Learn and Let Learn:
Comparative Cognition and Social Learning in Bats

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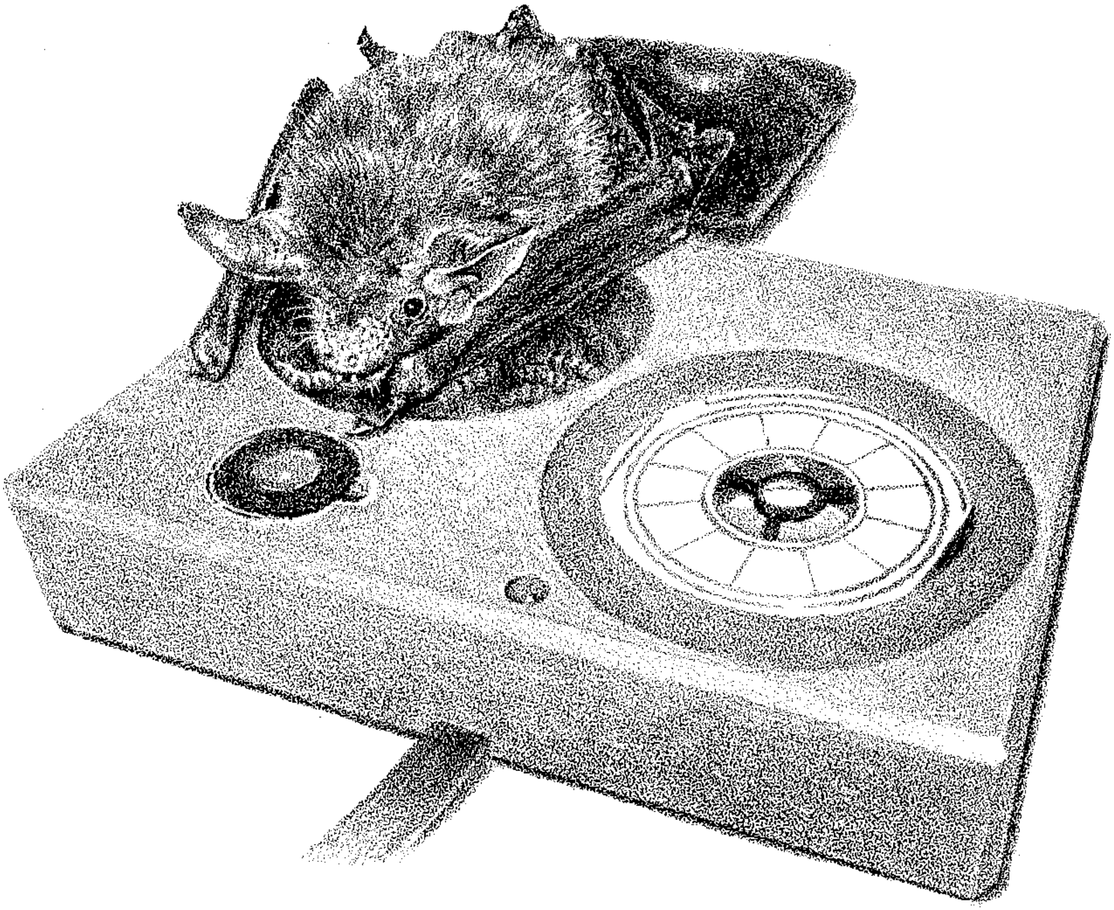

Die geistigen Fähigkeiten der Flatterthiere sind keineswegs so gering, als man gern annehmen möchte, und strafen den auf ziemliche Geistesarmuth hindeutenden Gesichtsausdruck Lügen. [...] Alle Flatterthiere zeichnen sich durch einen ziemlich hohen Grad von Gedächtnis und einige sogar durch verständige Ueberlegung aus.

(**Brehm**, A.E. **1864**. *Illustrirtes Thierleben: eine allgemeine Kunde des Thierreichs*).

The intellectual abilities of the bats are by no means as low as one would think and give the lie to the expression of their faces, which is indicative of a certain poverty of mind. [...] All bats stand out by a rather high degree of memory and some even by the presence of reasoning powers.

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A CD containing the supplementary movie to Chapter 1 (S1) is enclosed along with the thesis. The movie is also available at:
http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0064823#s5

SUMMARY

In this thesis, I present work on cognitive aspects of bat behavior.

In my first study (Chapter 1: “Foraging ecology predicts learning performance in insectivorous bats”), I investigated the relationship between foraging ecology and cognitive performance in insectivorous European bats. I found that learning performance and behavioral flexibility in a foraging task can be predicted by the ecological background of a species in the genus *Myotis*. Species foraging in more complex environments were more flexible and learned a more complex task faster than a species foraging in a less complex environment.

In a separate project, I investigated the ability of mouse-eared bats to learn socially (Chapter 2: “Social learning within and across species: information transfer in mouse-eared bats”). I found that greater mouse-eared bats (*Myotis myotis*) are able to learn a new foraging task from conspecifics and that information transfer is enhanced by direct interaction with the demonstrator. I also found that lesser mouse-eared bats (*M. oxygnathus*) can learn a new foraging task from their larger sister species. Through the fortuitous recapture of an observer one year after it had learned the task, I demonstrated that bats are able to retain newly acquired information over a period of hibernation in the wild.

Under controlled laboratory conditions, I also tested the influence of daily torpor on learning performance of bats (Chapter 3: “Do bats experience a trade-off between energy conservation and learning?”). Here I showed that for relatively simple tasks learning is not impaired by daily torpor in greater mouse-eared bats.

In a final study on the flexibility in bats’ behavior in response to anthropogenic disturbance (Chapter 4: “Effect of different light conditions on *Myotis myotis* foraging behavior”), I found that greater mouse-eared bats respond negatively to disturbance from light of varying wavelengths and intensities. By testing each individual several times and by comparing a group of wild bats with a group of long-term captive light-experienced bats, I found no sign of short-term habituation and only very weak signs of long-term habituation.

I discuss my findings with regard to the four main questions that drove my research: “How and why do bat species vary in their learning abilities?”, “How flexible are bat species in coping with changing or new conditions?”, “How can bats exploit new information sources?”, and “How does daily torpor affect learning performance in bats?”.

With this thesis I have added to our knowledge about cognition in bats and our understanding of the ability of bats to adjust to changing conditions. It also opens up new and exciting directions for future research.

ZUSAMMENFASSUNG

(German Summary)

In dieser Dissertation präsentiere ich Untersuchungen der kognitiven Aspekte des Verhaltens von Fledermäusen.

In meiner ersten Studie (Kapitel 1: “Foraging ecology predicts learning performance in insectivorous bats” (Nahrungssuchökologie ermöglicht Vorhersagen über Lernleistungen von insektivoren Fledermäusen)) untersuchte ich den Zusammenhang von Nahrungssuchökologie und kognitiven Leistungen bei europäischen, insektivoren Fledermausarten. Mit einer Aufgabe zur Nahrungsuche fand ich heraus, dass innerhalb der Gattung *Myotis* Lernleistungen und Verhaltensflexibilität einer Art durch ihre Nahrungssuchökologie vorausgesagt werden können. Arten, die in komplexeren Habitaten jagen, zeigten sich flexibler und lernten eine komplizierte Aufgabe schneller, als eine Art, die in weniger komplexer Umgebung jagt.

In einer zweiten Studie untersuchte ich die Fähigkeit von Mausohren, sozial zu lernen (Kapitel 2: “Social learning within and across species: information transfer in mouse-eared bats” (Soziales Lernen innerhalb und über Artgrenzen hinweg: Informationsweitergabe bei Mausohren)). Ich fand heraus, dass Große Mausohren (*Myotis myotis*) in der Lage sind, eine neue Aufgabe zur Nahrungssuche von ihren Artgenossen zu lernen, und dass die Informationsweitergabe durch direkte Interaktion mit dem Vorführer wesentlich verbessert wird. Ich konnte außerdem zeigen, dass Kleine Mausohren (*M. oxygnathus*) die Bewältigung einer neuen Aufgabe zur Nahrungssuche von ihrer größeren Schwesternart lernen können. Da ich durch einen glücklichen Zufall einen Schüler ein Jahr später wieder gefangen hatte, konnte ich zeigen, dass Fledermäuse in der Lage sind, neu gelernte Informationen auch über einen längeren Zeitraum der Hibernation zu behalten.

Unter kontrollierten Laborbedingungen testete ich auch den Einfluss von täglichem Torpor auf die Lernleistungen von Fledermäusen (Kapitel 3: “Do bats experience a trade-off between energy conservation and learning?” (Müssen Fledermäuse zwischen Energiesparen und Lernen abwägen?)). Ich konnte zeigen, dass Lernen nicht durch täglichen Torpor eingeschränkt wird, zumindest wenn es sich um eine relativ einfache Aufgabe handelt.

In einer weiteren Studie über die Verhaltensflexibilität von Fledermäusen als Antwort auf menschliche Störungen (Kapitel 4: “Effect of different light conditions on *Myotis myotis* foraging behavior” (Über den Effekt von unterschiedlichen Lichtgegebenheiten auf das Nahrungssuchverhalten von *Myotis myotis*)) fand ich heraus, dass Große Mausohren negativ auf Störungen durch Licht unterschiedlicher Wellenlängen und Intensitäten reagieren. Indem ich jedes Tier mehrfach testete und wilde Tiere mit Tieren, die längere Zeit in Gefangenschaft gelebt und Erfahrungen mit Licht gesammelt hatten, verglich, konnte ich keine Habituation binnen kurzer Zeit und nur sehr schwache Zeichen für Langzeit-Habituation feststellen.

Ich diskutiere meine Ergebnisse im Hinblick auf die vier wesentlichen Fragen, die meiner Arbeit zugrunde lagen: „Wie und warum unterscheiden sich Fledermausarten in ihren

kognitiven Fähigkeiten?“, „Wie flexibel sind Fledermausarten darin, mit neuen und sich verändernden Umweltbedingungen umzugehen?“, „Wie können Fledermäuse neue Informationsquellen nutzen?“ und „Wie beeinflusst täglicher Torpor die Lernleistungen von Fledermäusen?“.

Mit meiner Arbeit erweitere ich unseren Wissensschatz über die Kognition von Fledermäusen und unser Verständnis für die Fähigkeiten von Fledermäusen, sich veränderten Bedingungen anzupassen. Sie öffnet auch neue Wege zu weiteren, aufregenden Forschungsarbeiten.

GENERAL INTRODUCTION

Across the globe, the human species predominates. Within roughly one million years our species has progressed its skill set from that which allowed us to control a fire in a cave (Berna et al. 2012) to one that enables us to sit on a couch surfing the internet with the aid of a superfast laptop. Our technical opportunities and our knowledge of the world are growing faster every day. When the first functional computer was build in the 1930s by Konrad Zuse, who would have thought of the computational powers nowadays incorporated in a small hybrid of telephone and computer called a smart phone? We are now able to "tweet" faster with a person on the other side of the globe than we are able to talk to a person just a walk down the hall. We owe all of these inventions to our highly developed intelligence that apparently sets us apart from the rest of the animal kingdom. The ability to intelligently advance our skills and knowledge and to communicate those advancements is closely linked to the concept of cognition and our perception of ourselves as the cognitively most advanced animal species on the planet.

It is not then surprising that the term "cognition", although widely used, is typically defined in very different ways for human and non-human animals. When concerned with the cognition of animals in general (including humans), definitions found most commonly comprise terms like: "neuronal processes concerned with the acquisition, retention, and use of information" (Dukas & Ratcliffe 2009), or "mechanisms by which animals acquire, process, store, and act on information from the environment" (Shettleworth 2010). Sometimes definitions of cognition are even broader and explain responses to the environment that stretch from behavioral into developmental responses (Godfrey-Smith 2001). These are rather mechanistic approaches that deal with incoming signals and their processing, which lead to outgoing actions. However, simply Googling the term cognition, one will find definitions mostly concerned only with human cognition, additionally including terms like "awareness", "perception", "reasoning", "judgment", "creativity", "planning", "imagination", "argumentation", "introspection", "will", or even "beliefs". No single definition will comprise all of these terms and most definitions will contain additional terms (e.g., About.com; The Free Dictonary; Oxford Dictonaries).

The concepts behind these terms all require certain degrees of self-awareness and reflection and are usually regarded as "higher cognitive abilities" by students of animal cognition. Throughout human history such higher cognitive abilities have been thought to be unique to humans and to separate humans from the rest of the animal kingdom. They are what make us special; they make us think about ourselves, about others, and about right and wrong. Perhaps they are what enable us to feel empathy. However, ever since Darwin published "The Origin of Species" some 150 years ago, we have known that cognition, like any other human trait, must have evolved gradually through natural selection (e.g., Heyes 2012). An ever-increasing body of literature describing higher cognitive abilities in non-human animals, mostly mammals and birds, now supports this once radical idea.

About the Study of Cognition in Animals

Testing for the presence of higher cognitive skills in non-human animals (hereafter referred to as "animals"), however, is challenging, sometimes impossible. Terms describing cognition are defined by humans and are based on human experience. This is, of course, a biased viewpoint and it might not be appropriate to describe the experience, perceptions, and ongoing mental processes in animals other than ourselves (Nagel 1974). A related difficulty is that animals generally do not speak and therefore cannot be asked, whether they "believe" something was the right or wrong decision, or whether they "imagine" or "plan" future actions.

Higher cognitive abilities are therefore usually attributed only to animals that perform actions that we believe to be based on awareness or reflection. Examples are species that recognize themselves in mirrors, such as some species of primates (Gallup 1970; Povinelli et al. 1993), dolphins (Reiss & Marino 2001), elephants (Plotnik et al. 2006), and magpies (Prior et al. 2008). Other examples for high cognitive abilities are theory-of-mind-like skills shown for instance by food caching ravens, where individuals act differently when observed than when not observed by a conspecific (Bugnyar & Kotrschal 2002). A now famous case is the grey parrot Alex. He had numerical competences at least up to the number 6 and communicated astonishingly well with his owner, Irene Pepperberg (Pepperberg 2006).

Comparative Research on Cognition

To best study cognition and its evolution it is not sufficient to test only several individuals of one species; instead it is necessary to compare several species with presumably similar or different cognitive abilities. In the case that a task is solvable for a given set of species, it might be a good task to test which species have better cognitive abilities, learn faster, or are more flexible in their behavior. This applies to all tests, whether they are about higher or not so high cognitive abilities. Using such an approach, we can try to answer questions like: How did certain cognitive skills evolve? Can we find factors that are necessary for their origination? Can we define key-factors that lead to higher development of cognition? Are there proximate mechanisms for the further development of cognition?

If we succeed in finding a task whose solvability depends only on cognitive skills alone and not on other species differences, such as sensory and motor abilities, then comparative studies are a strong tool to investigate the evolution and development of different cognitive tools and skill sets.

The Evolution of Cognition: Theories

It is widely assumed that human cognitive abilities are highly adaptive and a key factor that propelled the explosive expansion of our species. How our cognitive skills evolved and which factors ultimately lead to them is still a matter of discussion. The evolutionary history of a species and with this the phylogenetic relationships among species certainly play a major role in the development of cognitive skills. However, phylogenetic relationships do not always reliably predict cognitive abilities. To fully understand which part of the variation in cognition among different species is due to phylogeny and which part is due to other variables like the ecological background or differences in the social organization of species, we need large scale comparisons among a variety of species (MacLean et al. 2012).

The Social Intelligence Hypothesis

One theory on the evolution of cognitive skills is the "social intelligence hypothesis", first described by Jolly (1966) and Humphrey (1976). The idea is that group living favors the development of cognitive skills and is one of the key factors leading to higher cognitive abilities.

A number of comparative studies between closely related species that vary in their degree of sociality, focusing mainly on primates (e.g., Moll & Tomasello 2007; Sandel et al. 2011) and birds (e.g., Bond et al. 2007; Krasheninnikova et al. 2013), support the social intelligence hypothesis. However, there is some evidence that while cognitive skills that have a social component and are important for group living are enhanced by sociality, cognition in general is not necessarily more developed in social species (MacLean et al. 2008, 2013).

The Ecological Approach

Another approach to understanding the difference in the development of cognitive skills among species is the complexity of the environment in which a species lives and/or forages.

Environments can be complex in both space and time. Environmental variation can be a function of natural changes such as seasons, or the result of human activity. It is impossible to order all existing natural environments on a linear scale according to complexity. Complexity is also defined by the viewpoint taken. For example, what might be a complex environment for a small insect might not be complex for a large mammal and vice versa. Additionally, complexity depends on the species-specific sensory perception of certain aspects of the environment, which may be difficult for us to comprehend (Nagel 1974).

Comparatively, however, it is often possible to define certain environments as more complex than others at least for a specific species or group of species.

Such differences in the complexity of environments in which species live and/or forage can determine differences in the degree of difficulty of daily tasks that have to be solved, differences in foraging modes, and differences in life styles.

Fruits in a forest, for instance, often have a patchy distribution, varying in both space and time. Therefore, frugivory may lead to enhanced spatial skills compared to folivory (Milton 1981). By extension, foraging for a broad diet in a generally unproductive and seasonally changing environment could stimulate the development of intelligent tool use, while foraging on a more narrow diet in a productive and more constant environment may be less likely to do so (Parker & Gibson 1977). A foraging task might be sensorial demanding, e.g., if it is hard to detect certain prey items. The more sensorial challenging a foraging task, the better a species should be able to differentiate between sensory inputs (Siemers & Schnitzler 2004) and to learn new stimuli that could indicate a food item (Siemers 2001).

Ultimately, all these environmental factors could lead to different cognitive abilities even among closely related species inhabiting different environments. Similarly, these factors could lead to comparable cognitive abilities in very distantly related species groups as has been suggested for the generally relatively high development of cognitive skills in mammals, birds, and cephalopods (Vitti 2013).

A Combination of Both – The Environmental Complexity Thesis

Although it seems easy to distinguish between the social intelligence hypothesis and the ecological approach and to favor one over the other, combining the two attains a more likely explanation for the development of cognition. The "environmental complexity thesis", put forward by Godfrey-Smith (2001), argues that complexity does not consist solely of external factors not causally related to the individual in question, such as seasonal changes. Rather, complexity also includes the interplay between individuals of the same species (but not necessarily of the same social group), e.g., in terms of competition or reproduction as well as among different species, e.g., in predator-prey-interactions.

Living in a social group adds to the complexity of the environment a specific individual experiences; together these factors might lead to enhanced cognitive abilities (Godfrey-Smith 2001). The social intelligence hypothesis is therefore part of the environmental complexity thesis.

Food unpredictability in space and time might also be a driver not only of a more generalist diet but also of social foraging. If food is patchy, hard to detect, or hard to obtain by only one individual, it may favor the formation of groups searching or hunting for food together and sharing ephemeral food sources. Both a generalist diet and social foraging have been connected to enhanced cognitive skills. This approach also intertwines ecological and social aspects to explain the evolution of enhanced cognition (Overington et al. 2008 and references therein).

Bats as Study Species

Unfortunately, in an attempt to understand the extraordinary cognitive abilities of humans, most of the theoretical models trying to explain the evolution of higher cognitive abilities are founded on studies in primates (e.g., Reader & Laland 2002; Zuberbühler & Byrne 2006; Sterelny 2007; Byrne & Bates 2010). Birds have also received some attention (Balda & Kamil 2002; Emery & Clayton 2004). However, other social animals and specifically other groups of mammals have not been studied in as much detail yet. Therefore, it seems to be still questionable, whether or not these ideas can be transferred and confirmed or rejected in other animal groups.

Additionally "sociality" is not a uniformly used term. In many mammal species, individuals aggregate for specific purposes, e.g., for reproduction or to benefit from a dilution effect (Dehn 1990; Mooring & Hart 1992; Cappozzo et al. 2008). While these potentially unstable aggregations of individuals might aid in enhancing certain cognitive aspects of social living like social learning, they do not necessarily involve social bonding, active cooperation, or individual recognition beyond mother-pup-recognition. It is unlikely that under such circumstances cognitive differences between species (with similar social structures) are driven by social complexity. More likely, differences in cognitive abilities should be related to the complexity of the habitat the species are living and/or foraging in, as well as other challenges the species face when foraging.

Some tropical as well as temperate bat species are known to form stable social groups (e.g., *Myotis bechsteinii* (Kerth et al. 2011); *Eptesicus fuscus* (Willis & Brigham 2004); *Ectophylla alba* (Brooke 1990); *Rhynchonycteris naso* (Nagy et al. 2013); *Desmodus rotundus* (Wilkinson 1985)). Here, I will describe work I conducted with European species that often form large maternity colonies of up to several thousand individuals. Such colonies may consist of one species only or may be mixtures of several species. Whether the bats form stable social bonds within these large aggregations has not been studied in detail yet. However, because they all occur in such large aggregations, and therefore have presumably similar social structures, differences in their cognitive abilities are more likely shaped by environmental factors than by social complexity.

Compared to birds, apes, and, of course, humans, the cognitive skills of different bat species are relatively poorly studied. Therefore, before we can even think of investigating the possible occurrence of higher cognitive abilities as it is done in other mammalian groups and birds, we have to investigate their performance in gathering information from new sources, learning and memory, and behavioral flexibility. As argued above, to better understand cognition in bats and the evolution of cognition in general, it is necessary to combine research on single focus-species and comparative studies on cognition in several bat species.

The Bats

The Order Chiroptera is characterized by several outstanding features that provide us with ample opportunities to not only study cognitive abilities, but to compare these abilities in a phylogenetic-dependent and a phylogenetic-independent, ecological context.

First, after rodents, bats are the most species rich mammalian order, comprising about 1200 species in 18 families (Simmons 2005a, 2005b). Second, while almost all bat species share striking features such as nocturnality and flight, and while most bat species echolocate, they also show great ecological diversity (Fenton & Ratcliffe 2010). We know of nectarivorous, frugivorous, carnivorous, sanguivorous, insectivorous, and omnivorous species (Simmons 2005a). Nectarivorous and frugivorous species provide important ecosystem services as pollinators and seed dispersers (e.g., Arizaga et al. 2000). Frugivores might also play an important role in re-forestation and de-fragmentation of tropical forests (Kelm et al. 2008; Lewanzik & Voigt 2014). Insectivorous bats act as pest control that limits herbivory (Kalka & Kalko 2006; Kalka et al. 2008). In morphology and behavior, the Order exhibits both a wide variety of divergent developments in closely related species, as well as convergent developments in distantly related species (e.g., Norberg & Rayner 1987; Schnitzler et al. 2003; Jones & Teeling 2006; Jones & Holderied 2007). For example, the phyllostomids comprise of species that show a large variety of diets (e.g., Bogdanowicz et al. 1997; Freeman 2000), while substrate-gleaning of animal prey has independently evolved multiple times in different families of bats (Simmons & Geisler 1998).

Although most bats in the tropics are probably capable of using torpor to save energy during the day or under unfavorable conditions (Geiser & Stawski 2011; Stawski & Geiser 2011), only a few species have been shown to hibernate for several days (Geiser & Stawski 2011). In contrast, a temperate-zone, non-migratory bat's year is divided into distinct stages, related to its reproductive cycle and food availability. In many European bats, females gather in spring to build maternity colonies in which they give birth to their young in early summer. Once the pups are weaned and fly out by themselves in late summer, the adult bats start mating. The females store sperm internally, often for many months. In late autumn, bats move to their wintering roost, where they hibernate during the period of low food availability. After hibernation the females become pregnant and move to their summer roosts again (for species specific differences in the yearly cycle of European bats see Dietz et al. 2009). Additionally, temperate-zone bats use torpor on a daily basis during the warm months to save energy during the day and between foraging bouts at night.

It is likely that many bats visit the same summer and winter roosts every year. It is therefore important to understand how bats cope with changes in their environment, for instance such that make former roosts inhabitable. Changing environmental conditions, the loss of habitat or suitable roosts might affect species differently depending on their ability to cope with changing conditions, to find new resources or new ways to old resources. Understanding the flexibility of bat behavior, and their general cognitive skills will help us protect bat species and profit from the services they provide us.

Despite similarities, large differences exist even within dietary niches. Insectivorous species can hunt for their prey in open space or over water surfaces as well as in cluttered forests. They catch their prey in flight or from water surfaces, or glean them from substrate. These differences in foraging behavior within bats feeding on the same general source (e.g., insects) lead to the classification of bat species into distinctive foraging guilds (e.g., Schnitzler et al. 2003).

The genus *Myotis* is a very good example of this high variation. Within this genus, we find a diverse set of insectivorous foraging modes and different degrees of specialization, despite close phylogenetic relationships. Each of these foraging modes comes with their own challenges and accompanying morphological and sensory adaptations. In the following I will describe some European *Myotis* species and their respective foraging modes.

Myotis daubentonii and *M. capaccinii* both hunt for insects or small fish over water bodies (Siemers et al. 2001a; Aihartza et al. 2008). Both species share morphological adaptations to this foraging mode such as large feet to pick up insects or fish. To detect their prey both species use echolocation. This detection task is comparably simple as almost all sound energy of their echolocation calls is reflected away from the bat by the horizontal water surface. Only the echoes of the insects or fish protruding through the water surface are reflected back to the bat (Siemers et al. 2001c). Although insect abundance over water surfaces changes over the course of the year, it stays relatively high while bats are foraging (Ciechanowski et al. 2007, 2010).

Very different are for instance *M. myotis* and *M. oxygnathus* (sometimes referred to as *M. blythii*). Both species hunt for insects over open, accessible ground in forests or fields (Arlettaz et al. 1997). Other than over water, their foraging habitats contain obstacles in form of vegetation. While they don’t hunt in close proximity to vegetation they share morphological adaptations to these habitats like short, broad wings that enable them to perform maneuvered flight. Although they use echolocation to orient in space, they do not search for their prey by echolocation. Instead, they listen for prey-produced sounds to find their prey. Complementing this foraging style they have relatively large ears. The structure of their foraging ground as well as abundance and quality of the prey change drastically over the course of one year and different foraging grounds have to be visited over the year to ensure a large enough food intake.

Myotis nattereri and *M. emarginatus*, in turn, hunt close to vegetation in highly cluttered space. Like *M. daubentonii* and *M. capaccinii*, both species use echolocation to detect their prey. However, their foraging task is much more complex. Background-generated echoes from vegetation have to be distinguished from the echoes returning from the prey items (e.g., Schnitzler et al. 2003; Siemers & Schnitzler 2004). As in *M. myotis* and *M. oxygnathus* their wings are short and broad to aid highly maneuvered flight. Also like *M. myotis* and *M. oxygnathus* they face the problem of a rapidly changing environment and need to adapt their behavior accordingly. Both species seem to be capable of flexibly switching foraging modes between gleaning and aerial hawking (Krull et al. 1991; Swift & Racey 2002).

There is no exclusively aerial hawking *Myotis* species in Europe. However, the neo-tropical *M. nigricans* mostly hunts for airborne insects in open space (Siemers et al. 2001b) using echolocation for both spatial orientation and prey detection. Aerial hawking bats have relatively small ears and elongated, narrow wings that enable fast flight. Generally, the foraging habitat of open space hunters is rather unstructured and the distributions of prey unpredictable all year round.

These species are only examples to illustrate the ecological diversity and specific adaptations possible within one genus of bats (reviewed in Fenton & Bogdanowicz 2002). Given these sets of morphological and sensorial adaptations to different challenges specific to the foraging modes, we might expect that different foraging strategies also come with their own set of cognitive adaptations and skills.

Cognition in Bats – What Do We Know?

While by no means exhaustively, a number of studies have investigated cognitive abilities in bats. However, given the enormous diversity in dietary niches, foraging modes, and social systems in bats, the study of bat cognition is still in its infancy.

Approaches to study cognition in bats include the investigation of associative learning (Siemers 2001; Ratcliffe et al. 2003; Page & Ryan 2005; Stich & Winter 2006; Page et al. 2012), spatial learning (Holland et al. 2005), cue-directed search for food versus spatial memory (Thiele & Winter 2005; Carter et al. 2010), and spatial working memory (Winter & Stich 2005; Henry & Stoner 2011). These studies show that bats can be trained to associate echoacoustic or acoustic cues with food rewards and can memorize the location of feeders or perches. They can also remember which of several feeders have already been depleted and avoid visiting them again. Plant-visiting bats seem to prefer spatial over object cues. Generalization of associatively learned cues (von Helversen 2004; Barber et al. 2009) and long-term memory of a spatially learned task in *M. myotis* (Ruczynski & Siemers 2011) have also been shown.

