak in Malaysia in 1998 that affected 283 persons and caused 109 deaths (case fatality rate 39%) [24]. Direct contact with infected pigs was identified as the predominant mode of human infection. Subsequently, outbreaks of NiV have been observed almost every year in Bangladesh [25] and occasionally in India [26]. Bangladesh outbreaks were shown to be linked to consumption of fresh data palm sap contaminated by NiV-containing *Pteropus* bats' secretions and excretions [27]. In 1997, another member of the bat-borne *Paramyxoviridae* family, described as Menangle virus, was isolated from stillborn piglets in Australia; two of 250 humans living in contact with the infected animal showed febrile illness with measles-like rash and had high titer of anti-Menangle virus antibodies [28]. These people never get in contact with flying foxes, suggesting that this bat-borne virus was transmitted to the humans after infection of pigs/piglets [29]. Before 2002, although coronaviruses (CoV) were known to be agents of respiratory infections in humans (e.g.; common winter cold), they lent little attention. Human CoV (HCoV) strongly gained in notoriety after being identified as responsible for the severe acute respiratory syndrome (SRAS) outbreak in humans [30]. SRAS emerged in 2002 in China and spread across 29 other countries, causing more than 8000 infected patients and almost 800 deaths worldwide (case fatality rate about 10%). Serological analysis of healthy human samples collected in Hong Kong in 2001 revealed a prevalence of 1.8%, suggesting that the circulation of SARS-related viruses had occurred prior to the 2003 epidemic. Indeed, SARS-like CoV circulating in Chinese horseshoe bats had spread and adapted to wild Himalayan palm-civet often sold as food in Chinese markets [31]. After mutation, this CoV adapted to humans and became able to spread from person-to-person. During SARS outbreaks in Toronto and Taiwan, certain persons were very efficient at transmitting SARS-CoV and were named "Superspreaders" [32]. A few years later, the emergent Middle East Bats Respiratory Syndrome (MERS)-CoV was reported in Saudi Arabia in 2012) [33]. Once again, the human MERS-CoV likely originated from a bat-CoV-related virus and was likely transmitted through camel-human contacts [34]. The MESR epidemics displayed a limited spread to other countries in the Middle East (except in individuals traveling back from Middle East). So far, 2081 people were infected with MERS-CoV among which 722 died from the disease (case fatality rate 34.7%). It is worth noting that during the 2012–2014 outbreak of MERS-CoV, "superefficient" person-to-person transmission apparently did not occur. However, the MERS-CoV outbreak that affected the Republic of Korea in 2015 was caused by a single person (68 years old "index patient") who developed fever 2 weeks after returning from 2 weeks travel in the Middle East. Once back to Seoul, this person visited the Samsung Medical Centre on 17 May and was isolated the day after on suspicion of MESR before being finally diagnosed with MERS on 20 May. A total of 186 people were infected out of which 36 died; some 44.1% of the cases were patients exposed in hospitals, 32.8% were caregivers, and 13.4% were healthcare personnel. Interestingly, a total of 83.2% of the transmission events were epidemiologically linked to five "superspreaders," all of whom had pneumonia characterized at the first medical consultation. In August 2015, 1413 laboratory-confirmed cases of MERS have been reported worldwide of which 502 died [35]. The cause for superspreading events is still unclear and could be consequence of virus mutation, high viremia linked to higher level of virus shedding, environmental factors such as co-infection, or host-altered immune status. A recent study of a virus closely related to Middle East respiratory syndrome coronavirus (MERS-CoV) found in a *Pipistrellus* bat supports the bat-borne origin of MERS-Cov [36].