Other studies have looked into vocal learning (Esser 1994; Boughman 1998; Knörnschild et al. 2012) and individual recognition (Yovel et al. 2009; Kerth et al. 2011; Carter & Wilkinson 2013) especially in bats that form stable social groups. It seems that in at least one emballonurid bat species, *Saccopteryx bilineata*, young bats (like many young songbirds (Thorpe 1958)) need tutors to learn species- and group specific isolation calls, which in some cases are also functionally used by adults to assess group membership (Knörnschild et al. 2012). Bats living in stable social groups apparently recognize individuals within their social group and have preferred partners, e.g., for roosting together (*M. bechsteinii* (Kerth et al. 2011)), grooming, or, in the case of vampire-bats, food-sharing (Carter & Wilkinson 2013).

It has been shown that the horseshoe bat, *Rhinolophus ferrumequinum*, can assess profitability of prey by echoacoustic cues and the mechanism by which this perch-hunting bat decides to attack prey has been investigated (Koselj et al. 2011). Another study looked into large-scale cognitive maps (Tsoar et al. 2011) and showed that the pteropodid Egyptian Fruit bat (*Rousettus aegyptiacus*) can home over a distance of 84 km. A number of studies have investigated social learning abilities about foraging of different bat species from the families Vespertilionidae and Phyllostomidae in a variety of settings (Gaudet & Fenton 1984; Ratcliffe & ter Hofstede 2005; Page & Ryan 2006; Wright et al. 2011; also reviewed in Wilkinson &

Boughman 1999). One study has even shown that pteropodid bats reared in captivity can learn to follow pointing gestures by humans, a behavior frequently considered to be indicative of theory-of-mind-like capabilities (Hall et al. 2011).

To understand bat cognition, it is important not only to study species from a variety of different families, but also to study species from a variety of geographical areas. Additionally, the better we understand their ecological background, the better will we be able to investigate the link between cognitive performance and environmental complexity. However, most of the studies on cognition in bats described above were carried out on tropical or North American bats. Very few studies have investigated the cognitive skills of European bats. Except for one species (*M. bechsteinii*) that has been studied in much detail (e.g., Kerth et al. 2001; Baigger et al. 2013; Melber et al. 2013), surprisingly little is known about the size and stability of social groups, individual recognition, and information transfer in European bats. Also, studies on associative and spatial learning as well as flexibility in the assessment of learned cues have mostly focused on non-European bat species. Within the genus *Myotis*, the before mentioned *M. bechsteinii* as well as the Natterer's bat (*M. nattereri*) are exceptions in that at least a few studies focused on their social system and their associative learning capabilities (e.g., Siemers 2001; Page et al. 2012).

The ecology and prey finding mechanisms, the echolocation behavior, and sensory constraints on prey detection and its impact on niche differentiation of European bats has been extensively studied. *M. myotis* is an example of an exceptionally well studied species (e.g., Arlettaz 1996; Arlettaz et al. 2001; Schaub et al. 2008; Jones et al. 2010). However, except for two studies focusing on the possibility of individual recognition by distinguishing the echolocation calls of conspecifics (Yovel et al. 2009) and long-term memory (Ruczynski & Siemers 2011), we know little about its cognitive abilities, its behavioral flexibility, and its ability to cope with changing environmental conditions.

Cognition in Bats – What Do I Want To Know?

The scope of my thesis therefore is to investigate the cognitive abilities of European bat species and to compare certain aspects of these cognitive abilities in an ecological context. Because of its well-studied ecological background, my focus species, included in all projects of my dissertation, is the greater mouse-eared bat *M. myotis*.

I assessed learning speed and flexibility in three vespertilionid species and compared these with regard to their respective ecology. I wanted to know how bats are able to cope with changing environmental conditions and how they might react to alterations in their environment, be they of natural or human origin. Additionally, I investigated how bats can make use of new information sources. A fortunate coincidence gave me the opportunity to test whether newly acquired knowledge can be retained over a period of hibernation. The influence of daily torpor on learning performance was tested in a separate study. With human-induced changes on both local and global scales, it is becoming increasingly important to understand how animals' flexibility, cognitive skills, and ability to adapt behavior to changing conditions will affect their ability to survive in a changing world.

I expected species foraging in more complex habitats (in terms of temporal change and spatial structure) to be faster learners and to be behaviorally more flexible than species using less complex habitats. In species forming large, yet probably unstable, aggregations (although nothing is known about social bonding within these aggregations), I expected to find social learning among individuals of the same species, as this should be favored by living with large numbers of conspecifics. Additionally, I expected individuals of an ecologically similar species to also use information provided by individuals of their sister species. Furthermore, I expected to find that daily torpor would negatively affect learning performance of bats. In an explorative study I tested how bats react to human-made disturbance by light and whether they can habituate to certain light conditions.

I mainly worked with wild caught animals in Bulgaria on the Tabachka Bat Research Station (TBRS) (see fig. 1). I had the opportunity to study their behavior and their reactions to changing conditions under controlled laboratory conditions.

Bulgaria as a Study Site

Bulgaria is a small (111 910 km^2; 7.6 Mio inhabitants (European Union 2014)) south-eastern European country. The typical characteristics of a limestone area shape most of the Bulgarian landscape. Rivers and streams of various sizes have cut deep gorges into the area and excavated caves from the stone. Two mountain chains, the Balkan Mountains and the Rhodope Mountains run through the country (see fig. 1).

Although small in size, Bulgaria offers a variety of natural settings. Its altitude ranges from 0 m above sea level at its eastern coast to almost 3000 m, in the Rhodope Mountains. Cities and villages, agriculturally shaped and unused areas occur at all heights. Its climate is strongly influenced by its continental position; hence, it has hot summers and severe winters.

The caves that have been excavated from the sides of the river gorges provide shelter for a variety of animal species. Egyptian vultures have found one of their last resorts in Europe here. Bulgaria is also an important stop over site for migrating birds. However, bats make up a large group of the species that inhabit the caves in Bulgaria. 30 out of 52 European bat species (4 of which are endemic to small islands) are found in large numbers in Bulgaria. Although not all bat species use them, the caves offer excellent roosting sites. The variety of natural habitats offers each species its unique set of habitat requirements. A sadly famous example of the importance of Bulgarian caves for European bats is the Devetashka cave situated in north-central Bulgaria. A Hollywood movie production during the winter 2011/2012 caused about three quarters of the hibernating bats in this cave to disappear: that is, approximately 26,000 individuals (Hubancheva 2011). In total 30% of the area of Bulgaria belongs to the protected areas of the “Natura 2000” network. About 5% of the area of Bulgaria is protected either as national parks or as natural parks (MOEW & ExEA 2010).

One of these natural parks is the “Rusenski Lom Nature Park” in northern Bulgaria. The TBRS (see fig. 1), where most experiments described in this thesis were conducted, is situated at the border of this park and is run as a cooperation between the park and the Sensory Ecology Group at the Max Planck Institute for Ornithology in Seewiesen.

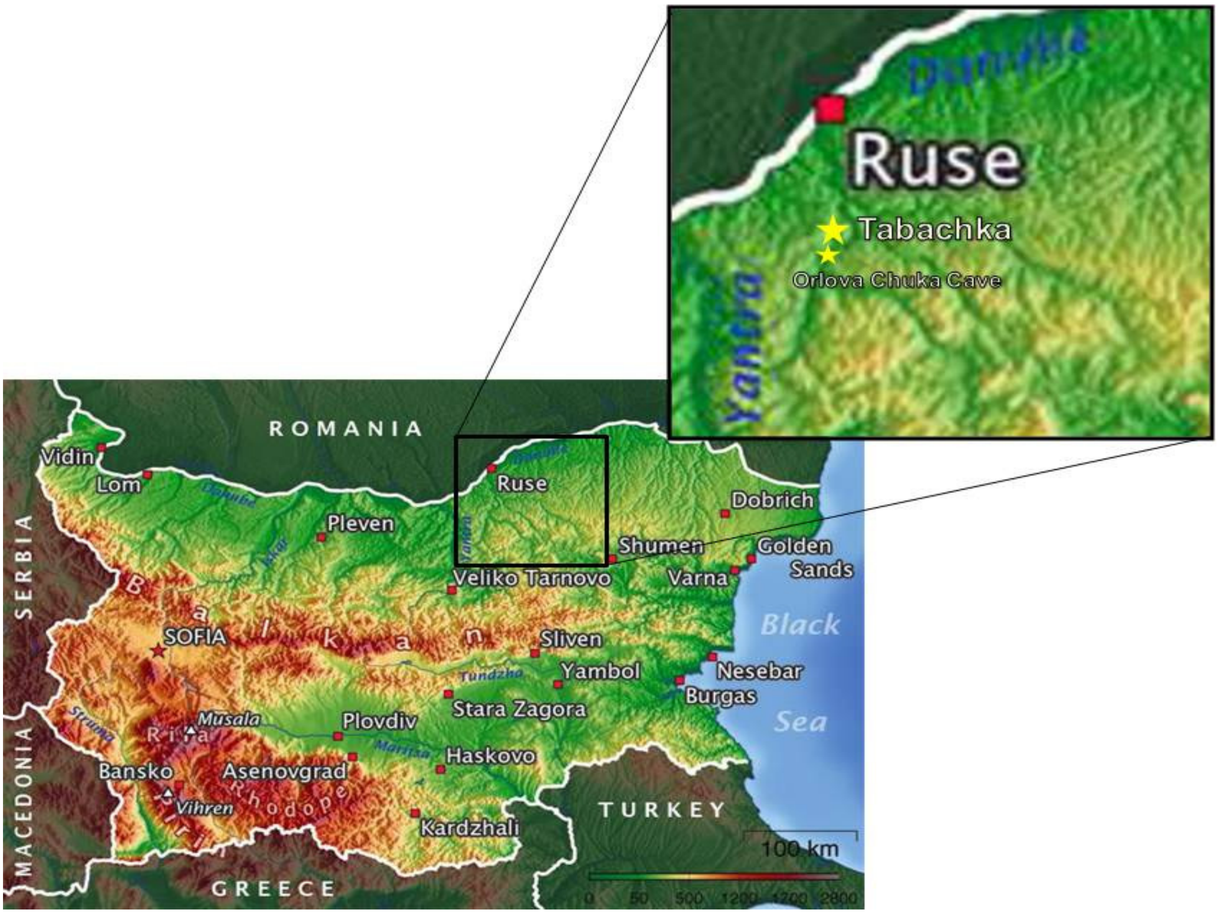

Figure 1 Position of Bulgaria in South-Eastern Europe. *The Tabachka Bat Research Station is close to the city of Ruse at the Romanian border.*

One of the caves in the park, the Orlova Chuka cave (“Eagle’s cave”) (see fig. 1), is used as a daily roosting site by six bat species from spring to autumn, namely *M. myotis*, *M. oxygnathus*, *M. daubentonii*, *R. ferrumequinum*, *Rhinolophus mehelyi*, and *Rhinolophus euryale*. Other species roost there as well, although in smaller numbers or only occasionally, specifically *M. emarginatus*, *M. nattereri*, *M. capaccinii*, *Miniopterus schreibersii*, *Nyctalus noctula*, *Eptesicus serotinus*, *Hypsugo savii*, and *Pipistrellus pipistrellus*. Other bat species can be found in smaller rocky niches nearby. Very few Bulgarian bat species cannot be accessed in the direct vicinity of the station and their capture requires longer trips, for instance into the mountains. Therefore, the Rusenski Lom Nature Park offers unique opportunities for the study of bats in general and for comparative studies that require several species in particular.

Thesis Outlook

In total, I worked with four species of European insectivorous bats. All of them can be found in the same area in northern Bulgaria. Sometimes they can even be found roosting in the same cave. However, they represent a range of ecological niches. They include species hunting over water surfaces (*M. capaccinii*), in open areas like fields (*M. myotis* and *M. oxygnathus*), or in highly cluttered forests (*M. emarginatus*). They differ markedly in size, maneuverability, and complexity of foraging task they face.

In my first chapter ("Foraging ecology predicts learning performance in insectivorous bats"), I address the question "How and why do bat species within the same genus differ in their learning abilities?" as well as "How flexibly can different bat species cope with changing conditions?" (Clarin et al. 2013).

With my second chapter ("Social learning within and across species: information transfer in mouse-eared bats"), I focus on two very closely related species and ask, "How can bats exploit new information sources and can this new information be retained?" More specifically, I investigated whether social learning in mouse-eared bats occurs within and across species and what level of interaction between individuals is necessary to lead to information transfer (Clarin et al. 2014).

In the third chapter ("Do bats experience a trade-off between energy conservation and learning?"), I investigated the question "How does daily torpor affect learning performance in bats?".

The fourth chapter ("Effect of different light conditions on *Myotis myotis* foraging behavior") deals with the question "How can a generally flexible species cope with human-made changes in its environment?" Specifically, I investigated the reaction to different light conditions and the possible occurrence of habituation to these light conditions.

CHAPTER 1

Foraging ecology predicts learning performance in insectivorous bats

Theresa M. A. Clarin, Ireneusz Ruczyński, Rachel A. Page, Björn M. Siemers

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Abstract

Bats are unusual among mammals in showing great ecological diversity even among closely related species and are thus well suited for studies of adaptation to the ecological background. Here we investigate whether behavioral flexibility and simple- and complex-rule learning performance can be predicted by foraging ecology. We predict faster learning and higher flexibility in animals hunting in more complex, variable environments than in animals hunting in more simple, stable environments. To test this hypothesis, we studied three closely related insectivorous European bat species of the genus *Myotis* that belong to three different functional groups based on foraging habitats: *M. capaccinii*, an open water forager, *M. myotis*, a passive listening gleaner, and *M. emarginatus*, a clutter specialist. We predicted that *M. capaccinii* would show the least flexibility and slowest learning reflecting its relatively unstructured foraging habitat and the stereotypy of its natural foraging behavior, while the other two species would show greater flexibility and more rapid learning reflecting the complexity of their natural foraging tasks. We used a purposefully unnatural and thus species-fair crawling maze to test simple- and complex-rule learning, flexibility and re-learning performance. We found that *M. capaccinii* learned a simple rule as fast as the other species, but was slower in complex rule learning and was less flexible in response to changes in reward location. We found no differences in re-learning ability among species. Our results corroborate the hypothesis that animals' cognitive skills reflect the demands of their ecological niche.

Ecological demands have been postulated as a driving factor in the evolution of cognitive complexity and intelligence (Parker & Gibson 1977; Overington et al. 2008). The cognitive abilities of animals are often well adapted to the requirements of their ecological niche (e.g., Rozin & Kalat 1971; Dukas & Ratcliffe 2009). Migratory bird species, for example, have much longer long-term memory than non-migratory species, and food-storing bird species show better spatial memory than non-storing species (Mettke-Hofmann & Gwinner 2003; Gibson & Kamil 2005). The ecological context of feeding affects learning abilities in crabs: mobile species show experience-dependent modifications of foraging behavior while sedentary species do not (Micheli 1997). In lizards, congeneric species with different foraging strategies display the same learning abilities but actively foraging species performed better in a reversal visual discrimination task than sit-and-wait predators (Day et al. 1999). The spatial learning abilities of voles reflect the complexity of their foraging habitats and their dietary specializations, with slower learning and decreased flexibility in more specialized species that forage in less complex habitats (Haupt et al. 2010). Game theory modeling also indicates that the unpredictability of food resources increases social foraging as well as generalism in diet; factors which can shape the evolution of cognition (Overington et al. 2008). According to the environmental complexity thesis (Godfrey-Smith 2001), the heterogeneity of an environment in space and time is thought to be one of the key factors that determine the rate of the evolution of cognitive skills (Godfrey-Smith 2001; Overington et al. 2008; Tebbich et al. 2012). In our study, we compare learning and flexibility in insectivorous bats to investigate the influence of an animal's ecological niche – specifically the complexity of its foraging habitat and the degree of stereotypy in its foraging behavior – on its cognitive abilities.

Bats are especially well-suited for investigations of ecological adaptations. Following rodents they are the second most species rich mammalian order (Simmons 2005b) and show great ecological diversity. Their diet ranges from nectar, pollen, and fruit to insects, small vertebrates, and blood (Simmons 2005a). We find high ecological diversity even among closely related species, and similar ecologies have developed convergently in many distantly related groups. Despite phylogenetic distance, similar wing morphology (Norberg & Rayner 1987) and echolocation patterns (e.g., Schnitzler et al. 2003; Jones & Teeling 2006; Jones & Holderied 2007; Weinbeer & Kalko 2007) have emerged in bats foraging in similar habitat types. *Macrophyllum macrophyllum*, for instance, is the only phyllostomid bat that forages exclusively over water (Meyer et al. 2005). It uses distinct terminal groups of echolocation calls prior to catching its prey, an echolocation behavior that is unique among phyllostomid bats but similar to distantly related trawling bat species (Kalko & Schnitzler 1989; Schnitzler et al. 1994) and is thus clearly shaped by the species' foraging behavior rather than its phylogeny (Weinbeer & Kalko 2007).

The similarities in morphology and behavior among distantly related but ecologically similar bats make it reasonable to expect that the cognitive abilities of bats are also shaped by the demands of their respective niche (Siemers 2001) and that closely related but ecologically divergent species will differ in their abilities to solve cognitive tasks. In bats, it has been shown that wing size, which reflects foraging habitat density, is correlated to larger hippocampi, which are known to relate to better spatial memory in a wide range of animal taxa (Safi & Dechmann 2005). We investigated whether learning performance and behavioral flexibility vary with foraging ecology by comparing closely related species that differ in their foraging behavior. Can one predict the learning performance of a species from the complexity of the habitat in which it forages? We hypothesize that species hunting in structurally complex habitats that fluctuate over time should learn faster and should be more flexible than species hunting in less complex, more stable habitats.

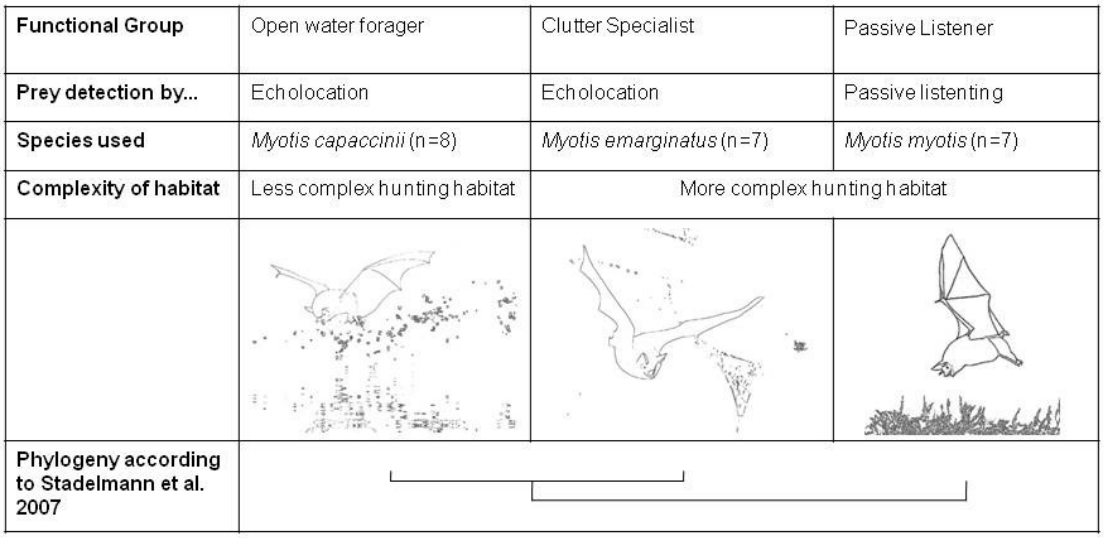
Insectivorous bats can be categorized into different functional groups according to habitat complexity, temporal habitat stability, and the sensory basis of prey detection. In a simplified overview, three groups can be distinguished: bats that use echolocation to forage in the open, either in open air or over water; bats that use prey-emitted acoustic cues to glean from vegetation or open ground; and bats that use echolocation to hunt prey near, but not on, vegetation (for a detailed review see Schnitzler et al. 2003). For our study, we chose one representative from each group, each from the genus *Myotis*. We experimentally tested flexibility and learning performance in these species of closely-related, congeneric European bat species to test the hypothesis that foraging ecology predicts cognitive ability.

Water foraging bats use echolocation to hunt insects over water surfaces (open water foragers). Their foraging task should be the least demanding within the three groups because the echoes reflected from insects are not masked by echoes reflected from background structures. A water surface acts as an acoustic mirror reflecting almost all the sound energy away from the bats and returning only the echoes of the bat's prey (Boonman et al. 1998; Siemers et al. 2001c, 2005; Greif & Siemers 2010). Bodies of water tend to be uniform and unstructured and do not undergo large changes in an observable time span; they usually do not change from night to night. Insect abundance over water surfaces also does not seem to alter the stereotyped behavior of water foraging bats: analysis of hunting behavior of the open water foraging bat, *Myotis daubentonii*, under natural conditions showed no effect of food abundance on flight activity. It is possible that the high degree of stereotypy in behavior in this group of bats is due to uniformly high insect abundance in water foraging habitats (Ciechanowski et al. 2007, 2010). We predict that associative learning between abundance of insect prey and specific locations or shapes plays little role in the hunting behavior of water foraging bats. As a representative of water foraging bats, we chose *M. capaccinii,* a species found in the Mediterranean region that hunts over water surfaces, with a preference for slow running rivers (Almenar et al. 2006; Biscardi et al. 2007).

Bats from the second group glean arthropods from open ground or vegetation. In this situation insect echoes are masked by strong background-generated clutter echoes. Gleaning bats are specialized to find their prey by listening for prey-generated sounds such as rustling noises or communication sounds (Jones et al. 2010) and are therefore termed "passive listeners". Their foraging habitats are highly structured and undergo large changes over the course of a year. Consequently, these bats must be adept at learning to recognize specific landscape features, such as a freshly cut meadow, as a good foraging ground (e.g., Arlettaz 1996). They could also learn to associate prey profitability with specific sensory cues, such as rustling noise amplitude (Goerlitz & Siemers 2007). We predict that associative learning should play a more important role in the foraging behavior of passive listeners than open water foragers. To represent the passive listening gleaners, we chose *M. myotis*, a species which hunts arthropods from open accessible ground in forests or fields (Arlettaz et al. 1997; Siemers & Güttinger 2006; Russo et al. 2007).

The third group, termed clutter specialists, consists of bats using echolocation to forage for insects in close proximity to vegetation. This foraging task is extremely challenging as it requires the ability to distinguish clutter echoes from the echoes of insects (e.g., Schnitzler & Kalko 2001; Siemers & Schnitzler 2004). Like passive listening gleaners, the foraging environment of clutter specialists changes rapidly: small plants and flowers appear and disappear, while trees grow leaves, blossoms and fruits and rapidly loose them again. Most important for bats, insect abundance changes in space and time as a function of plant phenology (e.g., Wang et al. 2010). Because flowering plants attract insects, the bats likely have to constantly build and rebuild associations with certain plants and places that are linked to high prey abundance (Siemers 2001). Associative learning of cues that indirectly indicate the presence of prey, and the flexibility to update these associations rapidly over time, should thus be more important in these bats than in the former two groups. As a representative of this group, we investigated *M. emarginatus*, a clutter specialist sympatric with the other two species in our study (Krull et al. 1991; Schumm et al. 1991; Flaquer et al. 2008; Zahn et al. 2010).

We specifically chose three closely related species (illustrated in fig. 1.1) to decrease the likelihood that species differences could be attributed to phylogenetic distance. Our species choice is conservative in that *M. myotis* and *M. emarginatus* are more similar in their foraging ecology, but more distantly related to each other than each is to the ecologically dissimilar *M. capaccinii* (Stadelmann et al. 2007).



Functional Group	Open water forager	Clutter Specialist	Passive Listener
Prey detection by...	Echolocation	Echolocation	Passive listenting
Species used	*Myotis capaccinii* (n=8)	*Myotis emarginatus* (n=7)	*Myotis myotis* (n=7)
Complexity of habitat	Less complex hunting habitat	More complex hunting habitat	
Phylogeny according to Stadelmann et al. 2007			

Figure 1.1 *The bat species used in the experiments were closely related European congeners representing three distinct foraging guilds.*

Based on the hypothesis that the complexity of the foraging habitat predicts cognitive ability, we expected open water foragers to display relatively stereotyped behavior, slow learning and low flexibility. In contrast, we predicted that passive listening gleaners and clutter specialists would be fast learners and highly flexible (Siemers 2001). To compare learning performance and flexibility, we used a purposefully artificial and thus species-fair plastic maze in which the animals had to crawl and search for food. A similar crawling paradigm has been successfully used for bats in other simple learning tests (Ruczynski & Siemers 2011; Page et al. 2012). We quantified the bats' behavior on four tasks: exploration, simple rule learning, a reversal learning task that tested for flexibility, and complex rule learning. We predicted that the two species hunting in or near vegetation would be faster learners and show greater flexibility than the water foraging species.

Materials and Methods

Ethical statement

Capture and husbandry were conducted in accordance with the species-specific recommendations of the Canadian Council on Animal Care on bats (Canadian Council On Animal Care 2003) and were licensed by the responsible Bulgarian authorities (MOEWSofia and RIOSV-Ruse, permit numbers 193/01.04.2009 and 205/29.05.2009). Officials from the Bulgarian Ministry of Environment and Water (MOEW) inspected our work in accordance with Section 8, Article 23, Paragraph 3 and 4 of the Bulgarian Biodiversity Law. According to Bulgarian laws no further ethical approval by a committee is required for a non-invasive behavioral study. No bats were harmed. All bats were released in good health, at or above capture weight, at their respective capture sites after the experiments.

Animals

Bat capture and experiments were conducted in Bulgaria. We used experimentally naïve, wild-caught adult male bats of the species *M. myotis* (n = 7), *M. capaccinii* (n = 8) and *M. emarginatus* (n=7). We captured *M. myotis* and *M. capaccinii* in or near the entrance of caves in northeastern Bulgaria. *Myotis emarginatus* were mist-netted in the central Balkan Mountains near Gabrovo. The animals were then transferred to the Tabachka Bat Research Station (Bulgaria) of the Sensory Ecology Group (Max Planck Institute for Ornithology, Seewiesen, Germany), which is run in cooperation with the directorate of the Rusenski Lom Nature Park in the district of Ruse. *Myotis capaccinii* (7-10 g) and *M. emarginatus* (6-9 g) were housed together in a screen tent (2.2 m x 0.9 m x 1.1 m). *Myotis myotis* (20-27 g) were kept in a holding cage (50 cm x 35 cm x 40 cm). All animals had *ad libitum* access to water. For individual recognition, we gave all bats a within-species individual-specific haircut by cutting a small stripe of hair on one part of the back. After capture, the bats were hand-fed live mealworms (*Tenebrio molitor*) for two nights before starting training in the maze, to allow them time to adjust to the environment and the new food source. *Myotis myotis* received 4 g of mealworms per day, while *M. capaccinii* and *M. emarginatus* received 1.5 g and 1.7 g respectively. All bats readily accepted mealworms as food. When experiments began, bats were only fed in the experiment (with the exception of night 1, see below). The body mass of the bats was measured before and after each session to ensure that the animals maintained their weight. The dark-light-cycle and temperature in captivity mirrored ambient, natural conditions. The experiments with *M. capaccinii*, *M. myotis*, and four *M. emarginatus* were conducted in July and the first half of August. The experiments with the other three *M. emarginatus* took place in September of the same year. After the experiments all bats were released at their respective capture sites.

Experimental setup

Experiments were conducted in a plastic maze. The simple form consisted of 4 plastic boxes (20 cm x 13.5 cm x 10 cm) connected to a large center box (24 cm x 16.5 cm x 12.5 cm) by plastic tubes (25 cm long, 7 cm internal diameter). All bats could easily crawl and turn in the tubes. One of the four boxes always served as the starting box while the other three contained mealworms (see fig. 1.2a). In all experiments, we placed the same amount of live mealworms in each feeding box to prevent the bats from receiving different acoustic, visual or olfactory cues from the three boxes. *Myotis myotis* was presented with normal-sized mealworms (approx. 0.1 g each) while the two smaller species received small mealworms (approx. 0.05 g each). The mealworms could crawl in the feeding boxes, but could not move back into the plastic tubes, as the entrance to the tubes was elevated by about 0.5 cm. The entrance to each box could be closed with a plastic slide. Additional arms could be added to the maze for the complex task (see fig. 1.2b). To remove possible olfactory cues, the mazes were cleaned after each experimental session with detergent and water and a clean set-up was used for each bat. Experiments were conducted in near darkness. The only light source was dim red light from the observer's headlamp (Tactikka plus, PETZL) and an infrared light (CONRAD, 1/3'' CMOS colour camera with IR) mounted on the ceiling to enable video recording. A camera (Watec, WAT-902H2 Ultimate) was placed above the maze to record all experiments. The videos were recorded on miniDV tapes with a camcorder (Sony DCR-TRV80E recorder).

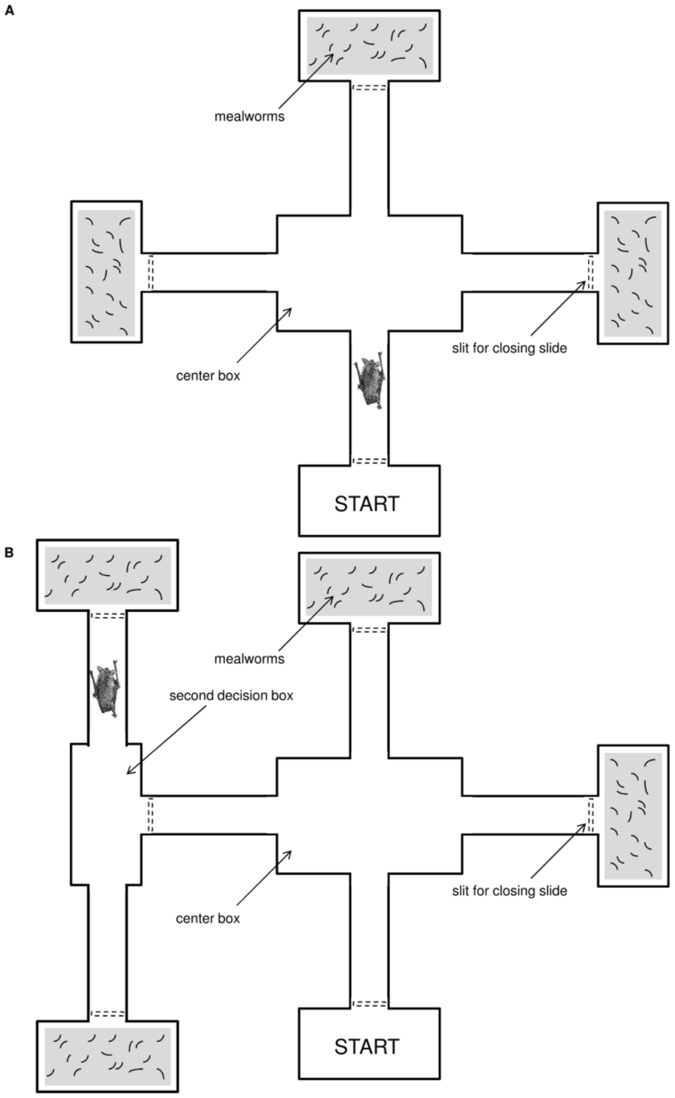


Figure 1.2 Mazes used in experiments. (a) Maze used in experiments 1 to 3. *"Exploration", "Simple Rule Learning", "Flexibility and Re-learning"* (b) Extended Maze used in experiment 4. *"Complex Rule Learning"*.

Procedure

Experiment 1: Exploration

On night 1 we conducted an exploration experiment. The experiment began when a bat was placed into the maze and left there for 15 minutes. Prior to placing the bat in the maze, each box, including the center box, was baited with three mealworms. The bats were allowed to move freely and eat as many of the mealworms as they wanted to. Thus, the bats had the possibility to acclimate to the plastic maze and we were able to use video analysis of movement in the maze to assess the possible effect of species differences in body size and crawling performance on the results of the following experiments. After 15 minutes of exploration, the bat was removed from the maze and was additionally hand-fed up to the normal daily amount of food taking into account the number of mealworms eaten during exploration.

We analyzed the videos of the exploration experiment for several behavioral parameters to control for differences in crawling abilities. “Small scale exploration” was defined as the amount of time an animal spent exploring one of the boxes or exploring an arm systematically by moving back and forth. In contrast “fast walking” was defined as the amount of time an animal was crawling straight through the maze; and “immobile” referred to times when the animal was not moving. We also quantified the “number of boxes visited” (excluding the start box), the “number of mealworms eaten”, and the “latency to exit the start box”. We additionally examined whether an animal explored the center box thoroughly or only crossed it when crawling from one arm to another. Two videos from *M. capaccinii* were lost due to technical failure. We analyzed the data using Anova, Kruskal-Wallis-test and Chi-square-test where appropriate.

Training

During the next two nights, the bats were trained to find rewards in one of the boxes (half of the bats were trained to the right box; half of the bats to the left box; balanced within species, fig. 1.2a). To train the bats to feed from the rewarded box, the other two arms were blocked by slides. In this training phase and all following experiments, each night, one session of 10 trials (one trial being one searching event) was conducted for each animal. At the beginning of each trial the bat was placed into the starting box. When it reached the target box it was allowed to eat two to four mealworms. Afterwards it was removed from the target box and the next trial started. If a bat did not move for more than five minutes (either did not leave the starting box or stopped in the center box), the trial was aborted. Then, after a break of two to five minutes, the next trial started.

Experiments 2 – 4

We conducted three additional experiments with all bats. All experiments were conducted in the same order. Each bat was tested in each experiment for at least three sessions (one session per night). Within each session after trial 4 and 7 the arms of the maze were interchanged to prevent the bat from following its own scent. After trial 7 the center box was rotated 180°.

If a bat made 8 out of 10 correct decisions, it was considered to have learned the task. To give the animals the opportunity to better consolidate the newly acquired information, individuals were required to make 8 out of 10 correct decisions on two consecutive nights before moving on to the next experiment. If a bat did not learn a task after 15 sessions, it was removed from the experiment. This rule only had to be applied for one *M. capaccinii*. The whole study required each bat to stay in captivity for a minimum of 14 nights (two nights of hand-feeding, one night in experiment 1, two nights training and three nights for each of the experiments 2-4). Theoretically, the study could take as long as 50 nights (2 + 1 + 2 + 15 + 15 + 15) for one individual, although no bat required the maximum amount of time in the experiments.

Experiment 2: Simple rule learning

On night 4 the second experiment started. For this and all subsequent experiments, all four arms of the maze were open. After reaching the center box, the bat was required to enter the arm in which it had formerly been trained to find mealworms (fig. 1.2a). In the target box it was again allowed to eat two to four mealworms before the next trial started. If a bat entered an unrewarded arm, the entrance to the box was blocked with a plastic slide. Subsequently, the bat was removed from the maze without receiving a food reward and the next trial started. We scored the number of days that an animal needed to meet the learning criterion of 8 out of 10 correct decisions.

Experiment 3: Flexibility and re-learning

To test flexibility and re-learning we conducted a reversal experiment in which the bats had to learn to visit the box opposite the formerly rewarded one (fig. 1.2a). If a bat entered the formerly rewarded arm it was denied access to the mealworms by closing the entrance to the box. We recorded how many trials were required for a bat to investigate a new arm; either straight ahead or the opposite box; we used this metric as a measure of flexibility. After visiting the newly rewarded arm for the first time, an animal could learn where to find the reward. We then analyzed the number of days it took an animal from the first correct visit until making 8 of 10 trials correct in one session, and used this as a measure of re-learning. One *M. capaccinii* did not learn the new position within 15 sessions and was therefore excluded from the second part of experiment 3 as well as from experiment 4.

Experiment 4: Complex rule learning

For experiment 4, two additional arms were added to the maze (fig. 1.2b). Upon choosing the same arm as was rewarded in experiment 3 the bat now entered a second decision box and had to turn in the opposite direction as before (either left-right or right-left) to obtain the mealworm reward. We used the same criterion and analysis as in experiment 3 to quantify how quickly the bats learned this more complex task. Due to the length of the study (see above) and constraints on the timing and use of the field station, logistical reasons made it necessary to release two *M. emarginatus* before they could participate in this experiment.

Statistical analysis was conducted in R (R Development Core Team 2012). For the post-hoc analysis following a Kruskal-Wallis-test, we followed Dunn's (1964) suggestions for a test for multiple comparisons using rank sums.

Results

Experiment 1: Exploration

For most behavioral parameters we did not find any differences between species in the exploration experiment. We compared the latency to exit the start box ($F_{2;17} = 1.20$; $p = 0.325$), the time spent with small scale exploration ($F_{2;17} = 0.75$; $p = 0.489$) (see fig. 1.3), the time spent walking fast ($F_{2;17} = 0.06$; $p = 0.943$), and the time spent immobile ($F_{2;17} = 0.56$; $p = 0.581$). All box-and-whisker-plots show median, 25 percentile, 75 percentile, minimum, and maximum. Outliers have values at least 1.5 times the interquartile range (IQR) larger than the 75 percentile or 1.5 times the IQR smaller than the 25 percentile. On average it took the bats less than one minute to leave the start box and begin to explore the maze (mean = 0.58 min ± SD = 0.80). They spent ten minutes on small scale exploration (10.37 min ± 2.71), two minutes on fast walking (1.8 min ± 1.34), and three minutes immobile (2.75 min ± 2.94). Three *M. capaccinii*, four *M. emarginatus*, and five *M. myotis* visited all three boxes. There was no difference in the number of boxes visited among the species (Kruskal-Wallis: $\chi^2_{[2]} = 0.51$; $p = 0.776$). We only found differences in the absolute number of mealworms consumed (Kruskal-Wallis: $\chi^2_{[2]} = 8.714$; $p = 0.013$) with *M. myotis* eating the most and *M. capaccinii* eating the least. To

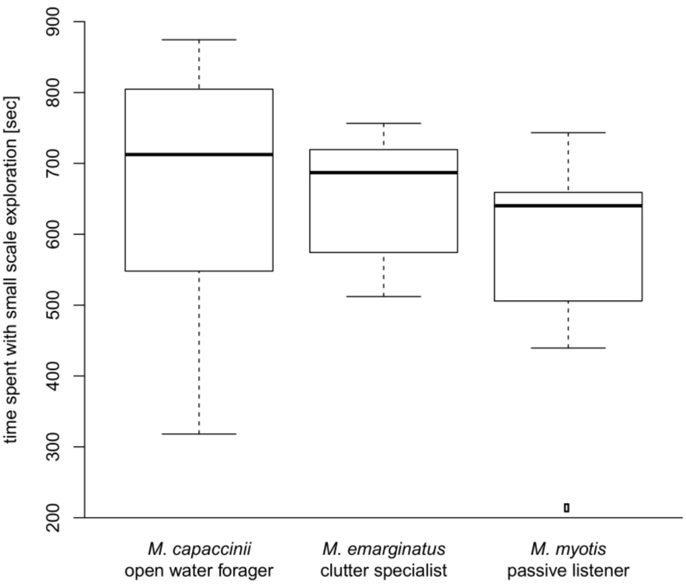


Figure 1.3 Experiment 1 ("Exploration"). *Time spent with small scale exploration: There was no difference among the species in the time the bats spent with small scale exploration (p = 0.49). We found no difference in other parameters measured, except for the total number of mealworms eaten (not shown here).*

control for the effect of body mass we calculated the number of mealworms eaten per gram body mass of the bat and still found a difference in the relative number of mealworms consumed ($F_{2;17} = 7.73$; $p = 0.004$) with *M. emarginatus* eating the most and *M. capaccinii* eating the least.

Experiment 2: Simple rule learning

All species learned the task quickly (see fig. 1.4). After two days of training, there were no differences among any of the species in the number of days the bats needed to make 8 out of 10 correct decisions (Kruskal-Wallis: $\chi^2_{[2]} = 2.16$; $p = 0.340$).

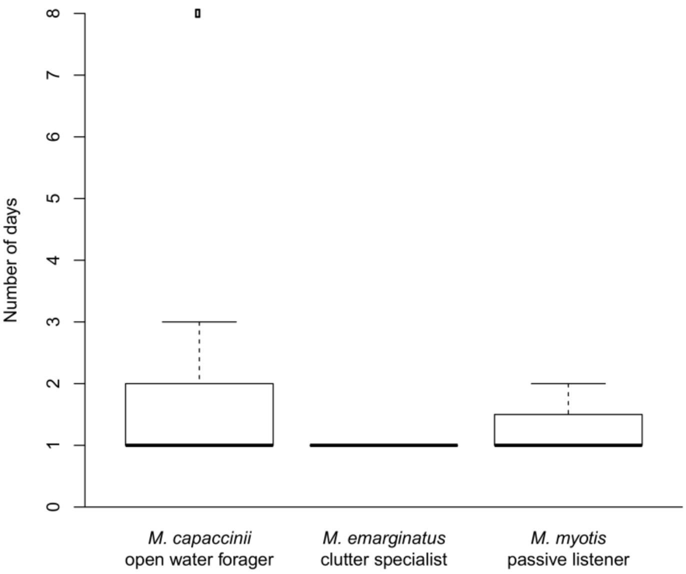


Figure 1.4 Experiment 2 ("Simple Rule Learning"). *Number of days to reach criterion: There was no difference in learning performance among the three species (p = 0.34). Most animals reached the criterion on the first day after pre-training.*

Experiment3: Flexibility and re-learning

Most *M. emarginatus* and *M. myotis* visited a new arm on the first day (trial 1 to 10), while most *M. capaccinii* required at least two days to visit a new arm for the first time (fig. 1.5 and supporting information Video S1). A Kruskal-Wallis-test showed significant differences between the species ($\chi^2_{[2]} = 7.68$; $p = 0.022$). One *M. capaccinii* was an extreme outlier that required 78 trials to try a different arm. To ensure that the difference between the species was not due to this single individual, we tentatively excluded it from analysis and still found significant differences among the species (Kruskal-Wallis: $\chi^2_{[2]} = 6.30$; $p = 0.04$). We did a post-hoc analysis following Dunn (1964) to find out if there were differences between *M. capaccinii* and the other two species, as well as differences between *M. emarginatus* and *M. myotis*. *Myotis capaccinii* required significantly more trials to change its strategy and search in a new location than did the two other species. There was no difference in the number of trials required for *M. emarginatus* and

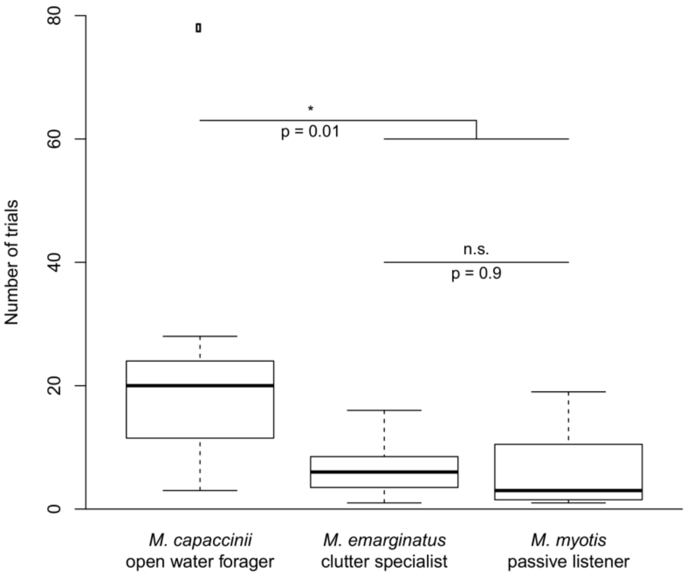


Figure 1.5 Experiment 3 ("Flexibility"). *Number of trials until the animals visited a formerly unrewarded arm for the first time.*

M. myotis (fig. 1.5 and supporting information Video S1).

We found no difference among species in re-learning speed (Kruskal-Wallis: $\chi^2_{[2]} = 4.14$; $p = 0.126$, fig. 1.6). However, when the *M. capaccinii* outlier (which needed six days to achieve 8 of 10 correct trials) was removed from the analysis, we found a significant difference among the species (Kruskal-Wallis: $\chi^2_{[2]} = 6.91$; $p = 0.032$), with a faster re-learning speed in *M. capaccinii* than in the other species (Dunn: $p = 0.022$).

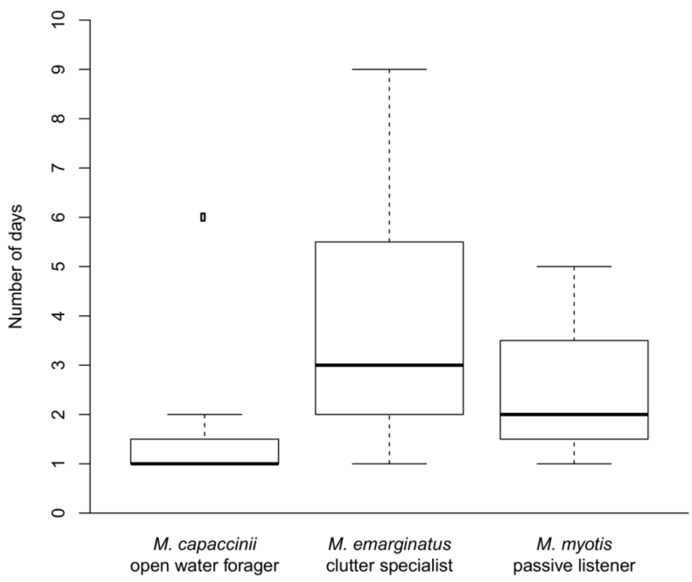


Figure 1.6 Experiment 3 ("Re-learning"). *Number of days from visiting the newly rewarded box for the first time to reaching criterion (turning 8 out of 10 times in the opposite direction than before): There was no difference in learning performance among the species (p = 0.13).*

Experiment 4: Complex learning

A Kruskal-Wallis-test showed a borderline significant difference among all species ($\chi^2_{[2]} = 5.81$; $p = 0.055$) in the number of days needed to make 8 out of 10 correct choices. In the post-hoc analysis we conducted following Dunn (1964) we found a clearly significant difference between *M. capaccinii* and the other two species ($p = 0.03$), implying that it took *M. capaccinii* longer to learn this more complex task of turning twice than it took either of the other species. The two *M. myotis* and *M. emarginatus* outliers (fig. 1.7) coupled with a low overall sample size (7 *M. capaccinii*, 5 *M. emarginatus*, 7 *M. myotis*) lead to only borderline significance in the Kruskal-Wallis-test (Kruskal-Wallis without outliers: $\chi^2_{[2]} = 8.65$; $p = 0.013$). Again, there was no difference between *M. emarginatus* and *M. myotis* (fig. 1.7).

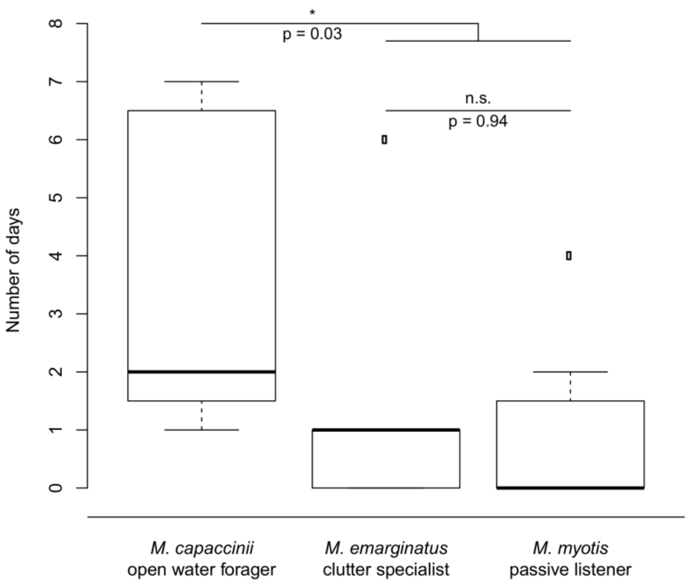


Figure 1.7 Experiment 4 ("Complex Rule Learning"). *Number of days from visiting the newly rewarded box for the first time to reaching learning criterion.*

For the experiments 2 – 4 we investigated whether there were differences among the individuals that were first trained to turn right versus the ones that were trained to the left box. We found no differences for any parameter between these two groups (all $p > 0.1$).

Discussion

We find strong evidence that bat cognitive skills reflect their ecological niche. By comparing the ability to find food in a species-fair, artificial crawling maze we tested the learning performance of three closely related species that naturally forage in habitats differing in complexity, stability, and food predictability. We found that bat species hunting in more complex, less stable habitats with lower food predictability perform better in more complex learning tasks and are more flexible when the food source is relocated than those hunting in simple, more stable habitats with highly predictable food resources. Our results confirm the environmental complexity thesis (Godfrey-Smith 2001) and are the first to directly link bat learning and flexibility with ecological foraging niche.

Learning in an artificial environment

The comparison of learning performance of different animal species is extremely challenging (Bitterman 1975). To allow for comparison all species should be tested in the same setup, while each species' unique set of sensorial and motor skills has to be accounted for to guarantee species-fairness. While a less artificial, more natural foraging task would have offered greater insight into the cognitive capabilities of these animals in nature, natural foraging tasks would have hindered cross-species comparisons. To compare learning and flexibility of taxa with widely disparate foraging ecologies (the goal of this study), we purposefully chose experimental tasks that were foreign to all. We used the exploration phase to assess possible differences in motor skills among the three species that might have hindered access and mobility within the maze. The lack of differences among the investigated species in the exploration experiment suggests that our results were not biased by any consistent species differences in the ability to cope with the maze. The difference in the number of mealworms eaten during exploration could be explained by body size differences or slight sensory inequalities. In the other experiments there were more mealworms in the boxes and the animals were given all the time they needed to consume two to four mealworms before the next trial started. This should have compensated for possible differences in detection and eating speed. We therefore conclude that the results of our experiments were not affected by differences in size or crawling performance among the species and that all animals had equal opportunities to learn about all the boxes and paths of the maze. The plastic maze was equally artificial for all bats and should not have posed a particular disadvantage to any one species. Because of its artificial novelty, it proved effective in elucidating consistent species differences in learning performance. Our results demonstrate that an artificial setup like ours can be useful to balance potentially biasing factors and to investigate cognitive abilities of different species in a species-fair manner.

Solving simple and complex tasks

Two days of pre-training were sufficient to teach the bats to find food in one arm of the maze. These results show that the process of learning a simple rule (experiment 2) is quick, and suggests that simple rule learning is not sufficiently challenging to elicit differential responses in the species tested. It suggests that differences in cognitive abilities might only be detectable in more complex tasks.

Indeed, when the bats were required to exhibit more complex behavior to obtain a food reward – to turn twice to find the rewarded box in the complex learning task (experiment 4) – we found differences among the species. *Myotis myotis* easily completed this task, and most individuals met the learning criterion on the first day of testing. *Myotis emarginatus* also quickly learned to find and remember the new feeding box, most individuals learning within days 1-2. *Myotis capaccinii* showed the greatest inter-individual variation. Of the seven *M. capaccinii*, four learned the task rather quickly within days 1-2 and three learned the task very slowly, requiring six to seven days. Intermediate learning performance was not observed in this species. Interestingly, the one *M. capaccinii* that required 78 trials to investigate a new arm in experiment 3 (flexibility and re-learning) was the fastest learner in this task and succeeded in finding the food reward in 8 out of 10 trials during the first night. Thus, the least flexible individual was the fastest learner in the complex learning task. Even though the sample size in the complex rule learning experiment was smaller than in the other experiments and the results only show borderline significance ($p = 0.055$), this trend suggests that *M. capaccinii* needed the greatest number of days to remember the newly rewarded box. A larger dataset would be needed to demonstrate clearly significant results. However, while *M. capaccinii* were able to learn a simple rule as quickly as the other species, a more complicated path was more difficult for them to learn and remember. Thus, as predicted, the species foraging in the least complex environment, open water, performed more poorly than the passive listening gleaner and the clutter specialist.

In experiment 4, a few individuals of each of the three species went straight through the center box several times, even though the end box of this arm had never been rewarded. This behavior rarely occurred in the other experiments. It would be interesting to investigate if the bats had developed a cognitive map of the maze and would have turned in the direction of the rewarded box at the end of the arm or would have been able to perform shortcuts or use a more direct route, had this been available. Further investigations are necessary to determine whether insectivorous bats use cognitive maps in foraging as has been recently shown for fruit-eating bats on a larger scale (Tsoar et al. 2011), and if so, the conditions under which they do so.

Flexibility and re-learning

As expected, we found a clear difference among the three species in the flexibility test (experiment 3). While most *M. emarginatus* and *M. myotis* tried new ways to find food on the first day when the familiar route was blocked, the open water forager, *M. capaccinii*, was persistent in visiting the formerly rewarded box. This supports the environmental complexity thesis (Godfrey-Smith 2001), which predicts that bats hunting in more complex and unpredictable habitats (for example, in or near vegetation) will show more flexible behavior than bats hunting in less complex and more predictable habitats (for example, over water surfaces). Game theoretical modeling suggests that individuals can enhance their probability of finding food by specializing on one food type when the location of their food sources is predictable in space and time (Overington et al. 2008). The stereotypic behavior of *M. capaccinii* together with what we know from natural history and dietary studies (Almenar et al. 2006; Biscardi et al. 2007) suggests that rather than specializing on a single food type, *M. capaccinii* has evolved to specialize on a specific and simple foraging habitat in which its particular foraging skills excel. The obstinacy of this species suggests that stereotypic behavior under natural conditions is beneficial and could be genetically determined. It is interesting that once the bats discovered the new food source in our artificial maze, there was no difference in the re-learning speed of a simple rule (e.g., always turn right or always turn left). There even was a trend that *M. capaccinii* learned the new position faster than the other species. This might be due to their greater persistence. This trend suggests that persistence can have evolutionary benefits. It is possible that in nature *M. emarginatus* and *M. myotis* continuously sample their surroundings for more and (potentially) better food sources, thereby making mistakes, while *M. capaccinii* persists in repeatedly visiting locations with a high probability of containing food. It is interesting to note that there is evidence that *M. capaccinii* in Israel have recently begun hunting fish adding this prey to their diet only within the last century. Especially during winter they forage to a great extent on *Gambusia affinis*, a species that was introduced in the area in the 1920s (Levin et al. 2006). Occasional piscivory is known in this species from other areas and seems to be a common foraging strategy in other trawling bat species in times of high fish abundance (Aihartza et al. 2003, 2008; Biscardi et al. 2007). In an experimental setup with *M. capaccinii* in the flight cage, dips into the water were not directionally targeting fish, but were carried out at random and seemed to follow stereotyped patterns (Aihartza et al. 2008), similar perhaps to the stereotyped foraging behavior we found in *M. capaccinii* in our maze experiment.

One *M. capaccinii* could not be included in the full set of experiments because it failed to complete the re-learning task within 15 sessions (experiment 3). This individual visited a new arm in the second night of experiment 3 (trial 20) and found the new food source for the first time in the fifth night of experiment 3 (trial 42), but even after ten additional nights of testing, never learned to consistently visit the newly rewarded box. This particular individual also required the most time of all bats to complete the simple rule learning task (see fig. 1.4; one *M. capaccinii* requiring eight days). This behavior differs from the other *M. capaccinii* which showed learning and re-learning within one or two nights once they found the food source, and highlights the potential for high inter-individual variation even within a species. Apart from this individual we did not find that any other bat consistently showed a different performance from its conspecifics (i.e., the outliers in different experiments were different individuals).

The relationship between flexibility and stereotypy and food predictability has been studied on an intraspecific level in the context of animal personality research. Studies of intraspecific variation in exploration speed, flexibility, and novelty response in birds (Verbeek et al. 1994) and small mammals (Benus et al. 1991) show that individuals that are more persistent and do not change their behavior when presented with changes in food positioning site have the advantage of finding more food under stable conditions. On the other hand, once they find a reliable food source they develop inflexible, routine-based behavior. Therefore, under more variable conditions, they have a disadvantage compared to less persistent individuals. Depending on how variable a specific environment of an individual or a population is, we predict a selective pressure to shape foraging behavior either towards more stereotypy or towards more flexibility. Because in our maze experiments we see predictable differences across species despite favorable conditions to the contrary, we further predict a genetic basis for stereotyped versus more flexible behavior, similar to the genetic basis for stress and novelty response (Ruiz-Gomez et al. 2011), exploration propensity (Dingemanse & de Goede 2004), and aggressive behavior (Benus et al. 1991). It is possible that within-species differences on the flexibility-stereotypy gradient ultimately translate into species differences in these traits, as shown in the present study, through allopatric or even sympatric speciation with differential microhabitat selection.

Brain-size and cognitive abilities

Ratcliffe et al. (2006) categorized predatory bat species into groups based on their natural foraging modes. They found that bat species they categorized as more flexible in their hunting strategies and ground gleaning species like *M. myotis* have larger relative brain sizes and a larger neocortex than less flexible species, such as open space aerial hawking bats. Eisenberg and Wilson (1978) also found that aerial insectivores have smaller relative brain sizes than other insectivores, which in turn have smaller relative brain sizes than frugivorous bats. Several studies in birds and mammals show that the relative size of the neocortex as well as the relative size of the whole brain are strongly related to cognitive abilities and enhanced novelty response (e.g., Reader & Laland 2002; Sol et al. 2005; also reviewed in Lefebvre & Sol 2008). We thus predicted that *M. emarginatus* and *M. myotis* should have larger relative brains and neocortices than *M. capaccinii*. As data on brain sizes of *M. emarginatus* and *M. capaccinii* are not available yet, this prediction remains to be studied. However, available data on skull morphology indicate that *M. capaccinii* indeed has the smallest relative skull and hence potentially the smallest relative brain of our three species followed by *M. emarginatus* and then *M. myotis* (condylobasal length divided by forearm length and zygomatic width divided by forearm length; data from Krapp & Niethammer (2011)).