Ebola hemorrhagic fever is also caused by a zoonotic virus discovered during an epidemic outbreak that affected people in villages of Democratic Republic of Congo (DRC; more than 300 infected people) and Sudan (almost 300 people infected), in 1976 [37]. Ebola virus is responsible for a severe and frequently fatal illness characterized by a nonspecific viral syndrome followed by a fulminant septic shock, multi-organ failure, and coagulopathy resulting in severe bleeding complications). Though silent during a few years, Ebola virus continued to circulate in these regions and re-emerged in Sudan in 1979 (34 infected people) and Gabon and DRC in 1994–1995 (more than 350 infected people). Between 1996 and 2014, several outbreaks were reported in different African countries, each episode affecting from a few people to thousands for the 2014 epidemic, case fatality 52% [38].

Although the recent emergence of viruses known to be carried by bats have not led to very large epidemic outbreaks (a few hundred to a few thousand infected people), the fact that some of these viruses can adapt to spread from person-to-person, and the high mortality associated with these infections (case fatality frequently above 30% of infected persons) has contributed to consider them a major public health risk by international medical authorities. This partly explains why after a period of relative disorganization in the face of the threat (e.g. SARS, MERS and Ebola outbreaks), each emergence was subject of a rapid response by the health authorities. In some cases, treatment of the disease is largely limited to supportive therapy and requires appropriate control measures. This proved true for the 2014′ Ebola outbreak in West Africa, which was the largest in history. Ebola hemorrhagic fever was diagnosed in Guinea in December 2013 and outbreaks next appeared in Liberia, Nigeria, Senegal, and Mali. By 18 September 2014, WHO reported of 5335 cases with 2622 deaths (case fatality around 50%). Early 2015, additional cases were reported in Mali and

Sierra Leone. On April 2015, the Ebolavirus outbreaks had already resulted in more than 10,880 deaths among 26,277 cases [38]. On March 2016, WHO reported a total 11,323 deaths among 28,646 cases, indicating a decrease in the spreading of the virus in human. There is no direct evidence that bat is the reservoir for ebolavirus-inducing disease in humans. Yet, Ebola-related virus were found in tissues of several bats (the hammer-headed fruit bat: *Hypsignathus monstrosus*; the Franquet's epauletted bat: *Epomops franqueti*; and the little collared fruit bat: *Myonycteris torquata*) [9], and experimental infections of the Angola free-tail bat (*Mops condylurus*), little free-tail bat (*Chaerephon pumilus*), and Wahlberg's epauletted fruit bat (*Epomophorus wahlbergi*) with a Zaire strain of Ebola virus led to viral replication in these bats [39]. Widespread infection of cave-dwelling bats by Crimean Congo hemorrhagic fever virus (CCHFV) has also been reported, suggesting a role of bats in the life cycle and geographic dispersal of this virus [40].

It is generally admitted that bats are a source of high viral diversity that may directly or indirectly (following genomic recombination, gene mutations, gene duplication loss/gain) cause a new outbreak. Since the past 20 years, a massive international effort was devoted to the identification of viruses in different families of bats. As shown in **Figure 2**, the total number of bat-associated sequences in GenBank has grown exponentially in the last 20 years. A review of articles referring to bat-borne viruses (**Figure 3**) indicates that rabbies (55,000 persons infected each year, case fatality nearly 100%) is the most prominent topic with 2792 articles (33%). Surprisingly, as shown in **Figure 3A**, the virus family that rank second is *Coronaviridae* with 2622 articles (31%), while the total number of cases accumulated the different episodes remains relatively low (cumulative cases about 8000 individuals; mean case fatality around 10%). Moreover, the number of scientific report about virus family indicates that Coronavirus rank first in terms of publications when MeSH terms concern viruses and