Ecology and sociality

Animal cognition researchers generally attribute the evolution of brains and intelligence to either ecology (e.g., Parker & Gibson 1977) or to social structure (e.g., Byrne & Bates 2007). Recently, however, there are models that combine the two (e.g., Overington et al. 2008). In our case, we have chosen bat species that differ widely in ecology, but are quite similar in their social systems. In all three species, females congregate in large maternity groups of up to several thousand individuals while males roost singly or in smaller bachelor colonies in summer; in winter, males and females from all three species hibernate singly or in small clusters (Dietz et al. 2009: *M. capaccinii* p. 213; *M. emarginatus* p. 244; *M. myotis* p. 254). In some cases pregnant or lactating females of all three species can be found in the same cave at the same time in Bulgaria (TC, personal observation). By choosing species with very similar social structures and other aspects of their biology, but disparate foraging ecologies, we can infer that the differences we find in learning and flexibility reflect ecology and not sociality.

Conclusion

Results from this study confirm our prediction that open water foragers are more stereotyped and hence less flexible than species hunting in more complex habitats. Contrary to our expectations, there was a trend that open water foragers learn simple rules more quickly than clutter specialists and passive listening gleaners. Given a more complex task involving two decisions, however, passive listening gleaners and clutter specialists showed a tendency to outperform bats hunting over water. Due to their unstructured foraging habitat, we would expect results from bats hunting in open space to be similar to those of open water hunters. More subtle differences between passive listening gleaners and clutter specialists might only be revealed in a yet more complex task.

Our data support the hypothesis that cognitive abilities of animals are shaped by the demands of their ecological background. Our results concur with those of recent studies on nectar-feeding bats that differ in their spatial working memory performance depending on their degree of dietary specialization, in which a specialized nectarivorous bat foraged more efficiently at artificial flower patches than a generalist that also includes fruits and insects in its diet (Henry & Stoner 2011). They are also in line with recent findings for birds (e.g., Mettke-Hofmann & Gwinner 2003; Gibson & Kamil 2005) and mammals (Haupt et al. 2010).

Supporting Information

Video S1: Video clips demonstrate *M. capaccinii* navigating the maze in the flexibility and re-learning task and in the complex learning task. For comparisons of crawling performance, video clips demonstrate *M. myotis*, a much larger species, in the flexibility and re-learning task. The video can be found on the CD enclosed in this thesis and accessed at: http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0064823#s5

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CHAPTER 2

Social learning within and across species: information transfer in mouse-eared bats

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Abstract

Social learning describes information transfer between individuals through observation or direct interaction. Bats can live and forage in large groups, sometimes comprising several species, and are thus well suited for investigations of both intraspecific and interspecific information transfer. Although social learning has been documented within several bat species, it has not been shown to occur between species. Furthermore, it is not fully understood what level of interaction between individuals is necessary for social learning in bats. We address these questions by comparing the efficiency of observation versus interaction in intraspecific social learning and by considering interspecific social learning in sympatric bat species. Observers learned from demonstrators to identify food sources using a light cue. We show that intraspecific social learning exists in the greater mouse-eared bat (*Myotis myotis* (Borkhausen, 1797)), and that direct interaction with a demonstrator more efficiently leads to information transfer than observational learning alone. We also found evidence for interspecific information transfer from *M. myotis* to the lesser mouse-eared bat (*Myotis oxygnathus* (Monticelli, 1885)). Additionally, we opportunistically retested one individual that we recaptured from the wild one year after initial learning and found long-term memory of the trained association. Our study adds to the understanding of learning, information transfer, and long-term memory in wild-living animals.

Social learning has been defined by Heyes (1994) as “learning that is influenced by observation of, or interaction with, another animal (typically a conspecific) or its products”. Social learning has been investigated with respect to predator avoidance (reviewed by Griffin 2004), habitat use (e.g., Rossiter et al. 2002; Slagsvold & Wiebe 2007), mate choice (reviewed by White 2004), and most often the exploitation and acquisition of new food sources (reviewed by Galef & Giraldeau 2001). Advantages of social learning about food include the rapid acquisition of information about safe, nutritious food (Galef 1976), avoidance of unpalatable food (Galef & Clark 1971), and perhaps the relocation of ephemeral food items (Ratcliffe & ter Hofstede 2005) faster than by individual learning. In general, social learning about food tends to lead to adaptive consumptive behavior (Galef 1995).

Social learning about food within species is a widespread phenomenon across vertebrate groups, from fish (e.g., Brown & Laland 2003), to amphibians (Ferrari et al. 2007), reptiles (e.g., Wilkinson et al. 2010), birds (e.g., Fritz et al. 2000; Heyes & Saggerson 2002; Aplin et al. 2013), and mammals (Gaudet & Fenton 1984; Cook & Mineka 1989; Heyes & Dawson 1990). Social learning has been reported in a number of bat species. For example, female Bechstein's bats (*Myotis bechsteinii* (Kuhl, 1817)) transfer information about suitable roosts among group members (Kerth & Reckardt 2003). Female greater spear-nosed bats (*Phyllostomus hastatus* (Pallas, 1767)) learn group-specific contact calls from resident group members (Boughman 1998) and use them as rallying cries when foraging and defending food resources from other groups (Wilkinson & Boughman 1998). Fringe-lipped bats (*Trachops cirrhosus* (Spix, 1823)) not only learn novel foraging behaviors socially. When foraging with a trained conspecific, they can also learn to associate a usually aversive acoustic cue with a reward (Page & Ryan 2006). Further studies on social learning in bats are reviewed by Wilkinson and Boughman (1999).

Social learning across species has been documented in the context of predator avoidance in amphibians and fish (e.g., Mathis et al. 1996; Ferrari & Chivers 2008). It has also been shown in the context of food acquisition and nest-site preferences in birds (e.g., May & Reboreda 2005; Seppänen & Forsman 2007). To our knowledge, cross-species social learning in bats has been investigated in only one study, but the results were confounded by interspecific aggressive behavior (Gaudet & Fenton 1984). In the two cases of social acquisition of a novel foraging task or a novel food source outlined above, observers seemed to react to demonstrators' chewing noises (Gaudet & Fenton 1984; Page & Ryan 2006), but once the observers' attention had been elicited, many possible explanations for learning are possible including direct interaction with the tutor, stimulus enhancement (the drawing of attention towards a novel object by a demonstrating individual; Heyes 1994) or observational conditioning (where the unconditioned response of a demonstrator acts as the unconditioned stimulus for the observer; Heyes 1994) (Page & Ryan 2006).

Greater mouse-eared bats (*Myotis myotis* (Borkhausen, 1797)), our primary study species, congregate in maternity roosts of up to several thousand individuals, and several individuals can forage in the same area at the same time (Rudolph et al. 2009). They are primarily passive listening gleaners hunting for arthropods over open accessible ground in forest and field. Often, these bats land on the ground to pick up prey that they then consume in flight (Arlettaz 1996). Their foraging habitats are complex and change over the course of the year, and the bats may be able to recognize specific landscape features, such as a freshly cut meadow, as good foraging grounds (e.g., Arlettaz 1996). *Myotis myotis* live in large groups, hunt close to each other, and are presumably capable of associative learning, as they likely associate ephemeral but recurring landscape features with productive patches of food. Additionally, laboratory studies have shown that congeners readily perform associative learning tasks in captivity (e.g., Siemers 2001; Page et al. 2012). Thus, information transfer may well occur between *M. myotis* individuals with respect to food. We tested this prediction. Specifically, we tested whether *M. myotis* could acquire information about food location associated with an artificial cue from conspecifics. We also tested whether direct interaction between individuals is necessary for information transfer to occur. Through the fortuitous recapture of a previous observer from the wild a year after release, we were also able to assess memory retention of a socially learned sensory cue - reward association about food after a period of prolonged hibernation.

To investigate interspecific learning, we used the lesser mouse-eared bat (*Myotis oxygnathus* (Monticelli, 1885); sometimes referred to as *Myotis blythii* (Tomes, 1857)), the sister species of *M. myotis*, as a congeneric observing species (i.e., with *M. myotis* as demonstrator). Although the preferred diet of *M. oxygnathus* differs significantly from *M. myotis*, there is also considerable overlap in diet and habitat use by the two species (e.g., Arlettaz 1996; Arlettaz et al. 1997; Siemers et al. 2011). Ecology, morphology, and foraging behavior of these two species are therefore relatively similar (Arlettaz 1999). We assumed that if interspecific social learning occurs, it would most likely occur between similarly sized, closely related species with similar foraging ecology that are regularly found roosting and, although less often, foraging together. By choosing a similar-sized sister species, we also expected to minimize the risk of interspecific aggressive behavior (Gaudet & Fenton 1984). In birds, social learning in mixed species groups of unrelated individuals has also recently been shown (Aplin et al. 2012).

We selected these two closely related sister-species for our study because of their similarity in ecology, their habit of regularly roosting together, and their accessibility in our study region, northern Bulgaria.

Materials and Methods

Animals and housing

We used experimentally naïve, wild-caught adult male bats (*M. myotis*, n = 22; *M. oxygnathus*, n = 12) captured in caves in northeastern Bulgaria. Species were discriminated by morphological traits, including forearm length (Arlettaz et al. 1991) and CM^3 (the length of the upper row of the bat's teeth between canine and third molar) (Bachanek & Postawa 2010). In our test individuals, *M. myotis* forearm length ranged from 60.0 to 63.8 mm and CM^3 ranged from 9.8 to 10.4 mm. In *M. oxygnathus*, forearm length ranged from 54.9 to 59.6 mm and CM^3 ranged from 8.7 to 9.7 mm. In addition to these morphological measures, for *M. oxygnathus* we only used individuals in the observer group that had a clearly visible white spot on the forehead, which is a diagnostic characteristic of this species (e.g., Arlettaz et al. 1991).

Animals were transferred to the Tabachka Bat Research Station (TBRS) of the Sensory Ecology Group (Max Planck Institute for Ornithology, Seewiesen, Germany), run in cooperation with the directorate of the Rusenski Lom Nature Park in the district of Ruse (Bulgaria). Bats were kept in holding cages (50 cm x 35 cm x 40 cm) in groups of two to six individuals; demonstrators and observers were housed separately. Animals had *ad libitum* access to water. After capture, bats were hand-fed for two nights before training to allow them to acclimate to captivity and mealworms (larvae of *Tenebrio molitor* (L., 1758)) as food. The next two nights the bats were fed from feeding boxes (see "*Training to feeding boxes*" below). Throughout, they received 4 g of mealworms per night, consumed either entirely during that night's experiment or as a supplement of an additional 2–4 g of mealworms at least 2 hours after that night's experiment (see "Noninteractive observers (six *M. myotis*)"; "Interactive observers (six *M. myotis*; six *M. oxygnathus*)", and "Control bats (four *M. myotis*; six *M. oxygnathus*)" below). Before and after each session, we measured the body mass of each bat. We ensured that the animals did not lose more than 2–3 g over the course of their time in captivity because of food deprivation, figures corresponding to 5%–10% of their original mass (*M. myotis* - median: 27.1 g, range: 24.0–28.6 g; *M. oxygnathus* - median: 24.7 g, range: 20.8–27.6 g). Temperature and photoperiod in captivity reflected outdoor conditions; experiments were conducted at night and at ambient temperature and humidity. After experimentation, bats were released at their sites of capture, at or above their body mass at time of capture.

Experimental setup

We used custom-made feeding boxes (13 cm long x 9.5 cm wide x 2.5 cm high) as novel food sources. Each contained a white LED and a lid-covered feeding hole. The closing-opening mechanism consisted of an electromagnet that kept the box closed and a spring to open the lid once the magnet was turned off. The box could display a light when opened (fig. 2.1). We controlled the boxes using a custom-made 60-channel switchboard positioned outside of the room.

During the experiment, 20 boxes were distributed uniformly across the flight-room floor (3 m wide x 8 m long x 2 m high; fig. 2.2). The reward was accessible in only 1 box out of the 20 boxes at any given time during the experimental sessions. Theoretical chance level of finding the box with the reward (i.e., rewarded box) was therefore 5%. To eat a mealworm, a bat would land on or near a box, pick up a mealworm, and subsequently consume the insect during flight, resembling these bats' natural foraging behavior. The exact positions of the boxes were changed every 2–4 nights to avoid potential spatial learning. Half the boxes contained mealworms, while the other half contained rubber dummies to ensure that the bats were not using visual or echo-acoustic cues to detect the mealworms. To remove olfactory cues, boxes were cleaned regularly. However, we could not absolutely exclude the possibility that the bats were using potential olfactory or acoustic cues produced by the mealworms to decide which boxes to visit. Further controls for this are discussed below. The order in which boxes were opened changed nightly. Each night a different subset of boxes contained mealworms.

Experiments were conducted in near darkness. The only visible light sources were the LEDs on the feeding boxes. Four infrared lights and four infrared-light-sensitive cameras (Watec, WAT-902H2 Ultimate) were mounted on the four corners of the room to video record the experiments. An omnidirectional broadband microphone (MIC-48; Speed-Shanghai Industrial Co., Ltd., Shanghai, China) was placed midway along the long side of the room near the wall, allowing the experimenter to listen to bats' chewing noises and thereby determine how many mealworms were left in a given box (fig. 2.2).

Demonstrator training took place in a different room, half the size of the experimental flight room used in the social learning experiments (3 m wide x 3.1 m long x 2.3 m high). All other conditions (light, recording system, microphone) were the same as in the experimental flight room.

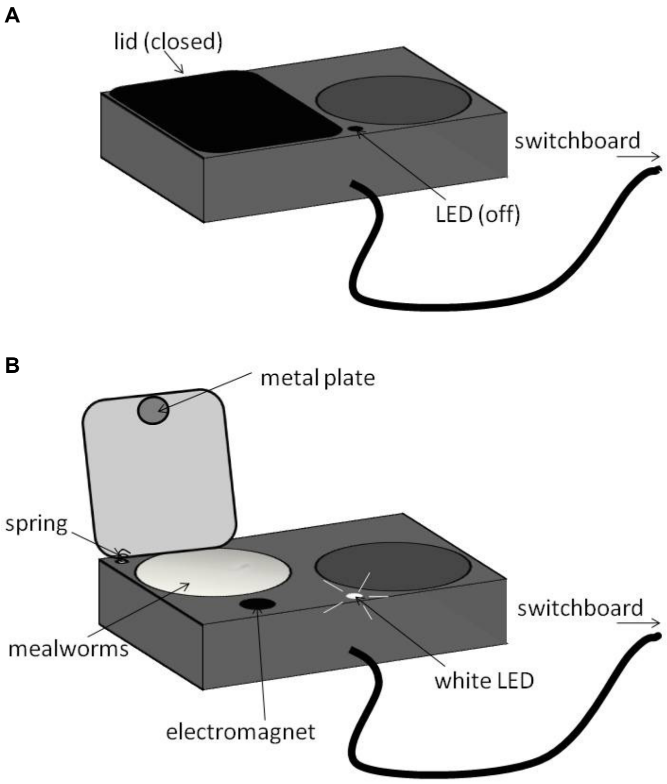

Figure 2.1 Schematic diagram of the feeding boxes used in the experiment studying greater mouse-eared bats (*Myotis myotis*) and lesser mouse-eared bats (*Myotis oxygnathus*). (a) Closed box. *Visible are the closed lid and the switched off LED light.* (b) Opened box. *Visible is the opening mechanism of the box (electromagnet, metal plate, spring). The 2 cm deep feeding hole contained mealworms or rubber dummies.*

Procedure

Training to feeding boxes

After being hand-fed for two nights, the bats had their first experience with the boxes. The demonstrators were fed individually from feeding boxes in their home cages for two consecutive nights. On the first night, the light on the boxes was switched off; on the second night the light was switched on. All observers and control bats were also fed individually for two nights from the feeding boxes in their home cages prior to experiment. For them, the light was switched off on both nights.

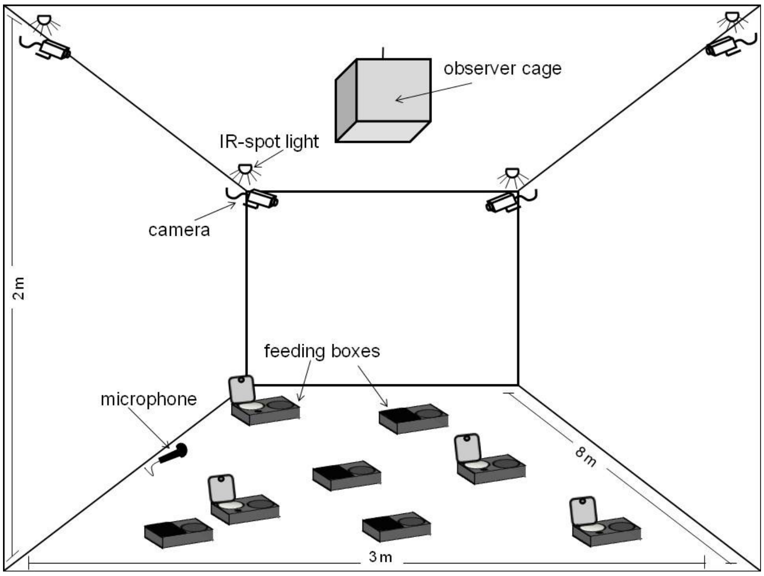

Figure 2.2 Flight room used during experimental sessions. *Twenty feeding boxes (not all shown) were distributed throughout the room (8 m x 3 m x 2 m). Their positions were changed regularly. The behaviour of greater mouse-eared bats (*Myotis myotis*) and lesser mouse-eared bats (*Myotis oxygnathus*) was monitored and recorded by four infrared (IR) cameras mounted below the ceiling in each of the four corners. For the purpose of video recording, four IR spotlights were mounted next to the cameras. In the middle, along one long side of the room, stood a microphone to enable the experimenter to detect and count the bat's chewing noises from outside the room. The noninteractive bat students were placed in an observer cage hanging from the ceiling in the middle of the room.*

Demonstrator training

We started by training six bats of the species *M. myotis* to become demonstrators. On the fifth night after their capture, in-flight training of the demonstrators began. Ten boxes were placed in the smaller flight room. All boxes were open, all boxes displayed light, and each box contained 10 mealworms. Each bat was allowed to fly alone and freely in the flight room for 20 minutes and eat mealworms. By listening to chewing noises, pauses, and scrambles for new prey, the experimenter could quantify how many mealworms the bat had eaten and from this deduce how many mealworms were left in which box from outside the room. If a box was emptied, its light was switched off. If a bat did not find mealworms within 20 minutes, we fed it 20 mealworms after placing it at a box with the light switched on.

After a bat found the mealworms and ate readily from the boxes (i.e., after 3-6 nights, depending on the individual), we increased the number of boxes in the room to 13. We gradually decreased the ratio of rewarded, light-displaying boxes to unrewarded, nonlight-displaying boxes from 10:0 to 8:5 and eventually to 7:6. If a bowl was emptied, we again immediately switched off the light. From then on, the demonstrators could only eat during training sessions and later experimental sessions. One of the six bats did not learn to land on the boxes after one week and was therefore not used for the experiments.

Once a bat readily fed in the paradigm described above and started to prefer lit over unlit boxes (additional 5-9 nights, depending on the individual), we introduced the opening mechanism of the boxes. When the bat started to fly, only two boxes displayed light and were rewarded. At this time, three unrewarded boxes were also open. Only when one of the rewarded boxes was emptied would another box be opened, making the mealworms accessible, and the light turned on. When a new rewarded box was opened, we waited until the bat ate 2-3 mealworms and only then opened an unrewarded box. We did this to prevent the bat from associating only the opening sound of the boxes with the reward. We eventually had seven rewarded boxes each containing seven mealworms and six unrewarded boxes containing rubber dummies in this training phase. As a result, a bat could eat up to 49 mealworms, which is equivalent to the 4 g that we usually fed them. From this point on, a single training session would last either 20 minutes or until the bat had eaten all of the mealworms, whichever came first. This stage lasted 3-11 days, depending on how easily the bat got used to the opening mechanism. In subsequent training sessions, we always opened an unrewarded and a rewarded box at the same time and decreased the number of mealworms per bowl to six.

Finally, we began training the demonstrators in what would be the experimental flight room (3 m wide x 8 m long x 2 m high; see fig. 2.2). Here, we placed 20 boxes on the ground. Each of 10 rewarded boxes now contained only two mealworms. An unrewarded and a rewarded box were now always opened at the same time. The LED on only one box was illuminated and only one reward offered at a given time. Each bat had two training sessions per night, separated by at least 2 hours. We noted the number of correct visits (to a lighted, mealworm-containing box) and incorrect visits (to an unlit box; i.e., a closed, rubber-dummy-containing, or emptied box) and calculated the percentage of correct visits within each session.

Once an individual consistently showed a performance of > 95% correct landings on boxes, the bat was assigned its first experimentally naïve observer. Three *M. myotis* were ultimately assigned as demonstrators (those three bats, from a total of six, that had reached > 95% correct associations between light and food most quickly). The two remaining bats that were trained to become demonstrators also reached performances of > 95%. However, it took them longer to show this high performance as consistently as the three individuals ultimately assigned as demonstrators. All observers in all groups were distributed equally among the three *M. myotis* demonstrators. Specifically, each demonstrator was assigned two conspecific noninteractive observers (*M. myotis*), two conspecific interactive observers (*M. myotis*), and two heterospecific interactive observers (*M. oxygnathus*). Each observer was paired with the same demonstrator for each of its sessions.

After completing experiments with demonstrators and observers, we conducted a final flight with the demonstrators. All boxes were open and all contained one mealworm. Light was only illuminated at one box at a time. Except for the LED light, all other olfactory, acoustic, or visual cues coming from the boxes were the same. Once the bat had found the mealworm, the light on this box was switched off and the light on another still baited box was switched on. This final flight served as an additional control to ensure that no cues other than the LED light were responsible for a bat's decision to visit a particular box.

Observers and control group

Six *M. myotis* were assigned to be noninteractive observers. Six more *M. myotis* were assigned to be interactive observers. Additionally, four *M. myotis* took part in the control experiment. As interspecific observers, six *M. oxygnathus* were assigned to be interactive observers and six *M. oxygnathus* were assigned to the control group. Each of them had one experimental session per night for 14 nights in a row (nights 5 – 18; for exceptions see below). Observers and control animals were never fed before the experiment.

During the experimental sessions, we counted how often a bat visited feeding boxes in total (including opened and closed ones) and how often each bat visited an opened rewarded box, and calculated the percentage of correct visits within one session for each individual. To prevent a bat from entering torpor, if a bat hung on the wall for more than 3 minutes, we encouraged it to fly by briefly entering the flight room and gently shooing it off the wall. If a bat ate more than 20 mealworms, it was not fed additionally after the experiment. Otherwise the bat was fed 2 g of mealworms at least 2 hours after its experimental session. If a bat was losing mass, we increased this amount to up to 4 g.

On night 19, we conducted a final flight with each individual (see below).

Noninteractive observers (six M. myotis*)*

Every night, the observer was placed in an acoustically transparent observing cage (20 cm x 20 cm x 20 cm) consisting of a wooden frame and six sides of green mesh (mesh size 3 mm). This mesh allowed the observer to locate the light source in the room. The cage was hung from the ceiling in the middle of the flight room (fig. 2.2). While its assigned demonstrator was performing its usual task, the noninteractive observer could watch, listen to, and potentially learn that the demonstrator always landed at the lit box and there always found food. After the demonstrator had eaten all 20 mealworms in the room, we caught it, refilled the rewarded boxes with 4 mealworms each, and let the noninteractive observer fly alone in the flight room for 20 minutes. The bat thus had potential access to 40 mealworms per session. At the beginning of the experimental 20 minutes, only two boxes (one rewarded with mealworms and the other unrewarded but containing rubber dummies) were opened. Only if the bat emptied the rewarded box, would two more boxes (one rewarded and one unrewarded) be opened.

On night 19, we conducted a final flight with the noninteractive observers. On this night, these bats were not put in the observation cage for 20 minutes prior to flight, but instead they were immediately released into the room to fly alone. If a bat was not flying, we left it undisturbed. Except for these two changes (no additional reinforcement by a demonstrating bat and no disturbance), the final flight followed the protocol of the previous experimental sessions. Because of logistical constraints, two noninteractive observers had to be released 2 days earlier than planned. Their final flight was conducted on night 17.

Interactive observers (six M. myotis*; six* M. oxygnathus*)*

Other than the noninteractive observers, the interactive observers were allowed to fly and interact with their respective demonstrator while the demonstrator was performing its task. To distinguish the demonstrator and the observer on video, the interactive observers each wore a collar that was made of soft wire with a yellow plastic stripe attached to it, similar to those described in Kunz and Weise (2009). This collar did not impair flight performance or any other behavior of the bats. As soon as the demonstrator had eaten 20 mealworms, the demonstrating bat was caught and removed from the flight room. The observer then had 20 minutes to fly alone in the flight room. To circumvent the disturbance that would have been caused by refilling of the boxes after the demonstrator had been caught and to account for the possibility that the interactive observer might eat while flying together with the demonstrator, we distributed 60 mealworms in the room (20 for the demonstrator, 40 for the interactive observer) and changed the number of mealworms per box. Specifically, the first four rewarded boxes to be opened now contained seven mealworms, the next two rewarded boxes contained six mealworms, and the last four rewarded boxes contained five mealworms.

Hence, like the noninteractive observers, the interactive observers potentially had access to 40 mealworms in total. The boxes that were already opened (and emptied) while the demonstrator was still in the room were not closed again after the demonstrator had been caught. Therefore, the number of opened and closed boxes at the beginning of the observers' 20 minutes varied according to the number of boxes that were opened while the demonstrator was still flying. However, during the observation period, all observers (interactive or not) experienced the same number of demonstrator-eating-mealworm-at-light-events (20) and the time spent at a lighted box by each demonstrator experienced by the observer was roughly the same.

On night 19, we again conducted a final flight. The interactive observer did not fly with the demonstrator and was released into the flight room alone. If the bat did not fly, we left it undisturbed. Except for these two changes, the final flight followed the protocol of the experimental sessions. Because of logistical constraints, one *M. myotis* had to be released 2 days early. We conducted its final flight on night 17. Similarly, two *M. oxygnathus* had to be released after 9 experimental nights and two *M. oxygnathus* had to be released after 12 experimental nights. Their final flights were conducted on nights 13 and 16, respectively. None of these bats had shown any incentive to visit the lit boxes at time of release. Before releasing bats back into the wild, the collars were removed and the bats were carefully checked for any possible injury caused by them. We did not observe any injuries in any of the bats.

Control bats (four M. myotis*; six* M. oxygnathus*)*

In most respects, the procedure for the control bats followed the procedure for the noninteractive observers. Briefly, each bat was placed in the experimental cage (20 cm x 20 cm x 20 cm) hung from the ceiling in the middle of the room. Every 30 seconds, a rewarded and an unrewarded box were opened simultaneously. The light at the box containing mealworms was left on for 30 seconds. After 5 minutes all boxes were closed again and the bat was allowed to fly for 20 minutes in the flight room with only one rewarded, light-displaying box and one unrewarded, dark box open. On night 19, a final flight as for the observer bats was conducted for each control bat.

Recaptured bat (one **M. myotis***)*

One of the noninteractive observer bats (*M. myotis*) was recaptured almost exactly one year after the first experiment (final flight in the first year was on 12 July 2011; first flight in the next year was on 9 July 2012). This individual had been ringed several years before the first year of this experiment and could therefore be identified. We conducted 14 experimental sessions with this recaptured individual. We started the experiment without any additional pretraining and without reinforcement by a demonstrating bat. The procedure was the same as it had been the year before. Two boxes were opened at the same time, one containing mealworms and displaying a light and one containing rubber dummies with the light switched off. Each of the 10 rewarded boxes contained four mealworms. On night 15, we conducted a final flight as for demonstrators.

Analysis

All calculations and statistics were conducted using R version 2.15.2 (R Development Core Team 2012). To analyze changes in performance and number of landings over time, we ran generalized linear mixed models using the glmer function of the lme4 package (Bates et al. 2012) (individual nested in days as random factor, family = Poisson or binomial where appropriate). We report p-values derived from log-likelihood ratio tests of the minimal adequate model and a model that differs from the minimal adequate model in not containing the fixed effect in question.

For the learning curves, we excluded sessions in which a bat did not land on any box. For modeling, we log-transformed the x-values (days) to account for asymmetry of the fitted curve. For fitting the learning curves, we transformed performance values below 5% (theoretical chance level) to 0; thus, y-values could range between 0.05 and 1 in the model. We back-transformed performance values for data visualization. P-values for multiple comparisons of number of landings during the first 5 days are Holm corrected.

Capture, experimentation, and care of bats while in captivity was carried out under license of the responsible Bulgarian authorities (MOEWSofia and RIOSV-Ruse, permit Nos. 193/01.04.2009, 205/29.05.2009, and 465/29.06.2012) and in accordance with the species-specific recommendations of the Canadian Council on Animal Care on bats (Canadian Council On Animal Care 2003).

Results

Once the demonstrators were being trained in the larger flight room on 20 boxes, 10 of which contained two mealworms, with two boxes (one rewarded and one unrewarded) opening at the same time, it took them 1-2.5 weeks to show a consistently high performance of > 95% correct landings. The three demonstrators used in our social learning experiments showed this high performance throughout. Since demonstrators did not differ in their performance, all else being equal, all observers presumably had an equal chance to learn the tasks from their respective demonstrators. During their final flights when all boxes were open but only one box displayed the light cue at any given moment in time, all demonstrators achieved a 100% performance, i.e., the bats were attending to the light cue only when making their decision which box to land on. When flying together with the interactive observers, we saw a variety of interactions between demonstrator and observer, ranging from observers following the demonstrator to demonstrators chasing the observer, demonstrators attacking the observer, and demonstrator and observer hanging side-by-side in nonaggressive contact.

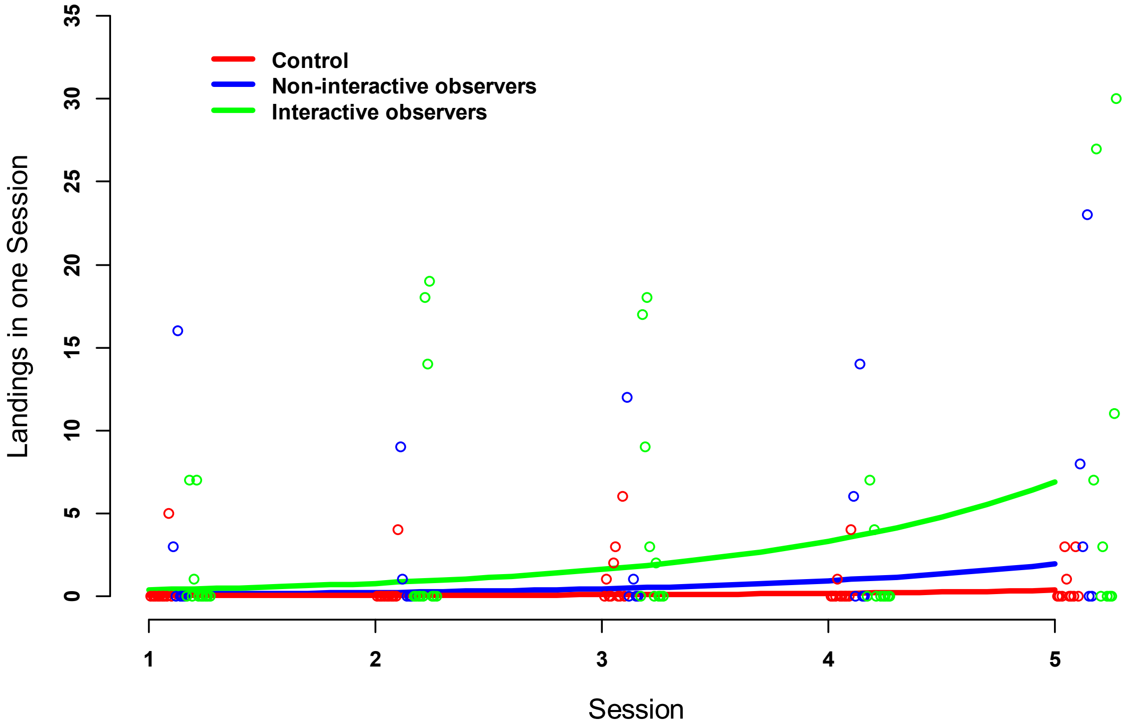

Figure 2.3 Total number of visits to boxes while flying 20 minutes alone are shown for all tested individual greater mouse-eared bats (*Myotis myotis*) and lesser mouse-eared bats (*Myotis oxygnathus*). *Color indicates groups. Open circles are single data points, whereas lines show curves derived from a generalized linear mixed effects model (minimal adequate model contains day and group as fixed effect and individual nested in day as random effect). There was a significant effect of group on the number of landings during the first five experimental sessions ($\chi^2_{[2]} = 7.06$, p = 0.029). Multiple comparisons with Holm correction showed that interactive observers landed significantly more often than control animals ($\chi^2_{[1]} = 7.05$, p = 0.024). Even though noninteractive observers neither differed significantly from control bats ($\chi^2_{[1]} = 2.83$, p = 0.185) nor differed significantly from interactive observers ($\chi^2_{[1]} = 0.81$, p = 0.367), the data suggest an upward trend, that is that their behavior resembled that of the other observer group more closely than that of the control group.*

Within each experimental group, some individuals visited the boxes during the first few sessions (4 out of 6 noninteractive *M. myotis*, 6 out of 6 interactive *M. myotis*, 5 out of 6 interactive *M. oxygnathus*, and 8 out of 10 control animals), although most of those visits were on unrewarded boxes and therefore did not lead to the bats finding mealworms. When an animal encountered rubber dummies in an open unrewarded box for the first time, it typically chewed them briefly before spitting them out again. After several encounters, rubber dummies were usually ignored. Figure 2.3 depicts the number of visits on boxes (whether open or closed; within the closed ones, whether containing mealworms or rubber dummies) during the first five experimental sessions by all experimental and control individuals. We suppose that once an animal successfully found a mealworm, its motivation to go on searching changed (i.e., increased immediately and rapidly). Therefore, animals that actually found mealworms only occur in the figure for those sessions before they found their first mealworm. Figure 2.3 also shows a comparison between the groups (noninteractive observers, interactive observers, and control bats). During these first five sessions, noninteractive and interactive observers visited the boxes more often than control animals. After experiencing only unrewarded visits, most of the bats stopped visiting the boxes after 2-3 days.

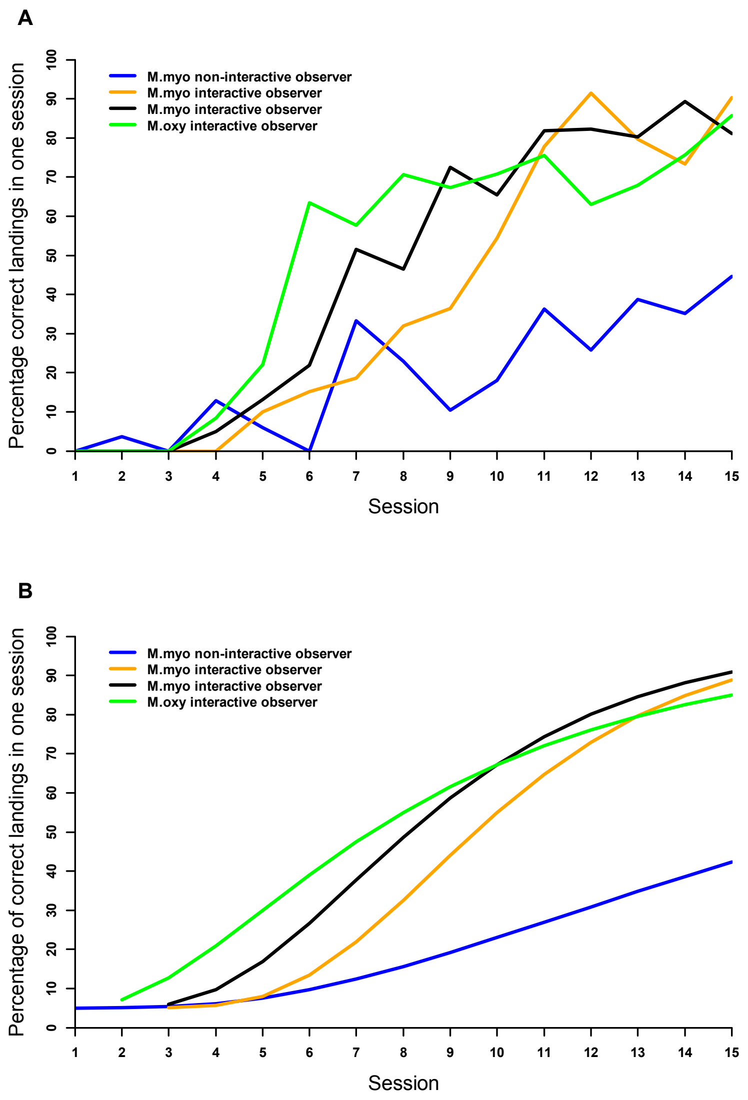

Figure 2.4 Percentage of correct landings while flying 20 minutes alone shown for the four individuals that increased their performance over time. *Three interactive students (two greater mouse-eared bats (*Myotis myotis*) and one lesser mouse-eared bat (*Myotis oxygnathus*)) reached a performance of about 90%. One noninteractive* M. myotis *learned the task up to about 50% correct landings and exhibited a shallower learning curve.* (a) Raw data. (b) Data from a generalized linear mixed effects model. *The two groups (noninteractive observer vs. interactive observer) differ significantly in their learning performance (minimal adequate model contains day and group as fixed effect and individual nested in day as random effect;* $\chi^2_{[1]} = 14.87, p < 0.001$*).*

None of the bats in the control group ever landed successfully at a lit box. Only four individuals (one noninteractive *M. myotis*, two interactive *M. myotis*, and one interactive *M. oxygnathus*) continued landing on the boxes after the first couple of days and increased their performance over time (fig. 2.4). It was these bats that had found mealworms during the first few sessions. Occasionally, other observer bats would visit lit boxes over the course of the experiment (in total 4 out of 6 noninteractive *M. myotis*, 2 out of 6 interactive *M. myotis*, and 2 out of 6 interactive *M. oxygnathus*). However, none of these individuals improved performance over time.

The total number of animals that visited lit boxes differed between control and observer bats (Fisher's exact test, p = 0.025). The total number of animals that improved their performance over time did not differ significantly between control (0 of 10 bats) and observer bats (4 of 18 bats) (Fisher's exact test: p = 0.265).

After 15 sessions of experimental trials, the total number of visits on boxes by the four individuals that improved their performance over time had leveled off at about 60-80 visits per session. The noninteractive observing *M. myotis* reached a performance of almost 50% (theoretical chance level: 5%); the three other individuals (two *M. myotis* interactive observers and one *M. oxygnathus* interactive observer) learned the task up to around 90% correct landings (fig. 2.4a). The learning curves of the three interactive bats of both species were significantly different from the learning curve of the noninteractive observer ($\chi^2_{[1]} = 14.87$, $p < 0.001$); hence, the interactive observers exhibited faster learning rates than the noninteractive observer (fig. 2.4b).

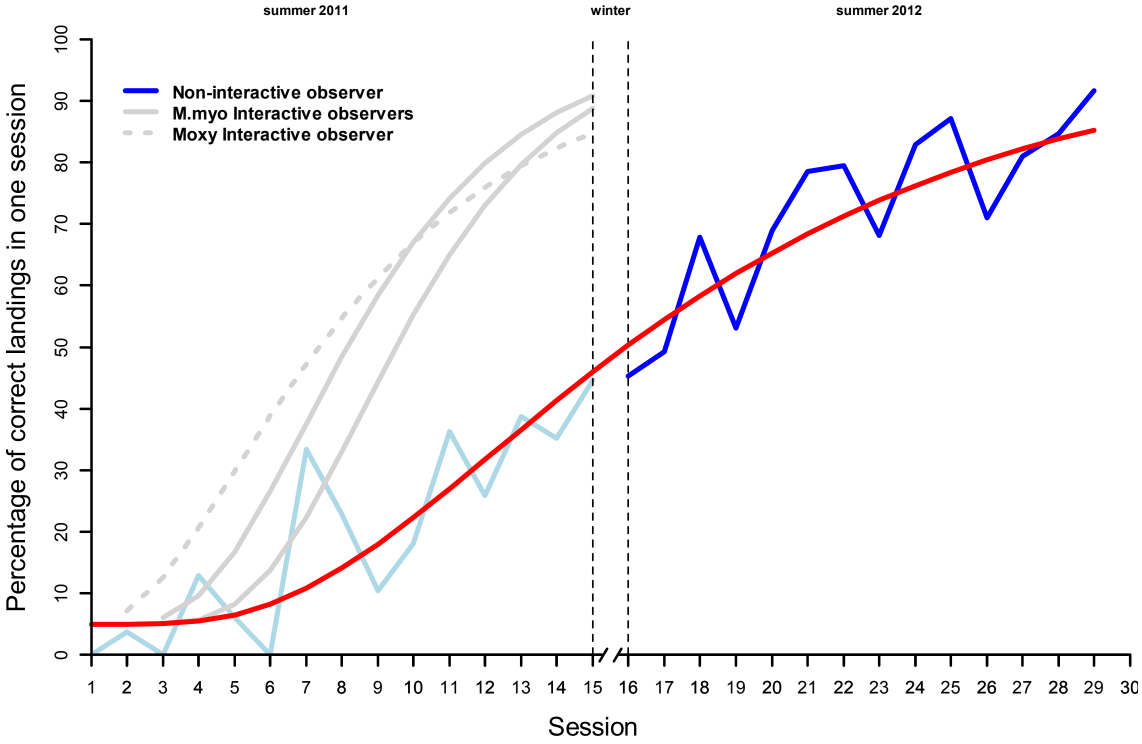

Figure 2.5 Percentage of correct landings per session while flying alone shown for the recaptured noninteractive observer (greater mouse-eared bat, *Myotis myotis*). *The learning performance of this individual continued to increase after recapture in the following summer. Shown are raw data from both years and a curve derived from a generalized linear mixed effects model including data for both years. For comparison, the learning curves of the three interactive observers that learned the task in the first year are also shown.*

The noninteractive observer that had improved its performance over time was recaptured 12 months after its release. Its initial performance after the year-long break was at the same level (45%) as its ending performance the year before (44%), and its performance increased continuously over the course of the 14 experimental sessions conducted during its second year until it also reached a performance of about 90%. The learning curve was a smooth continuation of the one it showed the year before (fig. 2.5). However, when performing a final flight as for the demonstrating bats at the end of the experimental period in the second year, the recaptured individual's performance dropped drastically from 91% to 62%.

Discussion

Although our sample sizes are small, our results suggest that social learning about food-associated cues occurs in mouse-eared bats and is positively influenced by direct interaction between demonstrator and observer. Our results also suggest that social learning may occur between bat species. We also found long-term memory retention of a novel task over a 1-year period including hibernation in a single, wild-caught *M. myotis*. Although the total number of animals that improved their performance over time did not differ between control and observer bats, we are convinced that the lack of statistically significant difference in performance across groups is due to our restricted sample size. If we had tested a larger number of bats and had maintained the same proportion of individuals that solved the task in each group, we would have seen a more prominent difference between observer and control groups. We believe that the difficulty of the task of associating an artificial cue with a food reward together with the fact that significantly more bats in the observer groups visited lit (rewarded) boxes at least once during the course of the experiment when compared with the control group supports this conviction.

We note that unambiguous species identification in mouse-eared bats can be difficult because of a tremendous overlap in all reliable measurements, as well as conflicting measurement information, in the literature. Additionally, hybridization between species might occur (Berthier et al. 2006), especially in southeastern Europe (Bachanek & Postawa 2010). Therefore, when possible, we used only individuals that did not fall into an overlap zone, as identified by measures of forearm length and CM^3. The possibility still exists that some *M. oxygnathus* from the control group were misclassified and actually were small *M. myotis* or hybrids. However, all *M. oxygnathus* in the experimental group (including the individual that increased its performance over time) could be clearly identified by morphological measurements and a white spot on the forehead. Similarly, all *M. myotis* were unambiguously identified.

None of the experimentally naïve bats in the control group learned the new task (light-food association); thus, we cannot compare trial-and-error learning (i.e., individual associative learning) alone to learning in either the noninteractive or interactive observers. Also, the learning curves of the demonstrators cannot serve as a template for trial-and-error learning, as the demonstrators were trained using a markedly different protocol than the one used for experimental and control animals. Similarly, the only individual from the noninteractive observer group (*M. myotis* only) that improved its performance over time showed a significantly shallower learning curve and did not reach as high a performance level during the experiment as did the interactive observers from both species. However, the total number of landings for each of the four individuals that improved performance over time (one noninteractive *M. myotis*, two interactive *M. myotis*, and one interactive *M. oxygnathus*) leveled off at about 60-80 landings by the end of their 15-session experimental period. This observation suggests that all four individuals were similarly motivated. Thus, the noninteractive bat did not show a poorer performance due to a lack of motivation, but most likely because it had not learned as much from its noninteracting demonstrator as had the interactive observers. In our experiment, only 1 out of 20 boxes was rewarded at any given time and theoretical chance level was therefore 5%. Our results thus suggest that in mouse-eared bats, effective social learning of a novel foraging task is improved by direct interaction between observer and demonstrator (see fig. 2.4), although we can only compare a learning curve from one noninteractive observer with learning curves from three interactive observers.

Other than in the control group, in the interactive and noninteractive observer groups, the total number of visits on boxes showed an upward trend over the first days of the experiment (fig. 2.3). This suggests that even though the noninteractive observers did not learn as much from their demonstrators as did the interactive observers, their attention was drawn towards the boxes. A potential, although speculative, explanation for the difference between the two groups could be that interactive observers could visit boxes while flying with the demonstrators. While the demonstrator was still in the room, the observers might have visited several unrewarded boxes but continuously received the information that the demonstrator was still finding food. Therefore, they would also continue searching despite several failures after the demonstrator had left the room knowing the situation of not finding food while there was still food available. The noninteractive observers could only experience unrewarded visits on boxes when they were alone in the room. After several unrewarded visits, it might have seemed to them as if the demonstrator had depleted the food source and they would have stopped searching faster than did the interactive observers.

A year after the initial experiments, we recaptured the single noninteractive observer (*M. myotis*) that had learned the task to an almost 50% performance level. Without any additional pretraining, this individual immediately showed the same performance as the year before upon reintroduction to experimental conditions, but this time without a demonstrator. The two summers in which the experiments with this individual took place were separated by winter, during which the bat was almost certainly hibernating in the wild. The longevity of species within the bat family Vespertilionidae averages 14.9 years (Barclay & Harder 2003), with a record of 41 years for Brandt's bat (*Myotis brandtii* (Eversmann, 1845)) (Podlutsky et al. 2005), a congener of *M. myotis* and *M. oxygnathus*, and a reported age record for *M. myotis* of 37 years in the wild (Gaisler et al. 2003). In long-lived animals like bats, long-term memory retention is thought to be of major importance to relocate roosts and feeding sites. However, it has been shown that the drop in core body temperature during hibernation alters the neurochemistry of the brain and can lead to synaptic degradation in shorter lived rodents (summarized in Ruczynski & Siemers 2011). This is in contrast to sleep, which is thought to consolidate long-term memory (Rasch & Born 2013). The individual recaptured in our study gave us the rare opportunity to observe long-term memory retention (12 months) over a period of hibernation (> 4 months in *M. myotis*; Meschede & Rudolph 2004, p. 215) in a wild bat. Similar results were obtained by Ruczynski and Siemers (2011) in a controlled indoor experiment over a shorter period of hibernation (10 weeks) before retesting. To our knowledge, ours is the first study to document long-term memory of an associative and socially acquired task over a period of hibernation in a wild bat. Even though results from only one individual might seem anecdotal, we feel that this is an interesting finding, highlighting the importance of further study of the mechanisms of memory retention in bats over hibernation.

Although the well-trained demonstrator bats performed at 100% during their final flight with all boxes open and only one box displaying light at a time, the recaptured individual showed a drastic drop in performance during its final flight in the second experimental year. This suggests that although the bat had learned this foraging task to a high level of performance, it was still sampling its surroundings for other potential food sources. Once rewarded at an unlit box, it fell back to sample the boxes more randomly. This supports the hypothesis that *M. myotis* is a behaviorally flexible species (Clarin et al. 2013).

When the final flight was more similar to the general experimental procedure and differed from it only in that there was no reinforcement by a demonstrating bat (as was the case for all observers during the first year of experimentation), the performance in the final flights was a continuation of the performance shown before (fig. 2.4, day 15). This supports our conclusion that the observers had learned the task from their demonstrators well enough to perform it even without observing an experienced demonstrator directly prior to the experiment.

We are confident that the bats that did learn to associate the rewarded boxes with food were attending to the LED light and not to other cues through other sensory modalities. We controlled for visual and echo-acoustic cues by the use of rubber dummies in the unrewarded boxes. *Myotis myotis* and *M. oxygnathus* are highly attuned to prey-emitted acoustic cues when foraging, such as prey rustling sounds (Arlettaz et al. 2001). However, we found no evidence to suggest that the movement of the mealworms against the smooth surfaces of the boxes provided sufficient acoustic information to elicit the bat's attention. It is also unlikely that bats used olfactory cues to find the prey. To our knowledge, olfaction can only play a role in foraging behavior at distances less than 20 cm in our two species (Bloss 1999). Additionally, had the bats used potential acoustic or olfactory cues produced by the mealworms, we would have expected that observer bats would preferably visit boxes which contained mealworms; consequently, more bats would have learned the light-food association. Most convincingly, not a single control bat found the mealworm reward in the open lit box. All demonstrator bats, on the other hand, only visited the lit rewarded boxes during their final flights and never visited an unlit but still rewarded box. Although olfactory and acoustic cues could have been controlled for even more effectively, taken together, these results provide strong evidence that the bats that improved their performance over time were attending to the light cues offered by the LED alone.

In total only 3 out of 12 individuals (25%) in the interactive observer group learned the task up to a level of 90% correct landings within a session. Thus, our study offers only preliminary evidence of the importance of social learning about food in our two bat species. Our experimental design did not closely mirror the natural foraging situation of our experimental species. Both mouse-eared bats feed on arthropods (such as carabids or crickets) that do not always occur in large numbers at exactly the same spot, as was the case with prey in our boxes. Landing at the same spot where a conspecific or heterospecific was observed feeding before will therefore not necessarily lead to finding a prey item in a natural setting. However, such arthropods do not just passively produce acoustic cues like rustling noises; they also produce other sensory cues that bats can use to find prey items. Male field crickets (*Gryllus campestris* (L., 1758)), for instance, inhabit burrows with a very specific shape and a vegetation-free arena in front of it where they attract females for mating. Frequently, so called satellite males are found in close vicinity (Ritz & Köhler 2007). The specific shape and setting of these burrows could be learned by bats and could subsequently serve as a cue predicting prey occurrence for bats feeding on crickets. Additionally, crickets actively produce sound to attract mates. Like the light cue in our experiment, such acoustic cues can be used by bats to localize prey items. Therefore, our study reflects a situation in which specific sensory cues or landscape and vegetation features predict prey occurrence. Some insects capable of hearing bat echolocation calls have developed defensive strategies to escape attacking bats (Fullard et al. 2005). Both our study species reduce their echolocation to whispering calls shortly before landing to catch a prey item, possibly to circumvent these defensive strategies (Russo et al. 2007). We therefore cannot rule out that in natural situations where finding food does not depend on an artificial, aversive – or at least nonattractive – cue, social learning may take place much more readily and frequently.

Social learning has been demonstrated in other bat species in a variety of ecological contexts. There is evidence that social interactions influence roost and habitat selection (e.g., Wilkinson 1992; Kerth & Reckardt 2003). Female Bechstein's bats and greater horseshoe bats (*Rhinolophus ferrumequinum* (Schreber, 1774)) inherit their foraging areas from their mothers (Kerth et al. 2001; Rossiter et al. 2002). Wright et al. (2011) found that the acquisition of a novel foraging task (catching a tethered mealworm) in the big brown bat (*Eptesicus fuscus* (Palisot de Beauvois, 1796)) is strongly enhanced by interaction with an experienced conspecific compared with individual trial-and-error learning. In evening bats (*Nycticeius humeralis* (Rafinesque, 1818)), naïve individuals follow experienced conspecifics to new food resources from the roost (Wilkinson 1992). Social learning could stimulate coordinated foraging, as may be the case in the Pallas's mastiff bat (*Molussus molossus* (Pallas, 1766)) (Dechmann et al. 2010).

Conclusions

Overall, our data from the control groups (two species), the noninteractive observer group (one species), the interactive observer groups (two species), and the 1-year retention of memory in a noninteractive observer, taken together with the difficulty the demonstrators had making the novel associative task, suggest the following. First, social enhancement (the drawing of attention towards a novel object or place by a demonstrating individual; Heyes 1994), is sufficient to motivate some naïve bats to inspect a novel food source more often than they would in the absence of a demonstrator. Second, bats that can observe but not directly interact with a demonstrator learn less about this experimental association between light and food initially than do interacting observers and this deficit is reflected even as time goes on. Third, transmission of information about a relatively difficult task can occur between individuals of congeneric species at about the same rate as within species (1 out of 6 versus 2 out of 6). Last, the retention of memory from one season to the next and the further improvement in performance without additional reinforcement by a demonstrator suggests that socially acquired knowledge is retained, and that after learning is initiated socially, the association can be refined through trial-and-error learning without further social interaction.

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CHAPTER 3

Do bats experience a trade-off between energy conservation and learning?

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Abstract

Some species of bats, rodents, and birds are able to save energy during the summer period by decreasing their body temperature and falling into torpor. Several studies indicate that torpor prevents animals from sleeping and causes effects similar to sleep deprivation. Impairment of processes stabilizing memory slows down learning accuracy and speed. We conducted two experiments to test whether greater mouse-eared bats, *Myotis myotis*, which commonly use torpor during the summer period, experience a trade-off between energy savings and learning abilities. We compared learning speed and accuracy in bats which were exposed to low (7°C) and higher ambient temperatures (22°C) between training and experimental sessions. Tests were conducted in experiments with food reward (food search) and without food reward (perch search). Time spent with skin temperature above 30°C was significantly longer for bats exposed to 22°C than 7°C and longer in experiments with food reward than without food reward. We observed only a very weak tendency for better accuracy and shorter search times in bats exposed to 22°C than in those exposed to 7°C. Our data indicate that memory consolidation of bats under natural conditions may not be adversely affected by daily torpor when bats are in good condition. We suggest that homeostatic processes connected with the circadian rhythm allow protecting the consolidation of memory for relatively simple tasks despite time spent in torpor.

Long term memory is important for many animals in a variety of different contexts (Roth et al. 2010). Good memory allows for quick and effective rediscovery of food resources and hiding places, the identification of conspecifics, and a variety of other adaptive acts (Stoddard et al. 1991; Shettleworth 2001). Storage of accurate memories is an active and costly process involving maintenance and repair of neural structures (Dukas 1999). Therefore animals may experience conflicts between the benefits and costs of memory retention (Roth & Pravosudov 2009; Chancellor et al. 2011). For example, food-caching birds living in harsh climates have developed a larger hippocampus volume than those from milder areas, which may result in enhanced spatial memory and improved survival. A memory is normally formed after repeated learning events (Smid et al. 2007) and sleep enhances this process (Palchykova et al. 2002; Roth et al. 2010). Sleep deprivation has negative effects on both memory consolidation and retention (Graves et al. 2003; Guan et al. 2004).

Recently, an interesting conflict between energy conservation and sleep was discovered in hibernating and torpor using mammals (for review, see Roth et al. 2010). Such mammals are able to decrease their body temperature to save energy during periods of food deficiency (Geiser 2008). Although torpor and sleep are characterized by short or prolonged inactivity, torpor and sleep are very different physiological states (Roth et al. 2010). Both REM sleep (Rapid Eye Movement sleep) and SWS (Slow Wave Sleep) are reduced during torpor and hibernation (e.g., Trachsel et al. 1991; Deboer & Tobler 1996, 2000, 2003; Millesi et al. 2001). Animals emerging from these states spend most of their time in sleep with brain activity typical for sleep-deprived animals (Palchykova et al. 2002). This suggests that torpid and hibernating animals experience sleep deficiency (Palchykova et al. 2002; von der Ohe et al. 2007), which might lead to deficiencies in memory consolidation and retention.

The influence of torpor on memory retention and consolidation has only been investigated in a handful of studies, primarily in rodents but also, in one recent study, in bats (Millesi et al. 2001; Palchykova et al. 2006; Clemens et al. 2009; Ruczynski & Siemers 2011). These studies tested the impact of hibernation on long-term memory and taken together provide conflicting results. The results of Millesi et al. (2001) provide evidence of memory loss. Specifically, spatial memory and memory of operant tasks were negatively affected by hibernation in European ground squirrels, *Spermophilus citellus* (Millesi et al. 2001). Social memory, in contrast to spatial memory, showed little to no impairment in European ground squirrels or in Belgin's ground squirrels, *Spermophilus beldingi* (Mateo & Johnston 2000; Millesi et al. 2001). In animals that live long and in complex environments, such as marmots and bats, memory was not affected by hibernation at all (Clemens et al. 2009; Ruczynski & Siemers 2011). Ruczynski and Siemers (2011) postulated that the ability to protect long-term memory through hibernation depends on memory type and life history of the respective animals. They further suggested that long-lived animals and those living in complex environments have better protected memory than those species which live relatively short lives and/or inhabit simple environments.