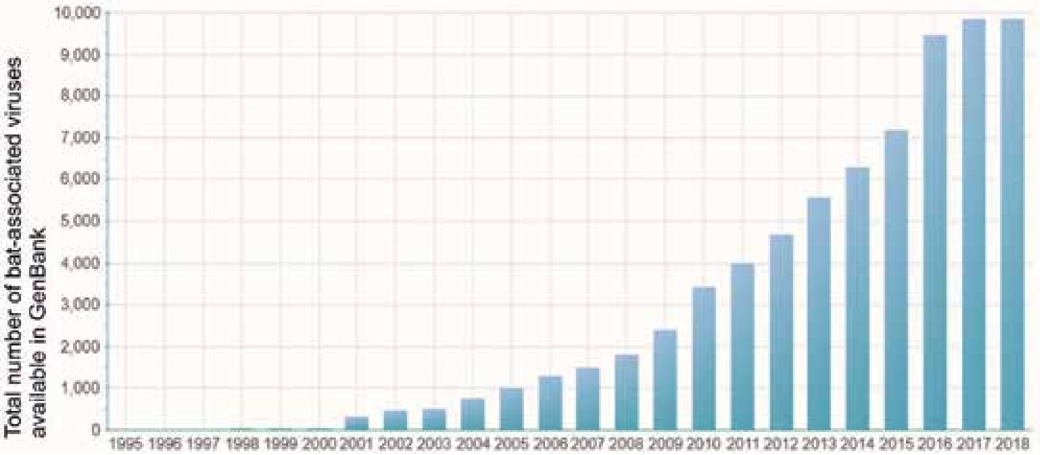

Figure 2. Data increase of bat-associated viruses during the past 20 years. This figure illustrates the total number of sequences of bat-associated viruses available in GenBank according to the database of bat-associated viruses (http://www.mgc.ac.cn/cgi-bin/DBatVir/main.cgi). During the same period (1997–2017), the total number of publications about bat-associated viruses in PubMed increased from 2 to 367 publications/year.

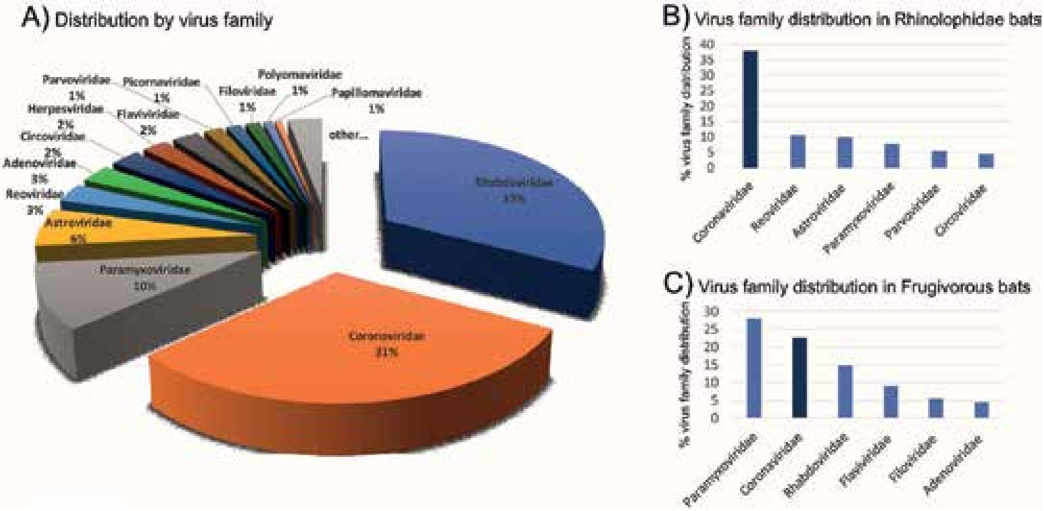

Figure 3. Distribution by virus family. (A) Overall data distribution by virus family. Adapted from the database of bat-associated viruses (http://www.mgc.ac.cn/cgi-bin/DBatVir/main.cgi, updated February, 18, 2018). Rhabdoviridae come first with 2792 articles (32.7%), followed by Coronaviridae with 2622 articles (30.7%), Paramyxoviridae with 839 articles (9.8%), Astroviridae with 494 articles (5.8%), Reoviridae with 244 articles (2.9%), Adenoviridae with 232 articles (2.7%), Circoviridae with 218 articles (2.6%), and Herpesviridae with 189 articles (2.2%). Others represent different virus families such as Flaviviridae (2.3%), Parvoviridae (1.5%), Picornaviridae (1.3%), Filoviridae (1.2%), Polyomaviridae (0.8%), Papillomaviridae (0.6%), and other virus families ranking 2.9%. (B) Ranking of virus family distribution (top 1–6) in Rhinolophidae. (C) Ranking of virus family distribution (top 1–6) in Frugivorous bats.

Rhinolophidae bats (**Figure 3B**) and second when MeSH terms concern viruses and frugivorous bats (**Figure 3C**). It suggests that the number of articles published concerning bat-borne virus does not correlate with the number of infected persons and the case fatality, but rather reflect the perception of a risk felt by the public authorities, health authorities, and funding agencies according to societal demand and presentation of the threat by the media. Even if the accumulation of knowledge through research works is probably influenced by these problems of perception of the risks, the example of coronavirus remains very interesting to tackle emergence phenomena. The increasing risk of pathogen transmission between bats, animals and humans in South East Asia is a consequence of the growing human population and of anthropization of environment (deforestation, agriculture) which have largely altered landscapes [41].

4. Coevolution between bats and viruses

The biological interaction of viruses and their hosts is usually antagonistic, with a delicate balance of actions and counteractions between host immune system and virus escape mechanisms. Parasite-induced reduction in host fitness enhances selection for host resistance mechanisms. On the other hand, novel host defenses increase selection on the parasite. A tight genetic interaction between hosts and pathogens can lead to ongoing host-parasite coevolution, defined as the reciprocal evolution of interacting hosts and parasites [42]. The antagonistic coevolutionary arms race of parasite infectivity and host resistance leads to adaptations and counteradaptations in the coevolution and also has a central role in the evolution of host-parasite relationships in the microbial world [43]. A key consequence of coevolution is the impact on genetic diversity of host and parasite populations. The host-parasite coevolution is widely assumed to have a major influence on biological evolution by imposing a high selective pressure on both host and virus. Selected traits, genes involved, and the underlying selection dynamics represent central topics of interest for understanding host-parasite coevolution [44].

The evolution of bats is a very successful singular history among mammals that have produced an enormous diversity of species with high mobility and great longevity adapted to a great spectrum of environments [42]. Bats host more zoonotic viruses and more total viruses per species than rodents, despite the fact that there is a lot more known species of rodents [45]. Furthermore, bats harbor a significantly higher proportion of zoonotic viruses than all other mammalian orders [46]. The antagonistic coevolutionary arms race of parasite infectivity and host resistance leads to adaptations and counteradaptations in the coevolution and also has a central role in the evolution of host-parasite relationships in the microbial world [47]. The origin of bats is estimated at about 64 million years ago or following the Cretaceous-Tertiary boundary [48]. The millions of years of bat evolution might have given rise to the coevolution processes between host and pathogen. The antagonistic coevolution between infectivity of viruses and resistance of bats is still poorly known. The ability of bats to harbor extremely lethal viruses for humans without apparent morbidity and mortality has long been discussed. The lack of abnormal ethology observed in virus-infected bats may be due at the selection of resistance mechanisms.