Most of these previous studies addressed memory retention over long-term hibernation. Here, we address a different question. Is the consolidation (shift from short- to long-term memory) of newly acquired memory impaired by low body temperature? When an animal moves into a hibernaculum, its memory is likely already consolidated. However, animals that employ short-term torpor on a daily basis may well experience a trade-off between energy savings and memory consolidation, because the latter is expected to require a warm, active brain. The process of memory consolidation invokes establishing new synapses and up- or down-regulation of existing synapses. These complex cellular processes will require normothermic conditions for the biochemical machinery to work (Palchykova et al. 2006). Furthermore, torpid animals may not be able to sleep in a neurophysiologial sense, or may only be able to sleep at a reduced level. As outlined above, this torpor-induced sleep deprivation should counteract memory consolidation. Experiments on Djungarian hamsters, *Phodopus sungorus*, indeed indicate that torpor has a negative influence on memory consolidation and may impair object recognition (Palchykova et al. 2006). In the poikilothermic snail *Lymnaea stagnalis*, the process of memory consolidation was also impaired by quick exposure to low temperatures (Sugai et al. 2007). These results indicate that the effect of decreasing brain temperature after training could be more pronounced on memory consolidation than on memory retention. Bats are a very interesting group of mammals in this respect. Temperate bats, in particular, decrease energetic costs by falling into torpor on a daily basis even during the summer period (Grinevitch et al. 1995; Turbill et al. 2003). Bats, however, are also very long-lived animals. Species of the genus *Myotis* live on average 14.9 years (Barclay & Harder 2003) and the reported age record for *M. myotis* in the wild is 37 years (Gaisler et al. 2003). Learning, therefore, most likely is crucially important in the behavioral ecology of bats (Gaudet & Fenton 1984; Page & Ryan 2005; Ruczyński & Bartoń 2012). As a result, bats could be especially affected by a trade-off between memory consolidation and energy savings using torpor.

To test if memory consolidation in bats is affected by the decrease in body temperature during daily torpor, we conducted two experiments. The first required the bats to learn the location of food and the second for the bats to learn the location of a perch. We tested whether learning performance depends on the duration of time during which bats stay at high body temperatures after training. We hypothesized that animals which are able to stay longer at high body temperatures after training would have a greater chance to consolidate memory and could learn faster than those animals that decrease their body temperatures faster, deeper, and for a longer period of time after training.

Materials and Methods

Animals and Housing Condition

For experiments we used male and post-lactating female greater mouse-eared bats (*Myotis myotis*, family Vespertilionidae). All animals were captured between 19 June and 15 August 2010 near Ruse in Bulgaria under license from the responsible authorities (MOEWSofia and RIOSV-Ruse, permit Nos. 193/01.04.2009 and 205/29.05.2009). The bats were kept for behavioral experiments at the Tabachka Bat Research Station (Bulgaria) of the Sensory Ecology Group (Max Planck Institute for Ornithology, Seewiesen, Germany), which is run in cooperation with the directorate of the Rusenski Lom Nature Park in the district of Ruse. Before starting experiments the animals were housed in small groups in cages (50 cm length x 35 cm width x 40 cm height) under the natural local light regime. Each bat was fed 4 g of mealworms daily (larvae of *Tenebrio molitor*). Animals in the “food search” experiment received their food during training and experimental sessions as reward. Animals in the "perch search" experiment received their food after the retention test (see below). All animals had access to water *ad libitum* in their cages. Additionally, bats received water after training in the "perch search" experiment.

Training and testing in "food search" experiment

Bats (16 adult males) were initially fed by hand and then trained to eat mealworms from small bowls for 2-3 nights after catching. Each day, bats were weighed before and after feeding and training. This allowed us to control for the motivation of the bats throughout the experiment. The training and testing maze consisted of four plastic boxes (20 cm x 13.5 cm x 10 cm), one of which was the starting box, while the other three were potential feeding boxes. The boxes were connected to a large central box (24 cm x 16.5 cm x 12.5 cm) by transparent tubes (25 cm long, internal diameter 7 cm); this diameter was sufficiently large to allow the bats to crawl and turn easily (for more details see Clarin et al. 2013).

Once the bats arrived in the central box, they had to decide which of three tubes to enter (left, right, or straight ahead). Each feeding box contained 10 g of live mealworms so that any prey-related sensory cues – smell, rustling sounds, etc. – emanating from the three feeding boxes were the same. We trained each bat to feed in only one of the boxes. To speed up training and decrease stress for the animals, we increased the difficulty of the task over three days (Day 1-3 below) and measured learning effects over the next three days (Day 4-6 below). Training and experiments were conducted during the natural activity hours of the bats (one hour after sunset until one hour before sunrise).

Day 1: Bats were placed in the starting box and subsequently allowed to explore the maze and all of its boxes for 15 minutes. In each box there were three mealworms so the bats were motivated to visit different boxes.

Day 2: Again, the bats were placed into the starting box and could crawl to the centre box. Here, only one arm was opened ("correct") while the two other arms were closed by slides ("wrong"). Each terminal box (three boxes) was baited with around 10 g of mealworms. When a bat went into the correct terminal box, it could eat mealworms. This procedure was repeated ten times. During the first four trials the bats received 4 mealworms per trial and 2 mealworms in the remaining six trials. If a bat turned back, stopped for a longer period of time (ca. 3 minutes), or successfully found and ate mealworms, it was removed from the maze for 1-3 minutes before the next trial started. The bats did not receive additional food after training.

Day 3: The procedure from day 2 was repeated. However, bats received 4 mealworms during the first three trials and 2 in the remaining seven trials. During the last (10th) trial the bats received additional mealworms, but all together not more than 40-45 mealworms during one training session, corresponding to ca. 4 g of mealworms. All mealworms were consumed in the maze. The number of mealworms eaten by each bat was noted after each trial.

Days 4, 5, and 6: All maze arms were opened. If a bat chose a wrong arm, closing the arm with a slide before the bat entered the terminal box prevented it from going further. After an unsuccessful trial the bat was removed and after a short break (1-3 minutes), the next trial started. During the last (10th) trial the bats received additional mealworms in the maze when necessary.

The bats were assigned to either the group kept at 7°C (±0.1°C) (8 bats) or at 22°C (8 bats). The temperature in caves used by *M. myotis* is around 15°C during the summer period (B.-Markus Clarin, pers. com.). We chose lower and higher temperatures for keeping the bats in order to differentiate between those conditions that could affect the duration of daily torpor. Half of the bats were trained to find food in the left terminal box and the other half to find food in the right terminal box (balanced within group). After each training or experimental session, the maze was cleaned with water and detergent to remove possible odor cues. Within a session with an individual bat, the different maze arms were interchanged to remove the possibility that a bat would simply follow its own scent cues.

After training and experiments, bats were placed in plastic boxes (1.3 l) (separate for each individual, numerous holes ensuring air exchange between the box and ambient air) and 30 minutes after training, they were transported to climate chambers (KB53, Binder, Möhringen-Tuttlingen, Germany). Bats spent around 22 hours per day in the climate chambers. The animals were removed from the climate chambers 1 hour before experiments and transported to the experimental room. During this hour the bats increased their body temperature to similar levels in the control (kept in 22°C) and experimental groups (kept in 7°C).

Air exchange between boxes and ambient air was fan assisted. Water was accessible in the boxes *ad libitum*. All experiments were filmed with a CCD camera (Watec, WAT-902H2 Ultimate) and recorded on miniDV tapes (Sony® DCR-TRV80E recorder). By a person blind to the experimental condition of the bats (experimental group or control group), the time that each bat took to complete each trial (i.e., time elapsed from leaving the start box to entering the correct feeding box) was scored off-line.

Training and testing in "perch search" experiment

For this second experiment, eighteen post-lactating females were caught early in the morning when returning from foraging. Training started the night after catching. Until the training started, bats had *ad libitum* access to water. Animals were not fed until the end of the retention test (see below). Naive bats were placed in the experimental setup at the starting point. The bottom of the arena was covered by 0.5 cm deep water. Behind a plastic wall, a dry perch was hidden. The perch was only accessible by crawling around the plastic wall either on the right side or on the left side. On the other side access to the dry perch was blocked by another plastic wall. If a bat made a wrong decision and crawled around the wall on the wrong side, it was not taken out of the arena, but allowed to turn around and further explore the arena. To analyze the number of correct decisions, we scored only the first choice an animal made when put into the arena. When analyzing the searching time, we counted the full time an animal needed to find the dry perch. Bats had three minutes to find the dry perch (fig. 3.1). If the bat did not find the dry shelter it was removed from the maze and dried for around one

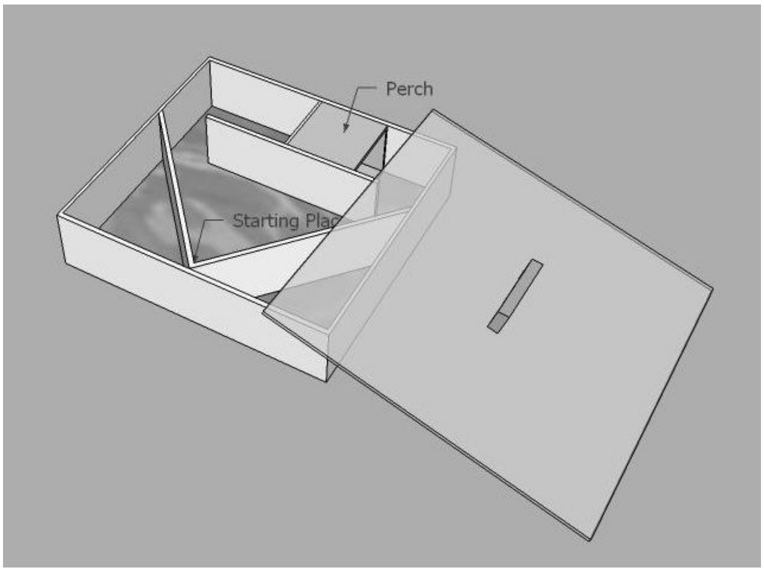

Figure 3.1 Experimental setup used in the perch search experiment. *Here, the dry perch is only accessible from the right side.*

minute in soft paper. When a bat found the perch it was allowed to stay there for three minutes.

Afterwards the bat was removed and a new trial started. Every bat had 3 trials within a training session (one night). Bats were dried after training in soft paper and transported to climate chambers 15 minutes after finishing the last trial. As in the food search experiment, bats were divided in two groups; one was kept at 7°C while the second one was kept at 22°C. In each group, 5 bats had to crawl around the plastic wall on the right side and 4 bats had to crawl on the left side to reach the dry perch. Bats stayed in the climate chambers for 22.5-23 hours. For the retention test bats were removed from the climate chambers one hour before the experiment and kept in small boxes in the training room (temperature between 22-25°C). Bats were weighed 10-15 minutes before the test and were checked to see if they were cold or warm to prevent starting experiments with bats still in torpor. The retention test was conducted in the same way as the training. Bats were fed after the last trial.

Measurement of skin temperature

All bats were tagged with iButtons ETL1 (Dallas, TX, USA). The iButton mass was reduced to 1-1.3 g by removing the metal capsule and covering it with rubber shrink tube (Robert & Thompson 2003; van Marken Lichtenbelt et al. 2006). We used iButtons although they produce ultrasound which may potentially disturb bats (Willis et al. 2009), because all bats were exposed to the same acoustic stimulus and the climate chambers produced continues noise to which the bats habituated quickly. Loggers were glued to the skin in the interscapular region using skin adhesive (Hanfred SauerGmbH, Labboch, Germany) at least 24 hours before starting the “food search” experiment and at least 12 hours before the “perch search” experiment. Skin temperature was measured every 5 minutes. We compared the duration of time during which the bats had a skin temperature (T_{sk}) above 30°C, because higher brain temperature favors the possibility of sleeping and memory consolidation (Palchykova et al. 2002; Roth et al. 2010). We used differences in time spent with $T_{sk} > 30$°C as an indicator of possibilities for potential memory consolidation. For comparisons we used only the times during which the bats were in the climate chambers. iBottons were taken off after the experiments were finished and before the bats were released.

Statistical analysis

All statistical analyses were conducted in R Version 2.15.2 (R Development Core Team 2012). For computation of mixed effects models, we used the lme4 package (Bates et al. 2012). To compare duration spent with $T_{sk} > 30°C$ we ran a linear model containing both experiment type (food search vs. perch search) and treatment (7°C vs. 22°C) as fixed factors. From the perch search experiment, we only had one measurement per individual. For the food search experiment we had five measurements per individual. To achieve a more balanced data set, we analyzed mean duration with $T_{sk} > 30°C$ for each individual in the food search experiment. To compare the proportion of correct decisions during one session, we ran generalized linear mixed effects models for binomial data with day and treatment as fixed factors and individual as random factor. To analyze search times, we computed linear mixed effects models with day and treatment as fixed and individual as random factors. All data on time were log-transformed to achieve equal variances and a distribution close to the normal distribution. All p-values reported are derived from log-likelihood ratio tests of the minimal adequate model and a model that differs from the minimal adequate model in not containing the fixed effect in question.

Results

Skin temperature

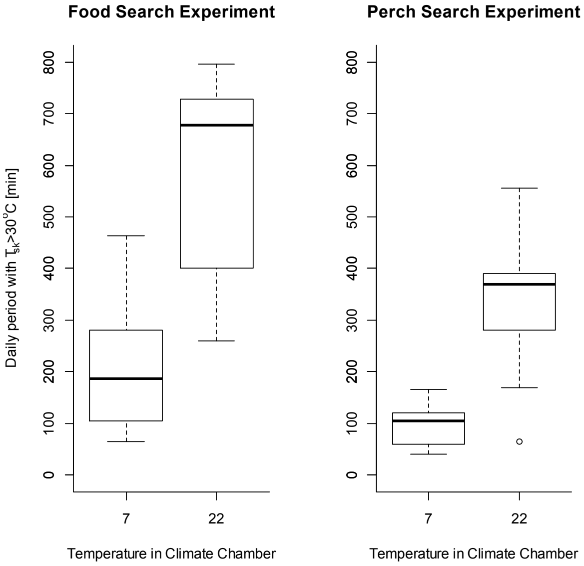

Figure 3.2 Time spent with Tsk > 30°C for both treatment groups in both experiments. *For animals in the food search experiment an average for each individual over the five days it spent in the climate chamber was used for the analysis.*

The duration of the daily period during which the bats maintained a skin temperature above 30°C ($T_{sk} > 30°C$) was significantly affected by experiment type ($F_{1;31} = 11.26$, $p = 0.002$) and temperature in climate chambers ($F_{1;31} = 37.05$, $p < 0.001$). Animals kept at 22°C between sessions spent more time with T_{sk} above 30°C than animals kept at 7°C (fig. 3.2). Bats in the perch search experiment spent less time with T_{sk} above 30°C than bats in the food search experiment (fig. 3.2). The mean duration from the end of the experimental trials to the moment when skin temperature dropped below 30°C for the first time was 148 minutes (± 101)/day in bats kept at 7°C and 520 minutes (± 216)/day in bats kept at 22°C in the food search experiment. In the perch search experiment the durations were 83 minutes (± 51)/day in bats kept at 7°C, and 257 minutes (± 155)/day in bats kept at 22°C.

Food search experiment

Neither treatment ($\chi^2_{[1]} = 1.12$; $p = 0.29$) nor training day ($\chi^2_{[1]} = 0.99$; $p = 0.32$) had an effect on how often the bats made a correct decision during the 2nd and 3rd day of training (fig. 3.3).

We did not observe differences in the proportion of correct choices made by bats kept at different temperatures during the 4th, 5th and 6th day (experimental sessions) (fig. 3.4). There was no difference between treatment groups ($\chi^2_{[1]} = 1.41$; $p = 0.23$) or days in experiment ($\chi^2_{[2]} = 3.39$; $p = 0.18$).

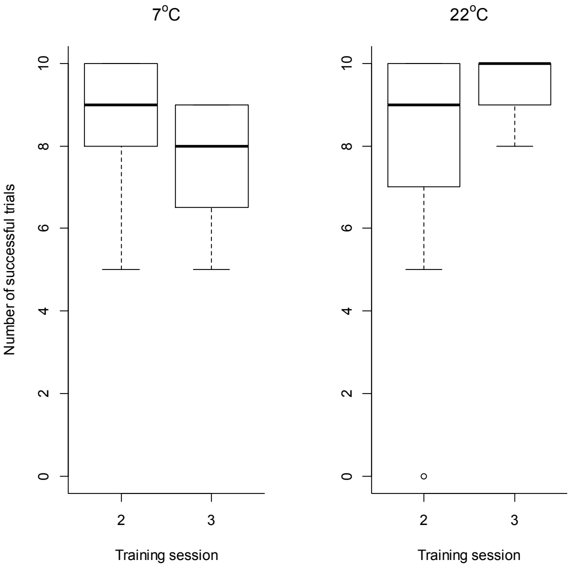

Figure 3.3 Number of successful trials during an early phase of training (day 2 and 3) in the food search experiment. *Only one arm of the maze was opened. Bats were exposed to 7°C or 22°C when placed in climate chambers.*

We also did not observe differences in search time between bats kept at 7°C and 22°C ($\chi^2_{[1]} = 0.34$; $p = 0.56$), as well as between days in experiment ($\chi^2_{[2]} = 3.13$; $p = 0.21$) (fig. 3.5). However, there was a slight trend for a decrease in search time over consecutive days in the group that was kept at 22°C between experimental sessions.

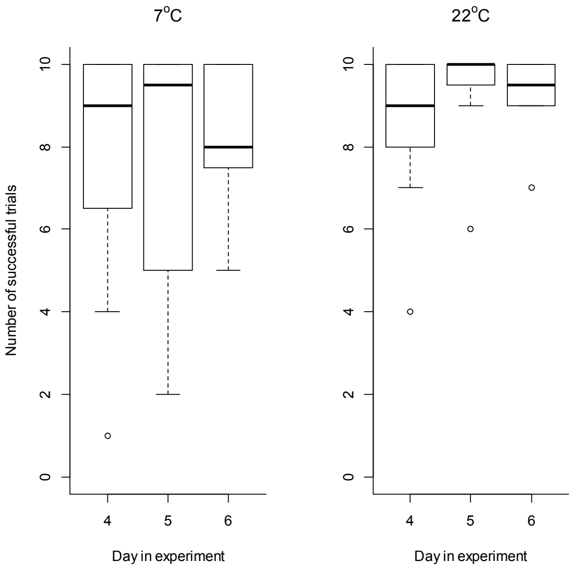

Figure 3.4 Number of successful trials during the 4th, 5th, and 6th day of the experiment with opened maze arms for bats exposed to 7°C or 22°C.

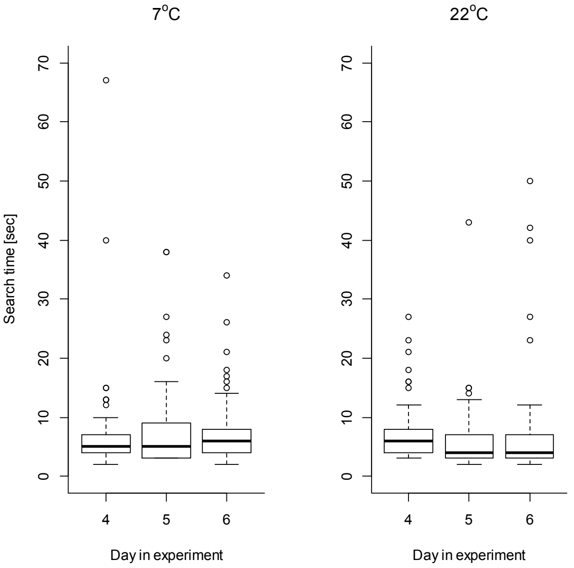

Figure 3.5 Time (in seconds) needed by the bats to successfully complete a trial in the food search experiment. *Between experiments bats were exposed to 7°C or 22°C.*

Perch search experiment

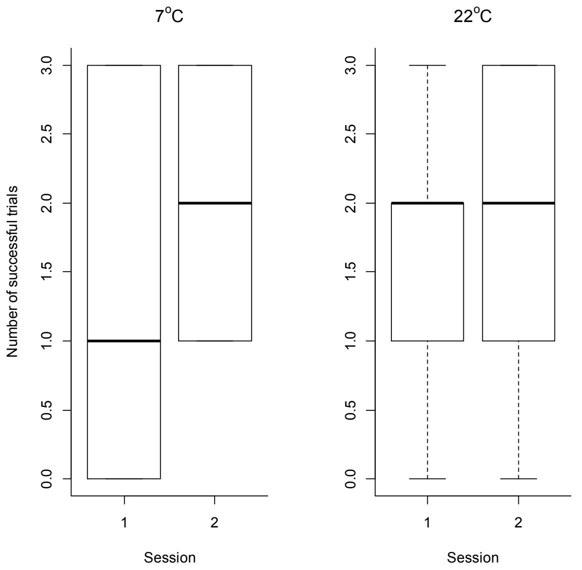

Figure 3.6 Number of successful trials on both experimental days in the perch search experiment. *Between experimental sessions, bats were kept at 7°C or 22°C.*

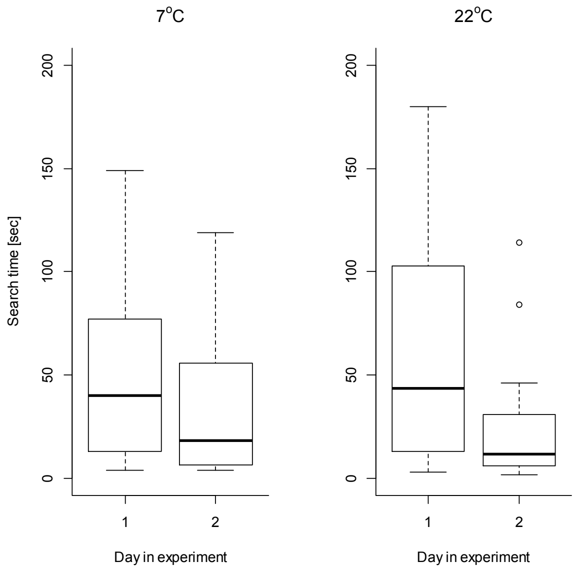

Figure 3.7 Time to find dry perch. *Between experimental days bats were exposed to 7°C or 22°C.*

We observed no difference in the proportion of correct choices made by bats kept at different temperatures in the perch search experiment ($\chi^2_{[1]} = 0.04$; $p = 0.84$). However, animals made more correct choices on the second day (retention test) than on the first day (training) ($\chi^2_{[1]} = 4.42$; $p = 0.035$) (fig. 3.6).

The time the animals needed to find the dry perch did not differ between treatment groups ($\chi^2_{[1]} = 0.37$; $p = 0.54$). However, on the second day animals found the dry perch faster ($\chi^2_{[1]} = 11.46$; $p < 0.001$) (fig. 3.7).

Discussion

Contrary to expectation, our study showed that daily exposure to lower temperature had no effect on the bats' learning abilities even though those bats spent less time with skin temperature above 30°C in comparison to bats kept at higher temperature. This suggests that for bats living under natural conditions daily torpor would have no significant cognitive consequence with respect to relatively simple tasks.

Although the role of sleep is not fully understood, it is known that sleep plays an important role in consolidation and reconsolidation of memory (Stickgold 2005) while torpor is a process that allows energy conservation compared to resting (Geiser 2004). The two states of sleep and torpor are mutually exclusive. When animals decrease their body temperature, the possibility of sleep is suspended and when they increase their body temperature to sleep the costs of sustaining that high temperature increase (Trachsel et al. 1991; Roth et al. 2010). We conservatively assumed that greater mouse-eared bats are able to sleep when their body temperature exceeds 30°C. Djungarian hamsters spontaneously sleep when body temperature rises above 20°C (Palchykova et al. 2002) after torpor. Unfortunately, the influence of torpor on the sleeping pattern of bats is not known (Zhao et al. 2010). Therefore, we can only speculate about the conditions necessary for bats to sleep and consolidate memory.

Our experiments of exposure to low and high temperatures did not reveal differences in the speed of learning between treatment groups, although the period of time with $T_{sk} > 30^oC$ was significantly different. This indicates that the duration of torpor does not play a role (or only a minor one) in the impairment of memory consolidation of a simple task. In other words, bats are able to avoid or minimize the conflict between energy conservation and memory consolidation. Torpor impairs object recognition in rodents in complex tasks while not in simple ones (Palchykova et al. 2006). Bats in our tasks had to associate spatial elements with food or a safe place, which may be a more complicated task than simple object recognition. Such a task demands skills of association of spatial elements with rewards. The extremely weak tendency for slower learning in bats kept at lower temperatures suggests that if torpor indeed affects learning abilities it is happening at a very subtle level.

The lack of clear cognitive effects caused by the decrease in body temperature could be explained by a bat's life history. Many bat species live in complex environments and knowledge about this environment is probably important in their long life (Ruczynski & Siemers 2011). Therefore behavioral and physiological mechanisms should have evolved in bats to minimize the negative effects of a trade-off between energy conservation and cognitive abilities.

Negative effects of torpor may be minimized especially when learning is associated with a food reward (which probably is the most common situation in nature). This is because digestion prevents the bats from falling into torpor quickly (Matheson et al. 2010) and thus may provide a suitable amount of time for memory consolidation, therefore decreasing potential effects of sleep deprivation by torpor. Subsequent falling into torpor might have no or only minimal effects on acquired skills or knowledge. The idea that recent feeding delays the onset of torpor is further supported by the fact that in both treatment groups, animals that were in the perch search experiment, which were not fed after their training session, entered torpor more quickly and spent more time with skin temperature below 30^oC, than bats in the food search experiment, which received food during training and experimental trials. Nevertheless, in both treatment groups dynamics of T_{sk} followed natural patterns (Dietz & Kalko 2006). Bats were active with high body temperatures for several hours after training and only subsequently decreased their body temperatures. Our data suggest that even 1-2 hours during which the bats keep their body temperature high is sufficient to consolidate memory about a simple task.

We conclude that under natural situations negative effects of torpor on cognitive abilities play only a marginal role, if any, in bats. However, we suggest that starvation may amplify potential negative effects on cognitive processes in bats. We argue on a more general level that although solving cognitive problems demands high brain temperatures, a period of decreased body temperature and inactivity does not necessarily impair cognitive processes that are actively underway before and after torpor.

Acknowledgements

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CHAPTER 4

Effect of different light conditions on *Myotis myotis* foraging behavior

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(Manuscript)

Abstract

Light pollution in form of night illumination of streets and buildings is increasing globally. This might have far reaching negative impacts on wildlife, especially on night active animals. In this study, we investigated the influence of seven different light conditions, varying in wavelength and intensity, on the foraging behavior of the greater mouse-eared bat, *Myotis myotis*. In a controlled laboratory experiment with wild and long-term captive bats, we compared foraging activity under these light conditions to foraging activity under dark conditions. We found that *M. myotis* responds by avoiding all light conditions equally and did not identify any indicators of short-term habituation (days/weeks) and only very weak signs of long-term habituation (years) to light in general. Our study emphasizes the need for further investigation of the influence of light pollution on night active animals.

With worldwide expanding industrialization and electrification of even the remotest areas, night illumination of streets and buildings in and around settlements and cities is constantly increasing. Over the past decades growing attention has been paid to this “light pollution” and its various impacts on human and non-human animals (reviewed in Longcore & Rich 2004). One negative consequence, for instance, is the resulting change in circadian rhythms in human and non-human animals (e.g., Kempenaers et al. 2010; Dominoni et al. 2013) potentially leading to drastic changes in hormone cycles with widespread medical consequences (Navara & Nelson 2007; Bedrosian et al. 2011). Another is the loss of protective darkness that many night active animals may rely upon to reduce predation pressures (e.g., Speakman 1995; Duverge et al. 2000). For such species the extension of illuminated areas may lead to a restriction of suitable habitats and/or their foraging time window.

A large proportion of night active mammals are bats. A field experiment showed that night illumination of buildings led to delayed emergence of bats from their roosts. As a consequence, lactating females missed the time of peak insect abundance, which in turn led to delayed development of their offspring (Boldogh et al. 2007). Another field study showed that lesser horseshoe bats (*Rhinolophus hipposideros*) reduced the use of traditional commuting routes when these were illuminated with streetlights. These bats also delayed the onset of commuting behavior in the presence of lighting with no evidence of habituation (Stone et al. 2009). Night lighting may also impair bats' ability to orient and avoid collisions with obstacles (McGuire & Fenton 2010; Orbach & Fenton 2010). Additionally, it may reduce seed dispersal in illuminated areas by the frugivorous bat *Carollia sowelli*, and thus impair reforestation and defragmentation of tropical forests (Lewanzik & Voigt 2014). Since some insects are attracted to lights (e.g., street lamps) their local abundance can change. Especially in rural areas and on country roads this might lead to higher insect densities around streets and lower insect densities over adjacent meadows, fields, or forests (e.g., Arlettaz et al. 2000). Such changes could have negative implications for night active insectivorous animals.