The evolution of flight in bats has been accompanied by genetic changes to their immune systems to accommodate high metabolic rates. The increased metabolism and higher body temperatures of bats during flight might have enhanced their immune system, increasing resistance and thus increase the diversity of viruses they host [2, 49]. This increase of metabolic rate in bats is estimated to be 15- to 16-fold, when it is only sevenfold for running rodents and twofold for birds [2]. Marburg, Angola, Ebola, and Makona-WPGC07 viruses were shown to efficiently replicate at flight temperature of bats, i.e. 37 and 41°C, indicating that flight-related temporal elevation in temperature does not affect filovirus replication [50]. Furthermore, many bat species display a daily torpor with decrease of body temperature which might be a virus-resistance strategy, interfering with optimal virus replication [2]. Bats also display a unique interferon system (IFNs) that may explain the ability of bats to coexist with viruses [51]. Mammals have a large IFN locus comprising a family of IFN-α genes expressed following infection. Conversely, bats display a contracted IFN locus with only three functional IFN-α, but constitutively and permanently expressed [51]. This constitutive expression could turn to be a highly effective system for controlling viral replication and explain the resistance of bats to viruses. Differences have also been observed in the immune response between bat species against the same virus. Important differences in percentage of seroconversion against European bat lyssavirus type 1 (EBLV-1) were observed between two species from two distinct families: *Rhinolophus ferrumequinum* (*Rhinolophidae*) and *Myotis myotis* (*Vespertilionidae*). The percentage of seropositive *Rhinolophus ferrumequinum* was much lower than that of *Myotis myotis* [45], suggesting differential rates of seroconversion. Turmelle et al. [52] reported that significant differences in seroconversion rates were found among bats depending on whether they had previously been infected, suggesting that long-term repeated infections of bats might confer significant immunological memory and reduced susceptibility to rabies infection. Immune competence in bats can vary with body condition (via nutritional status and stress) and reproductive activity and, as a consequence, can lead to a lower rabies seroprevalence between or within bat species.

5. Intra and interspecific transmission of bat viruses

Bats are considered major hosts for alphacoronaviruses and betacoronaviruses and they play an important role as the gene source in the evolution of these two genera of coronavirus [53]. Most, if not all, alphacoronaviruses and betacoronaviruses found in mammals are evolutionally linked to ancestral bat coronaviruses [54]. Different species of *Rhinolophus* bats in China carry genetically diverse SARS-like coronaviruses, some of which are direct ancestors of SARS-CoV and hence have the potential to cause direct interspecies transmission to humans [54]. A large-scale study conducted worldwide on 282 bat species from 12 families demonstrated the presence of coronaviruses on 8.6% of bats whereas the ratio was only 0.2% on non-bat species [36]. A relationship between viral richness and bat species richness was demonstrated, suggesting that the diversity of bat CoVs has been driven primarily by host ecology [36, 41]. Preferred association between viral subclade and bat family was also observed. Bat-borne Dependoparvoviruses are also suspected to be the ancestral origin of adeno-associated virus (AAVs) in mammals [55]. Similarly, bats are the primary reservoir for 15 of 17 species of lyssaviruses [56]. Lyssaviruses may have evolved in bats long before the emergence of carnivoran rabies [6, 57].

Dissemination of viruses among bat populations is a complex system affected by many traits of the seasonal bats life. Seasonality and environmental conditions determine birthing periods, migrations, gregarious behavior, and torpor of each bat species. Each one may affect population density, rates of contact between individuals, and consequently the basic reproductive number of virus (R_0) and virus transmission between species. The basic reproductive number (R_0) is an important parameter in the dynamic of diseases and is the average number of new infections that would arise from a single infectious host introduced into a population of susceptible hosts [58]. Understanding how pathogens spread within their host populations is a key factor in epidemiology. It is especially difficult to study the vertical transmission of viruses in bats. Bats are very sensitive to disturbances and environmental changes, especially during breeding period. A disturbance in a maternity colony can produce an important mortality in newborn bats that may impact in the demography of population. The per capita transmission rate depends on the infectivity of the virus, the susceptibility of the host, but also on the contact rate between susceptible hosts and infectious individuals. Social organization within the refuges thus plays a major role in virus transmission. Some bat species form a very large and tight monospecific or multispecific colonies of thousands individuals, e.g. the density of a hibernation colony of *Miniopterus schreibersii* near Barcelona was estimated at 1900 bats for square meter [58] (**Figure 4**). *Tadarida brasiliensis Mexicana* forms in Carlsbad Cavern (New Mexico), a colony with 793,838 bats [59]. This gregarious roosting behavior can provide large opportunities for viral exchange in bat colonies. Bat colonies are often composed by more than one species. Large colonies and multispecies associations are frequent among cave-dwelling bats, in particular during the maternity period. This colonial behavior confers thermodynamic and social advantages to reproductive females during pregnancy and lactation [60]. For instance, mixed colonies can be found in Southeastern Europe where *Miniopterus schreibersii*, *Myotis myotis*, and *Myotis capaccinii* are in direct physical contact. This cohabitation can facilitate virus transmission between species. The seroprevalence for EBLV-1 in *Myotis myotis* and *Miniopterus schreibersii* followed the same temporal pattern during 4 years [45], which could be explained by virus transmission between these two species. The size of the colony and species richness were two important ecological factors playing a major role in seroprevalence variability [45]. Virus transmission in colonies may follow different ways depending on the bat and virus species considered, i.e. aerosols, contact with feces, urine, blood, or other body fluids, or by bite. Ectoparasites should also be considered. There are almost no data on vertical transmission from mother to fetus. However, vertical transmission has nevertheless been reported. Transplacental transmission of Hendra virus (HeV) was shown in the fruit bat *Pteropus poliocephalus* [61]. Horizontal transmission is far more documented. Theoretical modeling of disease expansion has assumed large and well-mixed host populations. However, many wildlife systems have small groups with limited contacts among them. The distribution of seropositive bats against European Bat Lyssavirus type 1 (EBLV-1) is not random in bat colonies and follows a gregarious pattern, indicating a non-random transmission of viruses inside the colony. Most of gregarious species of bats have a metapopulation structure (consisting of periodically interacting, spatially discrete subpopulations) with variations in their subpopulations. The total number of individuals in the various subpopulations must be sufficient to maintain virus

Figure 4. Colony of *Miniopterus schreibersii* with individuals tightly close to each other.

circulation in the metapopulation over time, while immunity or death due to viral infection extinguishes transmission chains within individual subpopulations. In a longitudinal study in vampire bats of Peru, Blackwood et al. [62] found that persistence of rabies virus cannot occur in a single colony. Maintenance of rabies virus at levels consistent with field observations requires dispersal of bats between colonies, combined with a high frequency of immunizing non-lethal infections. The dynamic of virus infection in a bat colony usually produce periodic oscillations in the number of susceptible, immune and infected bats. The delay between the waves depends upon the rate of inflow of susceptible bats into the colonies as a consequence of new births, immigration of naïve animals from neighboring colonies, and expiration of immunity in previously infected animals. When a sufficient fraction of susceptible individuals in the bat population is reached, the virus spreads again if infected individuals joined the colony [63]. A high number of species might not only increase the rate of contact between bat groups and species but also could facilitate virus entry or spread through the higher mobility of individuals among colonies, especially if these bats exhibit a migratory behavior. The role of migratory species in virus dispersion is unfortunately poorly studied in spite of being very important.

6. Anthropization, human behavior, and dynamic of emergence

The main element for the emergence of an infectious disease is the contact. With no contact, there is no possibility for a virus to cross the species barrier. In the case of bat-borne diseases, a direct or indirect contact must occur for the disease to emerge and spread. Synanthropic bats are of course the first ones to be considered as a source of emerging viruses. However, they are far from being the only ones at risk for transmission to humans. It is not only the natural synanthropic behavior that matters but instead the whole complex of biology, ecology, behavior, landscape evolution, and anthropization.