Of the over 1200 bat species worldwide most species forage exclusively on insects (Fenton & Ratcliffe 2010). Some of these – especially aerial hawking bats – seem to cope with the changing environmental conditions in terms of night illumination by foraging systematically around street lamps (Lee & McCracken 2002; Rydell 1991). However, bats are not only predators of insects, but are also preyed upon by nocturnal birds of prey (Black et al. 1979; Speakman 1991). This may explain why some bat species are apparently light averse (e.g., Rydell 1992). For those species, light pollution may restrict suitable habitats to less illuminated areas where in turn insect density may be lower (Arlettaz et al. 2000).

Greater mouse-eared bats (*Myotis myotis*) prey upon ground dwelling arthropods such as carabid beetles, hunting spiders, and centipedes by passively listening for prey-produced rustling sounds to localize their food (Arlettaz et al. 2001; Siemers & Güttinger 2006). They hunt mainly over open, accessible ground, and land to pick up arthropods which they typically consume in flight (Arlettaz 1996). *Myotis* species in general are known to avoid light (e.g., Rydell 1992). Thus, light that causes little disturbance to greater mouse-eared bats would likely be little disturbing to bats in general.

However, not all types of light have the same influence on the behavior of insects or bats or both. Insects, especially moths, seem to be most attracted to light with high UV content. Consequently, such lights, or the moths flying around it, may also attract insectivorous bats (Ballasus et al. 2009). Furthermore, light with different combinations of wavelengths or intensities might disturb light sensitive bat species differently (Stone et al. 2012). Dim red light is generally thought to cause minimal disturbance to the behavior of bats and is therefore often used in behavioral experiments (e.g., Mistry & McCracken 1990). However, a number of studies offer evidence that many bat species not only perceive light up to wavelengths of about 680 nm (red) (Winter et al. 2003), but that many bat species possess two functional photopigment genes, one of which has a peak sensitivity at about 560 nm to 580 nm (yellow), but is also sensitive to longer wavelengths (e.g., Hope & Bhatnagar 1979;

Zhao et al. 2009). Therefore, red light can presumably be well perceived by bats. Whether it also disturbs them during, for example, cave visits by people or alters their behavior in experiments as much as white light has not been conclusively studied yet.

In this context a goal pursued by Philips Lighting is to develop a LED light that has low disturbance effects on bats. The aim of this project was to investigate the influence of light of different intensities and wavelengths on the foraging behavior and space use of *M. myotis* as compared to darkness. We conducted behavioral experiments with two independent groups of bats. The first was a cohort of freshly caught, wild bats. The second was a group of long-term captive bats. Generally, we expected the bats to forage more in darkness as compared to light. In order to test for a potential habituation to the different light conditions, we tested each bat over several days (short-term habituation) and compared the two groups of bats (long-term habituation). To answer the specific research question on the effect of light intensities and wavelengths on bat behavior, we tested for differences in foraging activity between light treatments. An ideal "bat-friendly" light would score foraging levels comparable to those observed for darkness.

Materials and Methods

Animals

The experiment with the wild bats took place in Tabachka, Bulgaria. We captured nine adult, post-lactating female *M. myotis* with a harp trap at the entrance of Orlova Chuka cave in northeastern Bulgaria and transferred them to the Tabachka Bat Research Station of the Sensory Ecology Group (Max Planck Institute for Ornithology, Seewiesen, Germany), which is run in cooperation with the directorate of the Rusenski Lom Nature Park in the district of Ruse. We kept the bats as a group in a holding cage (50 cm x 35 cm x 40 cm) with *ad libitum* access to water. The dark-light-cycle in the husbandry mimicked outside conditions. During day the bats were exposed to warm white light with an intensity of 12.5% (i.e., 1/8) of the least white-light intensity used in the experiment (see table 4.1). This resembled the conditions near the entrance of a cave. The temperature in the housing room was around 18^{o}C resembling the average temperature in a cave during summer. After the experiment we released the bats at their capture site in good condition at or above their capture weight.

We conducted the experiment with the long-term captive bats in Seewiesen, Germany. We used eight long-term (3 to 5 years) captive adult male *M. myotis*. Except one, none of them had ever participated in a study involving exposure to light before. However, over the course of their long-term captivity they had been exposed to various light conditions during experiments, handling, or medical checkups. These bats are kept in an aviary (2.4 m x 2 m x 2 m) under an inverted dark-light-cycle (8 h dark, 16 h light). They only received food during experimental trials, but had *ad libitum* access to water.

Light source

Philips Lighting provided the lamp. It was a computer controlled LED light source capable of emitting light of different wavelengths and intensities. The light settings used were predefined by Philips Lighting and are specified in table 4.1. While running the experiment, the experimenters had no information about the physical properties of the light settings used. They were also unaware of any *a priori* hypothesis regarding the levels of disturbance caused by each light setting. We tested the lamp for potentially disturbing ultrasound emissions with a bat-detector (Pettersson, D1000X). We found no ultrasound-noises emitted by the lamp.

Table 4.1 Light conditions used in the experiment. *Condition: names of the light conditions as referred to in the text; Color: color of condition as perceived by the experimenter; Wavelength: wavelength composition of the condition (short: 380 - 504 nm; medium: 505 - 589 nm; long: 590 - 780 nm); Intensity: Intensity of the light on the floor of the flight room (at the feeding platforms).*

condition	color	wavelength	intensity [lux] Tabachka (BUL)	intensity [lux] Seewiesen (GER)	picture
setting 1	Yellow	short = 0.14% medium = 0.46% long = 0.40%	1.99	1.24	
setting 2	White High Intensity	short = 0.20% medium = 0.38% long = 0.42%	1.00	0.63	
setting 3	White Low Intensity	short = 0.20% medium = 0.38% long = 0.42%	0.50	0.31	
setting 4	Orange	short = 0.05% medium = 0.57% long = 0.38%	2.50	1.56	
setting 5	Red Shade 1	short = 0.04% medium = 0.13% long = 0.83%	3.28	2.04	
setting 6	Red Shade 2	short = 0.02% medium = 0.06% long = 0.92%	3.78	2.35	
setting 7	Red Shade 3	short = 0.01% medium = 0.05% long = 0.94%	3.56	2.22	

Experimental setup

Wild bats (Tabachka, Bulgaria)

A flight-room (l: 8 m; w: 3.9 m; h: 2.4 m) was divided into two compartments by an opaque black curtain. In the following, the compartments will be referred to as *treatment compartment* and *control compartment*. The bats were allowed to fly freely in the flight room during training and experimental sessions. They could switch between the two compartments through a 1-meter opening between the curtain and the wall (see fig. 4.1a). The walls and ceiling were draped with sound attenuating material; the floor was covered with sand. The treatment compartment held four round feeding platforms (40 cm in diameter) arranged in a square on the floor under the lamp (see fig. 4.1a).

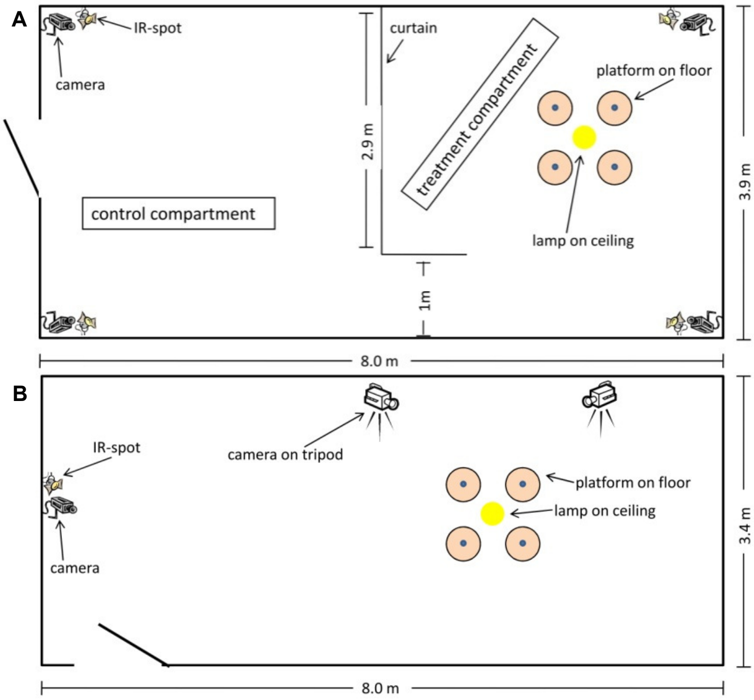

Figure 4.1 Flight rooms used during training and experiments. (a) Flight room in Tabachka (Bulgaria). (b) Flight room in Seewiesen (Germany).

Platforms consisted of foam and were covered with sand to make them echoacoustically similar to the surrounding floor. Each platform held a petri dish containing 4 g of mealworms (approx. 40 mealworms; larvae of *Tenebrio molitor*). The petri dishes lay in a circular notch of 9 cm diameter and had a round mesh-covered hole (4.5 cm in diameter) in the middle. A loudspeaker (Sennheiser, headphoneloudspeakers HD 555/595) was sunk facing upwards in each platform beneath the petri dish.

An omnidirectional microphone (MIC-48, Speed-Shanghai Industrial Co., Ltd., Shanghai, China) placed in the middle of the four landing platforms (i.e., directly under the lamp) that was connected to a computer and headphones (Pioneer, Stereo Headphones SE-M390) allowed recording of chewing noises to monitor the success of landings (i.e., if the bats found one or more mealworms while sitting on the platforms). We could clearly hear the sounds of landings and take-offs from the platforms as well as the chewing noises even when the bats flew into the control compartment while consuming the mealworm. The landing and eating noises were recorded on hard disk for future reference with Free Sound Recorder 2010 (Version 9.2.1, Cool Media, LLC, Redmond, WA, U.S.A.).

The only visible light source in the room was the lamp, illuminating the treatment compartment in the tested light conditions. Light color and intensity presented to the bats was controlled via a computer from outside the room. Four infrared sensitive cameras (Watec, WAT-902H2 Ultimate) were situated in each corner of the room directly under the ceiling. These provided almost complete coverage of the flight room to monitor the behavior of the bats. Four infrared LED spots next to them provided illumination for sufficient video quality in darkness. Bats are thought to be insensitive to infrared light and it does not appear to affect their behavior (Mistry & McCracken 1990; Winter et al. 2003). Videos were recorded on a computer with DigiProtect Version 6.246 (ABUS Group Security Center, Wetter, Germany).

Long-term captive bats (Seewiesen, Germany)

The flight room in Seewiesen (l: 8 m; w: 3.4 m; h: 3.2 m) was not compartmentalized (see fig. 4.1b). The same feeding platforms as described above were placed under the lamp; each held a petri dish with 2 g of mealworms (approx. 20 mealworms). The microphone was situated in the centre between the platforms to record chewing noises. One strong infrared spot was placed next to a camera that monitored almost the whole room. Two additional cameras were placed on tripods next to the platforms. Because the flight room ceiling in Germany was higher than in Bulgaria, but the same light settings were used, the light intensity at the feeding platforms was lower (see table 4.1).

Procedure

Training

Before training in the flight room started, we hand-fed the wild bats in Bulgaria 4 g of mealworms for two days. This gave the animals the opportunity to get used to the new environment and adjust to mealworms as food. After that they only received food in the training and experimental sessions. To attract the bats to the platforms we played back rustling sounds of beetles (*Carabus monilis* L.) over the loudspeakers in the feeding platforms. Such beetles are typical prey of *M. myotis* (e.g., Arlettaz et al. 1997). Each night a bat was allowed to fly for 15 minutes in the dark flight room. If the bat did not find the platforms during a training session, it was fed 2 g of mealworms at least 1.5 hours after training. During this feeding the bat was placed on one of the platforms and rustling noises were played back. If a bat lost too much weight (2-3 g, figures corresponding to 5%-10% of their original mass) because of food deprivation, we fed it up to 4 g of mealworms. After the bats first landed on a platform and found mealworms, they consistently found the platforms again and landed up to 12 times per minute. During the following experimental sessions no rustling sounds were played. Three of the nine bats did not learn to land on the feeding platforms to obtain food within 10 days and were therefore released untested. We present data from the six remaining bats. It took those six bats different amounts of time to learn to obtain food from the platforms. Time constraints made it impossible to conduct the same number of sessions with each bat. How many sessions were conducted with how many bats is given in table 4.2.

Table 4.2 Number of sessions conducted with the six wild Bulgarian bats.

number of individuals	number of sessions per individual
1	11
3	9
2	4

The eight long-term captive bats in Germany were already used to mealworms as food and experienced in obtaining them from the feeding platforms. We conducted six experimental sessions with each individual.

Experiment

After the bats had learned to retrieve food from the feeding platforms, we conducted one experimental session per night with each individual singly in the flight room. An experimental session lasted for 15 minutes. During each session the bats were exposed to seven different light-conditions in the treatment compartment. Philips Lighting predefined these conditions (see table 4.1). Every session started with one minute of darkness. Each of the seven light conditions was presented for one minute (light phase) followed by one minute of darkness (dark phase) (see fig. 4.2). Light conditions were presented in a pseudo-randomized order to control for the effect of the order of light presentation.

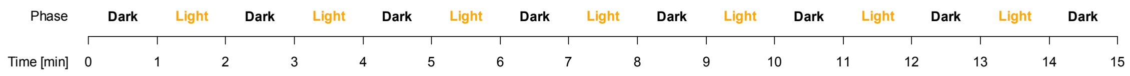

Figure 4.2 Time bar of one experimental session. *Each bat had one experimental session per night. The order of the light conditions was pseudo-randomized for each night.*

Data collection

Food was available *ad libitum* during experimental sessions, and some bats were apparently not motivated to feed during the last minutes of a 15-minutes session. In such cases, the last minutes of the session, in which the bat did not spent time on a platform anymore, were excluded from analysis. If the first minute during which the animal spent no time on the platform anymore was a dark phase, we could not be sure about the motivational status of the bat in the preceding light phase. In this case this previous light phase was also excluded. Experimental phases were not excluded from analysis if landings happened again in any of the following phases. As the sound recordings provided a better time resolution than video recordings, for the wild bats' data, we scored the bats' foraging activity for each light condition by analyzing the sound recordings for landings and take offs and calculating the time spent on the platforms. In the experiments with the long-term captive bats, we had cameras placed closer to the feeding platforms (see fig. 4.1b) and therefore used video recordings to calculate the time spent on platforms.

For analysis we discriminated between total time spent on platforms in a specific phase ("Total Time") and time spent on platforms during landings that actually happened in this phase ("Shortened Time"). This parameter excluded the time an animal stayed on a platform after a phase switch.

Data preparation

Data on time spent on platforms during one minute were not normally distributed, but strongly skewed towards low values. We therefore decided to use a binary variable, which received the value "1" if the bat was on the platform during a second, or "0" if not. Values for two consecutive seconds could not be considered independent from each other: if a bat sat on the platform during one second it was more likely to sit on the platform during the next second as well. To achieve a sampling interval with only independent samples, we calculated the mean and the 95% confidence interval of the durations of all landings and used a sampling interval of mean + confidence interval, rounded to the next higher integer. This resulted in a sampling interval of 8 seconds for both the wild and the long-term captive bats. We therefore conducted our analysis of foraging activity on our binary variable, sampled every 8th second. We are confident that our measure was conservative. Other means of finding an appropriate sampling interval (e.g., 3rd quartile of the duration of all landings) would have led to shorter sampling intervals.

Because only one wild individual participated in 11 sessions (see table 4.2), we excluded the last two sessions of this individual to achieve a more balanced data-set.

Statistical analysis

Analyses were done using R Version 2.15.2 (R Development Core Team 2012). We computed generalized linear mixed effect models with a binomial error distribution using the glmer function of the lme4 package (Bates et al. 2012). We included light condition, number of session, and the number of minutes elapsed (within each session) as fixed effects and individual as a random effect. Number of session was included as a numerical variable to test for a habituation effect over sessions, and as a factor, when comparing the response to the different light settings. To compare the data obtained from the wild (Bulgaria) and the long-term captive (Germany) bats, we additionally included "location" as a fixed effect in the model. To compare "Total Time" (total time spent on platforms) and "Shortened Time" (time spent on platforms for landings in this phase), we additionally included "dataset" as a fixed effect in the model. We report p-values derived from log-likelihood ratio tests of the minimal adequate model and a model that differs from the minimal adequate model in not containing the fixed effect in question. To test for specific effects of different conditions, we used the glht function for multiple linear hypothesis testing with Tukey contrasts of the multcomp package (Hothorn et al. 2008), which uses the single step method to adjust p-values in multiple comparisons.

Because of the large difference between dark and light conditions, we always found an effect of condition if we analyzed all 15 minutes of a session. We therefore analyzed dark and light phases separately. We compared dark conditions to test whether light conditions had an "After-Effect" on the bats' behavior in the following dark phase. To do so, we defined dark conditions by the previous light condition. "D1", for example, is therefore not the first dark phase, but the dark condition following presentation of light setting 1 (see table 4.1).

Capture, experimentation and care of the wild bats while in captivity was carried out under license of the responsible Bulgarian authorities (MOEWSofia and RIOSV-Ruse, permit numbers 193/01.04.2009, 205/29.05.2009). Experimentation and care of the long-term captive bats in Germany was carried out under license of the responsible German authorities (Landratsamt Starnberg, permit number 301c.4V-sä). All bats were kept in accordance with the species-specific recommendations of the Canadian Council on Animal Care on bats (Canadian Council On Animal Care 2003).

Results

Most of the animals foraged continuously for almost the whole duration of a session. To illustrate the bats' behavior figure 4.3 shows the duration and timing of landings on feeding platforms for one exemplary flight of a wild bat.

Single landing times ranged from 0.12 to 273.50 seconds in the wild-caught bats and from 0.10 to 455.81 seconds in the long-term captive bats, although long landings occurred very rarely.

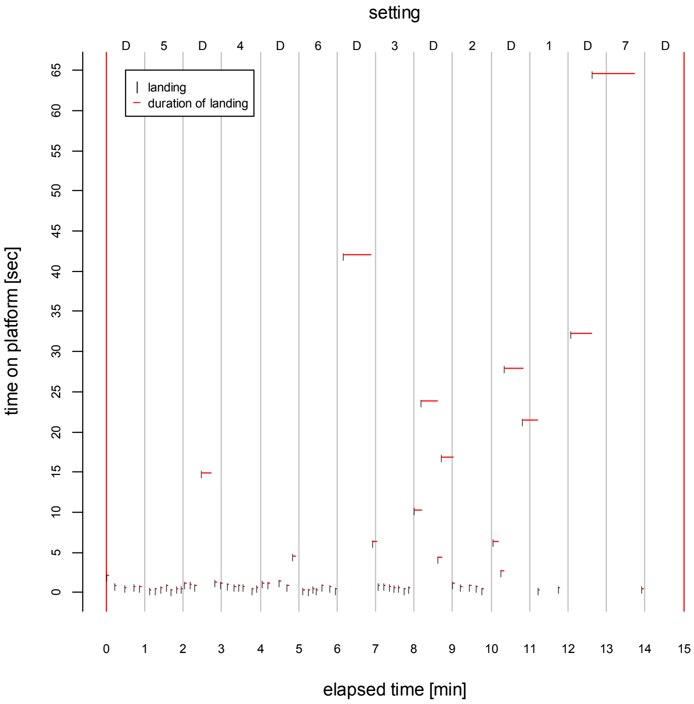

Figure 4.3 Example for the temporal structure of landings during one 15-minutes experimental session. *D = Dark Phase; 1 to 7 = numbers of the light settings as given in table 4.1. The duration of each landing is shown by the following red line as well as by their position relative to the y-axis.*

Even though there was considerable inter-individual variation in flight and landing behavior, within each session the bats spent consistently more time on the feeding platforms in darkness than in any illuminated phase. This effect was found when analyzing the "Total Time" and when analyzing the "Shortened Time" in both the wild and the long-term captive bats. When comparing the two locations (i.e., wild vs. long-term captive bats), we found that with respect to "Total Time" the locations differed in how much the bats' behavior differed between dark and light phases ($\chi^2_{[1]} = 12.62$; $p < 0.001$). In contrast, in "Shortened Time" we did not find this effect (i.e., dark and light phases still differed, but the two locations did not differ in how much dark phases differed from light phases) ($\chi^2_{[1]} = 1.02$; $p = 0.31$).

For both locations we created the "Shortened Time" data-set by subtracting the amount of time the animals stayed on a platform after a phase switch (i.e., from light to dark or from dark to light) from the "Total Time" data-set. Therefore, this result indicates that in one group of animals the amount of time they stayed on the platforms after a phase switch was larger than in the other group of animals. Specifically, long-term captive bats stayed longer on the platforms after a phase-switch from dark to light (see below and also figs. 4.4 – 4.7).

All values presented in the figures are the percentages of samples (see Methods – Data preparation) during which the animal was found on one of the feeding platforms during each phase. In the following, we present results from separate analyses of light and dark phases.

All figures show values for light and dark phases together. Data presented are means ± 1 SEM.

Light phases

In none of the analyses conducted did the light settings differ in their effect on the bats behavior (wild bats "Total Time": $\chi^2_{[6]} = 11.63$; $p = 0.07$; wild bats "Shortened Time": $\chi^2_{[6]} = 5.16$; $p = 0.52$; long-term captive bats "Total Time": $\chi^2_{[6]} = 7.77$; $p = 0.26$; long-term captive bats "Shortened Time": $\chi^2_{[6]} = 4.55$; $p = 0.60$). The only factor that always had an effect on the bats' behavior in lighted phases was the number of minutes elapsed; that is, the bats behaved differently at different time points during one session regardless of light condition presentation order (fig. 4.4).

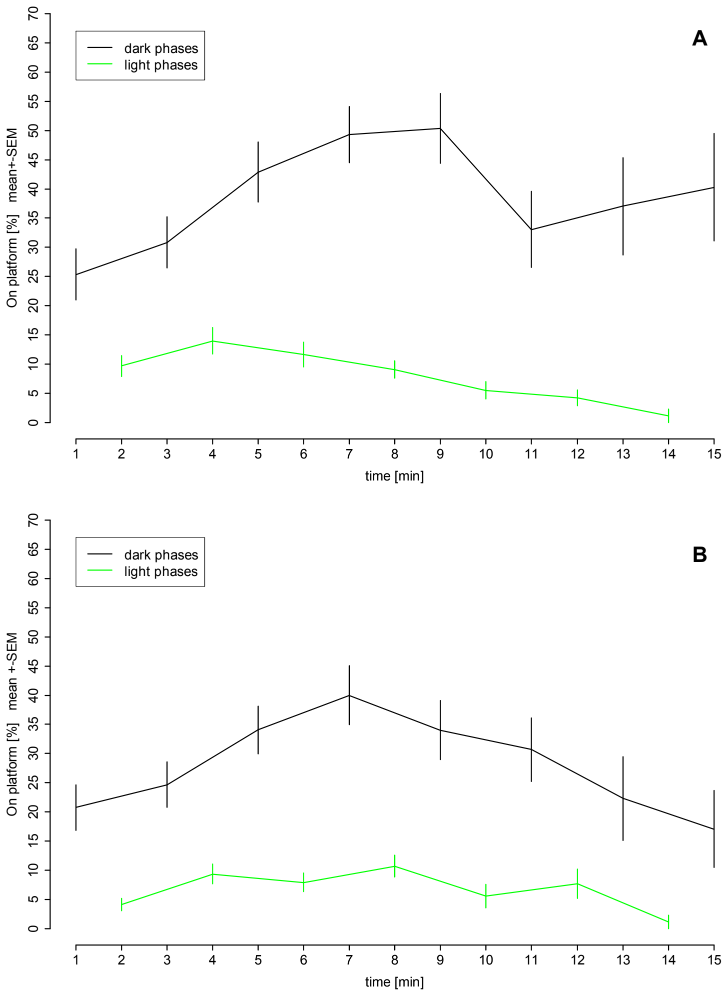

Figure 4.4 Temporal pattern of the time spent on platforms during 15-minutes experimental sessions averaged over individuals and sessions (data shown for "Shortened Time"). *Color indicates lit versus dark minutes. Shown are means ± 1 SEM. Only the number of minutes elapsed had an effect on the amount of time the animals stayed on the platform during lit phases. In dark the different phases also differed according to the number of minutes elapsed. However, other factors also influenced the bats' behavior in dark phases.* (a) Wild bats from Bulgaria. *The time spent on platforms in lit minutes decreased after phase 4.* (b) Long-term captive bats from Germany. *No constant decrease in time spent on platforms over time elapsed is visible. Still, the number of minutes elapsed had an effect on the bats' behavior in light phases.*

The bats did not change their response to the light conditions over the course of several experimental sessions (fig. 4.5). Although there is an effect of the number of session on the time spent on platforms in light in the "Total Time" data-sets (wild bats: $\chi^2_{[8]} = 17.78$; $p = 0.023$; long-term captive bats: $\chi^2_{[5]} = 65.28$; $p < 0.0001$), this effect is non-linear (wild bats: $\chi^2_{[1]} = 0.20$; $p = 0.66$; long-term captive bats: $\chi^2_{[1]} = 0.22$; $p = 0.66$), and not present in the "Shortened Time" data-sets (wild bats: $\chi^2_{[8]} = 6.33$; $p = 0.61$; long-term captive bats: $\chi^2_{[5]} = 10.61$; $p = 0.06$). Therefore, there is no indication for short-term habituation to light; in other words, there was no increase in the time spent on the feeding platforms in light phases over the sessions in both groups of bats.

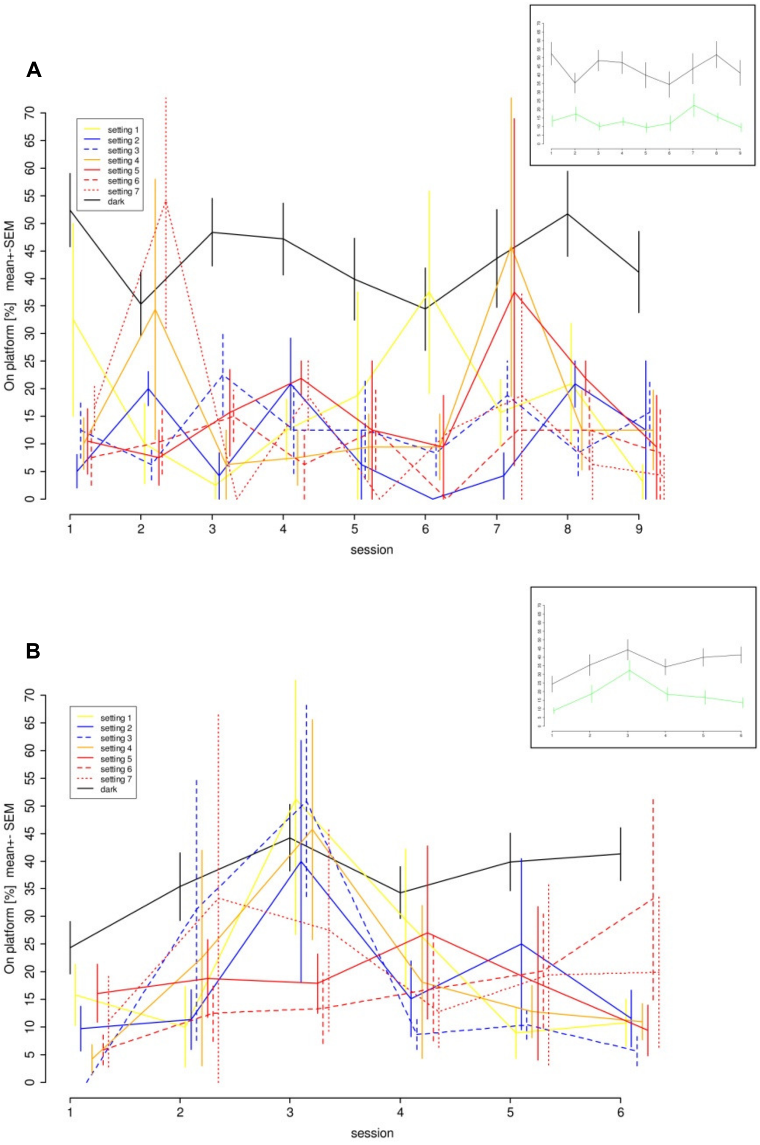

Figure 4.5 Temporal pattern of the time spent on the feeding platforms over the course of all experimental sessions averaged over individuals (data shown for "Total Time"). *Color and line type indicate light conditions. Shown are means ± 1 SEM. The main figure displays the light settings separately. The inlay shows the same data with all illuminated minutes pooled to reduce variance and further illustrate the difference between dark and illuminated phases. The black line shows again dark, the green line light phases. Although sessions differ from each other, there is no indication of habituation to any of the light conditions.* (a) Wild bats from Bulgaria. (b) Long-term captive bats in Germany.