The first interaction considered for transmission of bat-borne viruses to humans is hunting and consumption of bush meat [64]. This is a traditional interaction in which humans are potentially going towards bats and thus viruses. However, there is no documentation of direct origin of virus disease outbreak coming from bat hunting, butchering, and consumption. Bush meat has been for instance regularly considered for the emergence of Ebola [65]. However, there is no evidence of direct contact with bats and bats were not the primary bush meat. Bats might just be a reservoir involved in a sylvatic cycle involving other animals being the actual target of bush hunting. In places where bats are hunted and consumed such as Southeast Asia, there is no report of direct emergence of viral diseases coming from consumption or hunting. A more likely potential process of transfer of viruses from bats to humans might be the attractiveness of degraded environment for bats [41]. Indeed, a highest diversity of bat-borne viruses was demonstrated, as a consequence of a higher diversity of bats, in anthropized, degraded environments. Deforestation and anthropization, instead of leading to the elimination of bats as one would instinctively expect, generate conversely a higher diversity. This might be explained by the complexity of the anthropized environments, which offer opportunities to different groups of ubiquity bat species, whereas natural environments might be more selective and suited for species with stricter ecological requirements. Anthropized environment displaying a higher biodiversity, the risk of virus transmission is therefore increased [41]. The impact of land use change on the emergence of diseases has been modeled to two main processes: (1) the perturbation hypothesis in which "land use change perturbs disease dynamics in multihost disease systems by disrupting the cross-species transmission rate" and (2) the pathogen pool hypothesis in which "land use change allows exposure of novel hosts to a rich pool of pathogen diversity, influencing the cross-species transmission rate" [66]. However, the same authors stated that these hypotheses tend to be vague or case specific with lack of theoretical foundation. This makes sense since the emergence of an infectious disease is an accidental process or in other words a very low probability event resulting from the sum of low probability independent events. According to this accidental process, an emergence cannot be predicted and will always appear as case specific. In the case of bats, numerous viruses have been found in bats but no direct transmission to humans has been formerly described. Emergence of bat-borne viruses is therefore most likely the consequence of the accidental association of a chain of events favored by structural elements from the human society. Although traced as a bat-borne virus, the coronavirus responsible for SARS seems to have been initially transmitted by civet meat to humans [31]. The outbreak itself was most likely triggered by human-to-human transmission through aerosols. The epidemic of SARS in 2003 was limited to hotels, high population density areas, and hospitals. No direct contact with bats was involved in the outbreak. Similarly, the MERS epidemic in the Arabic Peninsula was attributed to a coronavirus probably initially present in bats but transmitted to humans by dromedaries [34]. MERS was also involved, like SARS previously, in major nosocomial outbreaks [67]. In this case, also the trigger for the epidemic was not a direct contact with bats but the human society organization, close proximity with domestic animals, and nosocomial transmission.

The main risk for emergence of bat-borne diseases is directly linked to the development of anthropized environment and reduction of natural environments. It is often understood that deforestation and anthropization will lead to the disappearance of species. This is not always true and anthropized environments can provide an acceptable habitat for a large range of bat species, generating thus a higher diversity of bats and in turn of bat-borne viruses next to human dwellings. Anthropization generates a highly diverse environment in the vicinity of human, characterized by differing forest densities. Bats of differing ecology can find in anthropized environments niches compatible with their roosting and hunting needs. Natural environments are highly selective and compatible only with adapted species over a large surface, usually away from human settlements. In the exact contrary, anthropized environments provide a mosaic of ecosystems, very close to each other, each one corresponding to the needs of a given group of bat host. Insectivorous bats will find large populations of insects due to the presence of water, animals, and humans. Furthermore, house lights attract large number of insects at night. Houses and barns offer shelter for cave-dwelling bats while orchard and field can attract frugivorous bats. This environment is favorable to the occurrence of key parameters identified for virus transmission in large colonies of cave bats, i.e. shared roosting areas, close contact of different species, and regular introduction of infected individuals [45, 58]. However, in this specific environment, there is an additional aspect, the proximity of humans and domestic animals. Another recent example is the first report of the presence of human and chicken blood in the diet of *Diphylla ecaudata* vampire bats living in the highly anthropized Caatinga dry forests of northeastern Brazil [68]. This attractive effect of anthropized environments on bats and the consequent promiscuity of bats, domestic animals, and humans are most likely to increase the risk of direct transmission of viruses and to the probability to trigger the accidental process of emergence.

7. Deforestation trends and increased risk of emergence

Bats have long rendered great services to mankind by acting positively on its environment and without living in a too close vicinity of human populations. However, by increasing the surface of cultivated areas and through the rapid growth of cities in the recent decades, men have drastically modified ecosystems which had remained in equilibrium for millennia. This evolution of ecosystems is even faster in Asia than in the rest of the world. Southeast Asia (SEA) is the region in the world that suffered the largest deforestation with a loss of 30% of forest surface over the last 40 years. In Thailand, agricultural lands represented 23% in 1960 and 40% since 1985 [69]. Similar trends were observed in other Southeast Asian countries [69]. In Cambodia, agricultural surfaces doubled from 15% in the 1980s to 30% in 2000. A similar trend was observed in Vietnam with an increase from 20% in 1990 to 35% today. In Indonesia, the growth was from 21% in the 1980s to 31.5% today. Deforestation is today linked to increased agricultural surfaces and to poorly managed urban growth. Owing to evolving land use, bat populations are setting in area closer to human dwellings [70]. Anthropized rural environments are characterized by a wide diversity of landscapes comprising houses, barns, fields, orchards, and woods of differing density. Human dwellings are also established close to water which along with the presence of animals is favorable for insects and insectivorous bats. Unlike natural environment which are highly selective, these altered landscapes are acceptable by a wide range of bat species, usually not encountered together, which establish close to human dwellings. This results in a higher density of bat-borne CoVs in the close vicinity of human dwellings [70–72], and thus a higher risk of human infection through direct contact or contamination by urine or feces. An aggravating factor is that the human population growth is higher in suburban and rural areas generating thus a higher pressure on land use, agricultural land, and deforestation with the most common activities being farming, logging, and hunting. The recent acceleration of deforestation in Southeast Asia and all predictions based on demographic burden on land use clearly indicate that the risk of contact and of transmission of new microorganisms which could turn pathogenic for humans will increase. It is thus just a matter of time, chance to encounter appropriated targets (human or animal in close contact with humans) and viral mutations to adapt to new hosts. Similar trends of deforestation are occurring in South America, but landscape organization is different, and the human population density is far lower than in SEA making thus the risk perhaps lower. If the exact time and nature of the emergence cannot be predicted, the increased probability of encounter and occurrence of emergence-leading chain of events yielded by anthropized environment must be considered seriously.

8. Prospectives

Bat-borne virus transmission is a complex issue associating at the same time viruses with a high potential for infectivity for humans and a lack of evidence of direct transmission from bats to humans. Hence, outbreaks have already occurred demonstrating the reality of this threat. An emergence cannot be predicted but some elements in the chain of events can and must be monitored, in particular: (1) the prevalence of the virus in wild species that inhabit the region; (2) the effects of environmental changes on the prevalence of pathogens in wild populations; and (3) the frequency of human and domestic animals contact with bats (including indirect contact with droppings, aerosols, saliva, or urine). The future of the viruses-bats-humans relationship seems to evolve in a dichotomic way: on one hand, the number of endangered bat species is growing and their natural habitat is decreasing. According to IUCN [73], 23% of bat species worldwide are considered to be decreasing. On the other hand, the increasing deforestation and extension of mosaic anthropized habitats will attract different bat species leading synanthropic behavior and contacts. The current mobility of people is unprecedented and is a very important epidemiological factor to consider, since it increases the risk of spreading diseases. Land modification, changes in vegetation patterns (deforested areas, new land crops), disturbances in vector and host species dynamics, and microclimate changes are most likely to increase the contact between human or livestock and wildlife [41, 74]. Monitoring bat-borne diseases and more importantly the environmental conditions bringing bats, viruses, and humans into contact will be crucial and should lead to the development of scenarios of risk management.

Conflict of interest

The authors declare the absence of any conflict of interest.

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Edited by Heimo Mikkola

Bats have a poor image for the public at large because they are often feared. This is usually due to ignorance. In this book, we have eight chapters on bats covering countries such as Algeria, Bulgaria, France, Pakistan, Poland, the UK and the USA and subjects ranging from acoustic monitoring of bat species for distribution and conservation purposes to various bat-borne and bat-carried diseases. These diseases cannot be taken lightly but should not be a reason for panic or to fear or even kill bats. Bats will not cause any harm if we let them live in peace. With the added knowledge through this book, we should know how best to cope with bats, which need all our support in the changing environments and climates.

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