Figure 4.6 shows the time the wild bats spent on the feeding platforms under each condition, averaged over animals and time. There was no difference in the bats' response to the different light settings neither in the "Total Time" nor in the "Shortened Time" data-set (see above). Compared to darkness, foraging activity was reduced by about the same magnitude in all seven light conditions. Figure 4.6a shows the total amount of time the bats spent on the feeding platforms ("Total Time") and figure 4.6b shows the time the animals spent on the platforms during landings that happened in the respective phase ("Shortened Time"). The time spent on platforms during light phases is reduced in "Shortened Time" ($\chi^2_{[1]} = 18.50$; $p < 0.0001$). In both data-sets, there seems to be an indication that the bats were more affected by setting 2 than by setting 3. Both are warm white light conditions with a higher intensity in setting 2 (see table 4.1).

Also in the long-term captive bats, compared to darkness, foraging activity was reduced by about the same magnitude in all seven light conditions (fig. 4.7). Again, time spent on platform during light phases was significantly reduced in the "Shortened Time" data-set as compared to the "Total Time" data-set ($\chi^2_{[1]} = 64.89$; $p < 0.0001$). However, the slight indication for a stronger disturbance effect of setting 2 as compared to setting 3 found in the wild bats is not visible in the long-term captive bats.

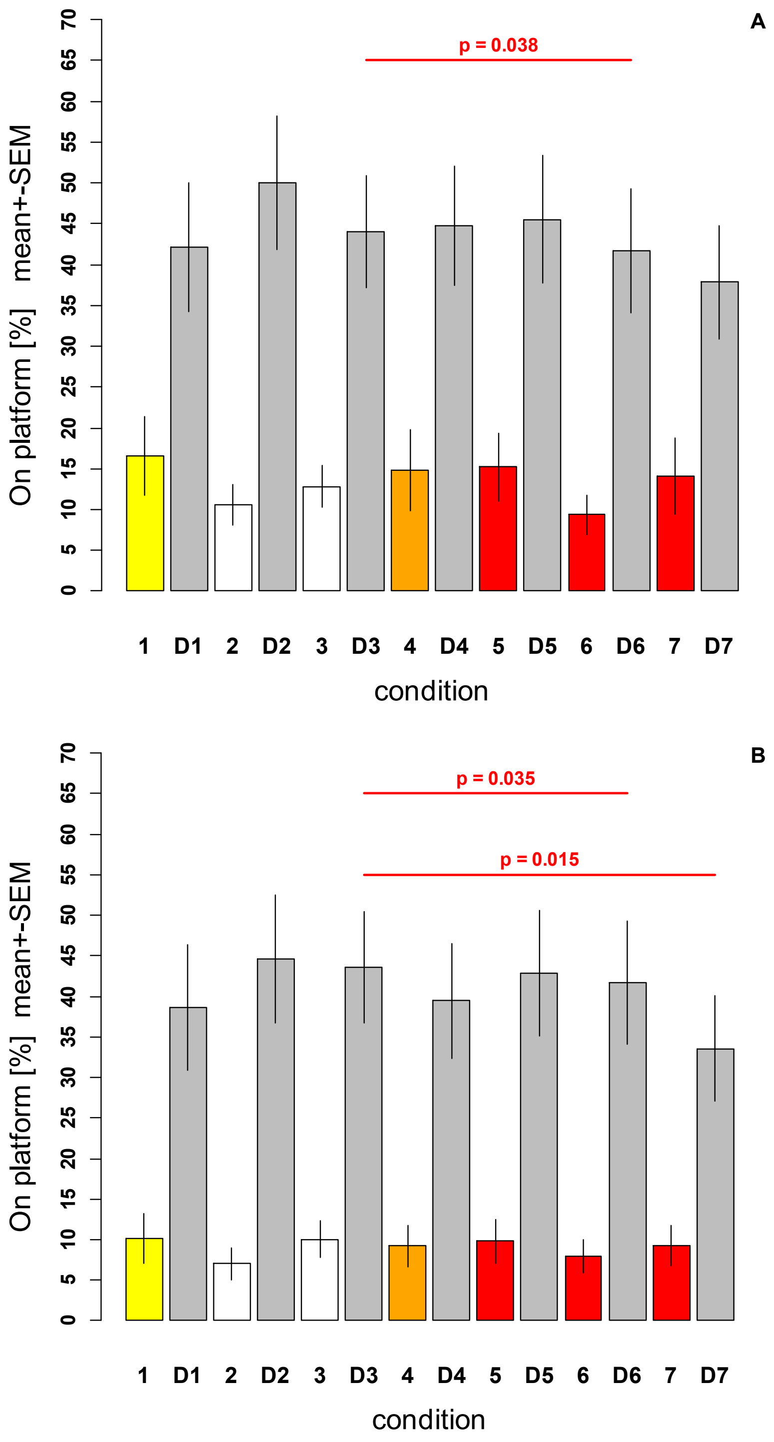

Figure 4.6 Time the wild bats spent on the feeding platforms in each condition. *Color indicates light condition. Grey bars represent dark conditions. Shown are means ± 1 SEM.* (a) Total time spent on platform. *There is no difference in the total time the bats spent on the feeding platforms in the different light settings, but there is a clear difference between dark and any of the light conditions. Additionally, the behavior of the bats differed between dark phases following presentation of light setting 3 and dark phases following the presentation of light setting 6.* (b) Time spent on platforms during landings that happened in the respective condition ("Shortened Time"). *We found no difference in the time the bats spent on the platforms for landings that happened in this condition in light, but there is a clear difference between dark and any of the light conditions. Within dark conditions, the behavior of the bats differed between dark phases following presentation of light setting 3 and dark phases following presentation of light setting 6 or 7. The difference between "Total Time" and "Shortened Time" is significant for light conditions, but not for dark conditions.*

There is no difference between wild and long-term captive bats in their response to the different light settings ("Total Time": $\chi^2_{[1]} = 0.16$; $p = 0.69$; "Shortened Time": $\chi^2_{[1]} = 0.44$; $p = 0.51$). However, it seems as if in total the long-term captive bats spent more time on the platforms during light phases (figs. 4.6a and 4.7a). Since this impression is not there in "Shortened Time" (figs. 4.6b and 4.7b), this means that the long-term captive bats stayed longer on the feeding platforms after phase-switches from dark to light.

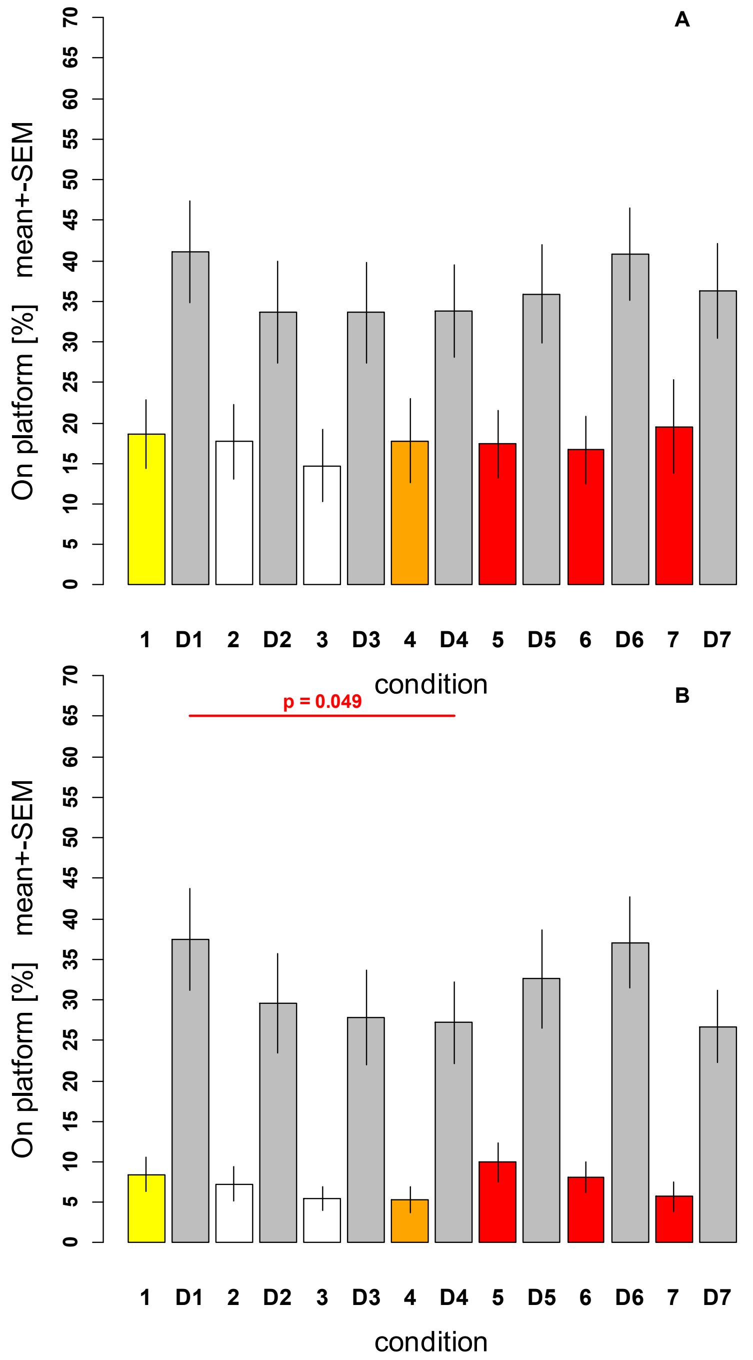

Figure 4.7 Time the long-term captive bats spent on the feeding platforms in each condition. *Color indicates light condition. Grey bars represent dark conditions. Shown are means ± 1 SEM.* (a) Total time spent on platform. *As with the wild bats, we found no differences between the times the bats spent on the feeding platforms in the different light settings, but a clear difference between light and dark phases.* (b) Time spent on platforms during landings that happened in the respective condition ("Shortened Time"). *There was no difference between the time the animals spent on the platforms during landings that happened in this condition in light, but, again, there is a clear difference between light phases and dark phases. Within dark conditions, the behavior of the bats differed between dark phases following presentation of light setting 1 and dark phases following presentation of light setting 4. The difference between "Total Time" and "Shortened Time" is significant for light conditions, but not for dark conditions.*

Dark phases

By analyzing the dark phases separately, we tested whether the preceding light condition had an influence on the time an animal spent on the platform during a dark phase. Dark conditions were defined by their preceding light condition (i.e., "D1" was defined as the dark phase following a presentation of light setting 1).

In contrast to the light phases, we found a general increase in time spent on platforms in dark phases over consecutive experimental sessions for the long-term captive bats ("Total Time": $\chi^2_{[1]} = 33.21$; $p < 0.0001$; "Shortened Time": $\chi^2_{[1]} = 28.84$; $p < 0.0001$) (fig. 4.5b). We did not find this general increase in the wild bats (fig. 4.5a).

Additionally, although the kind of light presented did not have an effect on how bats behaved during light phases, we found that the behavior of the bats during dark phases was in some cases influenced by the preceding light condition (wild bats "Total Time": $\chi^2_{[6]} = 13.99$; $p = 0.03$; wild bats "Shortened Time": $\chi^2_{[6]} = 14.64$; $p = 0.02$; long-term captive bats "Shortened Time": $\chi^2_{[6]} = 12.93$; $p = 0.04$) (figs. 4.6 and 4.7). In the "Shortened Time" data-sets more significant differences between dark conditions occurred than in the "Total Time" data-sets. However, these effects were different in the wild versus the long-term captive bats (see figs. 4.6 and 4.7). In contrast to light, the two data-sets ("Total Time" and "Shortened Time") did not differ, neither in the wild nor in the long-term captive bats (wild bats: $\chi^2_{[1]} = 3.5021$; $p = 0.06$, long-term captive bats: $\chi^2_{[1]} = 2.47$; $p = 0.12$). This means that the amount of time the animals stayed on a platform after a phase switch (light to dark), did not make up a substantial proportion of the total time the animals stayed on the feeding platforms in dark phases.

Discussion

We present four clear results from two independent behavioral experiments conducted with wild bats in Bulgaria and with long-term captive bats in Germany. First, all bats foraged more and longer in darkness than under any tested light condition. Second, all tested light conditions apparently disturbed the bats equally. Third, there was no indication of short-term (days/weeks) habituation to any of the tested light conditions. Fourth, we found no significant difference in the foraging behavior of freshly wild-caught and long-term captive *M. myotis* under the different tested light conditions.

Nevertheless, the long-term captive bats were apparently less startled by the onset of light as indicated by their longer stays on the platforms after a phase-switch from dark to light. Therefore, they also spent slightly more time on the platforms in light than the wild bats. This could be an indication for slight long-term (years) habituation to light. However, since this difference in time spent on platforms between the two groups of bats only concerns the response to the onset of the light but disappeared once we only considered the time the animals spent on the platforms during landings that happened in the respective phase, this very slight long-term effect would probably not affect the response of wild bats to the illumination of streets and buildings. Our findings confirm the apparent absence of habituation to night illumination of buildings used as roosting sites (Boldogh et al. 2007) or of commuting routes in wild bats (Stone et al. 2009).

We did not find a difference in the time spent on platform between the "Total Time" and the "Shortened Time" data-sets in dark phases. However, most likely this derives from the fact that bats landed less often in light phases and therefore there are fewer occurrences of bats sitting on the platforms during a switch from light to dark. We did find that the long-term captive bats spent increasingly more time on the platforms during dark phases over the course of the experiment. This is probably a general sign of adjustment to the experimental procedure and less a sign of "habituation" to dark phases.

However, we found that lights differed in the effect they had on the behavior of the bats in the following dark phase. This after-effect could potentially reflect a difference in disturbance the bats perceived by the different light qualities. Since these effects are weak, differ between the wild and the long-term captive bats, and we did not find differences between the light conditions themselves, our data do not permit inferences about the causes of this after-effect. They could also be false positive effects we detected despite correction of p-values. The same is true for the very weak (non-significant) indication that the white light with the lower intensity might have disturbed the wild bats less than the white light with the higher intensity.

The only factor we found to have a consistent effect on the behavior of bats in light phases was the number of minutes elapsed. This is best explained by decreasing motivation after the first minutes. After a bat had eaten mealworms during the first experimental minutes, it was less hungry and the perceived risk of landing in an illuminated area might have been higher than the perceived risk of starvation. The ability of bats to change their foraging strategy and become more selective in their prey choice under profitable conditions has been shown in *Rhinolophus ferrumequinum* (Koselj et al. 2011).

During their stay in captivity, the long-term captive bats are exposed to light in various situations. Prior to our experiment, during handling, medical checkups, or behavioral experiments, they have regularly experienced dim white light or dim red light without negative consequences. If long-term habituation to light occurs in greater mouse-eared bats, we would have expected to find stronger differences between the two groups of bats at least for white or red light conditions. That we did not find these differences is an argument in favor of no or only very weak long-term habituation to light in this species.

We note that direct comparison of the data from the wild and the long-term captive bats must be taken with caution for several reasons. First, while the wild bats had the opportunity to escape from the illuminated area by flying into the control compartment, in the experiment with the long-term captive bats no such control compartment existed. However, the long-term captive bats could have avoided staying in the illuminated area directly below the lamp by spending time in a darker corner of the room. Furthermore, because we scored time spent on feeding platform and not time spent in the treatment compartment or time spent flying, we are confident that our main results were not confounded by these differences in the setup. Second, because the flight room used for experiments with the long-term captive bats was higher than the flight room used for experiments with the wild bats but the light source was the same, the intensity of the light at the feeding platforms was slightly lower for the long-term captive bats (see table 4.1). Third, the two groups of bats not only differed in their experience with light, but also in other factors, that might have had an influence on our behavioral data. For example, long-term captive bats were more used to handling, and therefore presumably less stressed in general. All of the above mentioned variables, should they have had any effect on the bats' behavior, would however, most likely have led to less light avoidance in the long-term captive bats. Because, we did not find this effect, we are convinced that the behavioral responses of our two groups of bats are comparable.

Although we cannot draw conclusions regarding color perception in bats from our data, they offer additional evidence for the sensitivity of bats to long wavelength light. Mistry and McCracken (1990) showed that *Tadarida brasiliensis* responds behaviorally to light of wavelengths beyond 580 nm (red light), even if its intensity is considerably lower than that emitted by a 25-W red bulb, which are often used in behavioral experiments. However, they observed no response to light beyond 670 nm (far red). The intensity of the light conditions in our experiments was higher than those emitted by 25-W red bulbs. Nevertheless, given the very strong response in behavior it produced in the bats, we suggest that, in the future, bat researchers use only infrared lights in behavioral experiments to better ensure undisturbed behavior.

Our model species, the greater mouse-eared bat, often uses hunting grounds up to 10 km away from the roost (Audet 1990) and finds home quickly when released at a distance of 25 km from the roost (Holland et al. 2010). Single individuals have been observed commuting as far as 30 km from their roost each night (Borissov, Greif pers. com.). *Myotis myotis* shows strong light avoidance, as also evidenced by our data. Like other slow flying species *Myotis spp.* are known to avoid white LED light even at low intensity-levels (Stone et al. 2012). The lighting of streets and buildings is thus likely to affect the commuting behavior of this species and may disrupt the various, long commuting routes and potentially lead to habitat fragmentation. A study on pond bats (*Myotis dasycneme*) showed that a single lamp placed into a commuting route drastically altered the behavior of the bats and could potentially reduce foraging success along the route while increasing energy demands by the search for alternative routes (Kuijper et al. 2008). Our study complements such field studies by investigating the influence of different light conditions on the foraging behavior of bats under controlled laboratory circumstances. The design of a truly “bat-friendly” light requires that it minimize disturbance to such light-averse species. This will, if at all feasible, require further research and development. The avoidance behavior all our bats showed to the presented light stimuli indicates that the experimental paradigm we used is suitable to experimentally investigate illumination effects on and light avoidance in bats.

Because both the wild bats and the long-term captive bats in our experiments showed strong avoidance behavior towards all seven light conditions, we conclude that all of the tested light conditions were visible to them and not "bat-friendly". We found no strong evidence of habituation to light over several experimental sessions, neither in wild nor in long-term captive bats, and only a very weak indication of long-term habituation.

GENERAL DISCUSSION

The goal of this thesis was to contribute to our knowledge about cognition in bats. First, I wanted to increase our understanding of the selective pressures shaping cognitive skills in insectivorous bats. Furthermore, I investigated the abilities of mouse-eared bats to use new information sources, particularly to learn socially within and across species borders. I also wanted to know how daily torpor affects learning performance. Finally, I explored the ability of bats to cope with human-made disturbance, here with disturbance caused by light, and had a closer look on potential habituation to LED lights in a generally light-averse species.

I have shown that species-specific foraging ecology may predict learning performance and behavioral flexibility in insectivorous bats (Chapter 1; Clarin et al. 2013). I also demonstrated that mouse-eared bats can learn socially within and across species borders and that this socially acquired information can be retained over a period of hibernation (Chapter 2; Clarin et al. 2014). Complementing this finding I found that bat learning performance is not negatively influenced by daily torpor (Chapter 3). Finally, I found that *Myotis myotis*, a flexible, but light-averse bat species, does not - or only very mildly - habituate with respect to its foraging behavior to disturbance caused by light (Chapter 4).

Within my work as described in Chapters 1-4 I tried to approach the questions laid out in the introduction from different angles. These were: *How* and *Why* do bat species vary in their learning abilities? *How* flexible are bat species in coping with changing or new conditions? *How* do bats exploit new information sources? *How* does daily torpor affect learning performance in bats? I believe that my work is a valuable contribution to our understanding of bat behavior and cognition. In the following, I will discuss the main findings of my work with regard to those questions. Finally, I will summarize the implications of my work and give an outlook on possible future studies.

Main Findings

***How* and *Why* do bat species vary in their learning abilities?**

In Chapter 1 ("Foraging ecology predicts learning performance in insectivorous bats") I set out to understand how bat species differ in their learning abilities. I tested three species from the genus *Myotis* and compared their performance in learning a simple rule, their performance in re-learning that simple rule, and their performance learning a complex rule.

I hypothesized that the species hunting in the least complex environment, *M. capaccinii*, would be the slowest learner as compared to two species hunting in more complex environments. I worked with *M. capaccinii*, a species foraging over water surfaces, *M. myotis*, a species hunting over open areas in forests or fields finding prey by listening for prey produced sounds, and *M. emarginatus*, a clutter specialist.

I found that simple rule learning seems to be equally easy for all tested bat species, as almost all individuals learned a simple rule on the first day tested. There was a trend suggesting that *M. capaccinii* re-learned a simple rule faster than the two other species. However, in accordance with my expectations, it took *M. capaccinii* longer to learn a complex rule than *M. myotis* or *M. emarginatus*.

This latter result suggests that learning skills related to foraging can be predicted by species ecology. Bats hunting in more complex environments are able to learn complex rules faster than species foraging in less complex environments. This supports the idea that the complexity of the environment a species inhabits and forages in will influence the development of its cognitive skills.

***How* flexible are bat species in coping with changing or new conditions?**

In Chapter 1 ("Foraging ecology predicts learning performance in insectivorous bats") and in Chapter 4 ("Effect of different light conditions on *Myotis myotis* foraging behavior"), I wanted to test how flexibly bat species can cope with new or changing conditions. I tested the flexibility of three species with regard to their foraging behavior. Asking the question, how quickly will they alter their behavior if a previously successful behavior does not have the desired outcome (finding food) anymore? Additionally, I tested the response of a rather flexible species, *M. myotis*, to common human disturbance, in this case different light conditions of varying wavelengths and intensities. I searched for changes in behavior as a sign of habituation (or lack thereof) to the lights.

When I compared the behavioral flexibility of three *Myotis* species (Chapter 1), I predicted that *M. capaccinii*, hunting over water surfaces, would be the most stereotyped species. I compared it to *M. myotis* and *M. emarginatus*, two species foraging in more complex environments. In the explorative study testing for habituation to different light conditions in *M. myotis* (Chapter 4), I expected to at least find long-term (years) habituation to light in general and maybe even short-term (days/weeks) habituation to specific light conditions.

In the first experiment, I found that indeed the two species foraging in more complex surroundings were more flexible in their behavior than the species hunting in a less complex environment. Specifically, *M. myotis* and *M. emarginatus* tried out new solutions to the old problem of finding food and changed their behavior more quickly than did *M. capaccinii*.

However, when one of these more flexible species, *M. myotis*, was confronted with a genuinely anthropogenic disturbance, namely light, it did not alter its behavior quickly. Over the course of several experimental sessions the bats showed consistent avoidance behavior to the presented light conditions and even long-term captive bats showed the same inflexible avoidance behavior. The only long-term change in behavior we could find was that the bats seemed to respond less quickly to the disturbance than did the wild-caught animals.

In conclusion, I found that in tasks related to foraging, bat species that hunt in more complex habitats are indeed more flexible and - when unsuccessful - attempt new solutions faster than do species that forage in simpler environments. However, even a rather flexible species presumably needs relatively long time and a lot of experience with anthropogenic light disturbance before it changes its light-averse response even slightly.

How **do bats exploit new information sources?**

In Chapter 2 ("Social learning within and across species: information transfer in mouse-eared bats") I investigated whether mouse-eared bats are capable of social learning, what level of interaction is necessary between demonstrator and observer to lead to information transfer, and whether information about an associative task can be transferred across species boundaries.

It turned out that mouse-eared bats are able to learn socially and that this works even across species boundaries. Furthermore, information transfer was greatly increased by direct interaction between demonstrator and observer. However, only very few individuals in each experimental group acquired the task.

Conspecifics as well as closely related, ecologically similar congenerics seem to be a valuable source of information for bats. However, our study provides only very restricted evidence for the importance of social learning in the wild. To solve the task, bats had to learn to approach an unnatural and unattractive, possibly aversive cue. This was apparently hard to learn for the bats. Given that social learning did occur under these unfavorable conditions, it might well be more common in nature. In the wild, social learning probably does not depend on non-attractive cues and animals would be able to more freely interact with each other.

How **does daily torpor affect learning performance in bats?**

In Chapter 3 ("Do bats experience a trade-off between energy conservation and learning?") we studied how daily torpor affects the learning performance of *M. myotis*. Because torpor and hibernation are thought to impair learning performance in other small mammals (reviewed in Roth et al. 2010), we assumed that learning performance would be negatively influenced by duration and depth of daily torpor.

We found no difference in learning performance between animals kept at 7°C and animals kept at 22°C between experimental sessions. This suggests that daily torpor has no negative effect on learning in bats at least for relatively simple tasks.

These results complement data I fortuitously gathered during the social learning project, described in Chapter 2 ("Social learning within and across species: information transfer in mouse-eared bats"). One year after the initial social learning experiment, I recaptured one observer, who had previously learned the task up to a level of almost 50% correct choices (theoretical chance level: 5%). When reintroduced to experimental conditions and without any further reinforcement by a demonstrator this animal showed the same performance it had shown the year before, although it had most certainly spent about four months hibernating in the wild during winter. While in captivity again, it increased its performance at the same rate it had done during the experiments in the previous year. By the end of its second experimental year, the animal reached a performance level of around 90%.

Our results suggest that bats have developed effective mechanisms to circumvent the negative effects of torpor and hibernation on memory consolidation and prevent loss of memory during daily torpor and long-term hibernation.

Implications

For animals moving freely in three dimensions, we can assume that an environment full of structures and obstacles might be more complex than an open space. It likely adds to the overall complexity, if these structures change over time, as is the case with vegetation. If in turn these changing structures are potential predictors for patchy food sources (Siemers 2001), we would assume that complexity is again increased. For insectivorous bats that search for prey by echolocation, such structures add an additional level of difficulty. Specifically, echoes reflected from the background have to be distinguished from the echoes returning from potential prey items (e.g., Schnitzler et al. 2003; Siemers & Schnitzler 2004).

I therefore categorized foraging habitats including forests or fields as more complex than foraging habitats over water or in open space (see Chapter 1). I hypothesized that species hunting in more complex environments would be faster learners and more flexible in their behavior than species foraging in less complex environments.

I have shown that behavioral flexibility and learning performance of European bat species in a foraging task may be predicted by their foraging ecology. My results support the idea that cognitive skills are connected with environmental complexity (Godfrey-Smith 2001). Species foraging in more complex habitats develop more advanced cognitive abilities and show higher behavioral flexibility than species foraging in less complex habitats. At this point however, it is not possible to make inferences about the causal relationship between cognition and environmental complexity. We do not know whether species develop higher cognitive skills because they live in a more complex environment, or whether species are able to survive in a more complex environment because they have more advanced cognitive skills.

Nevertheless, I also found that in another situation in which an environmental change occurred that would not naturally happen in the wild, namely light at night, the in general flexible greater mouse-eared bat did not change its behavioral response.

When measuring behavioral flexibility in response to changes, there is a qualitative difference between changes that occur naturally, like a food source changing its place, and anthropogenic changes. When a previously successful strategy to obtain food was not effective anymore, I found that bat species differ in their behavioral flexibility and learning performance (Chapter 1). However, all animals eventually tried new paths to find food. This was as expected, given that regardless how simple a natural environment is, changes in food availability will occur eventually and individuals must be able to cope with such changes. Genuinely anthropogenic disturbances however, like light pollution, might have occurred and spread only recently. Animals might not have had the time to evolve strategies to cope with theses changes in their environment. However, changes caused by human disturbance are common and it is important to find out how bats respond to them.

Bat species of the genus *Myotis* are known to be light averse (e.g., Rydell 1992). I tested individuals of the species *M. myotis* on their response to light disturbance and found that although slight long-term habituation might occur, in general these bats keep avoiding lighted areas even after having experience with light for several years. With light pollution increasing globally this means that the available foraging grounds for such light-averse species may be decreasing. Additionally, insects attracted by lights might not be available as prey in unlit areas where the bats forage (Arlettaz et al. 2000). When trying to avoid lit areas, bats might be forced to forage in less productive areas or at places where other conditions, like predation pressure, are less favorable. Other bats, especially fast flying species like *Pipistrellus* or *Eptesicus* species, have learned to cope with light pollution and might even actively use areas around lights as foraging grounds (e.g., Schnitzler et al. 1987; Rydell 1991, 1992). However, it is important to know that certain species are not able to cope flexibly with light disturbance and this needs to be taken into consideration when planning how to illuminate streets and buildings at night.

I also found that mouse-eared bats are able to learn socially and that information transfer can occur across species boundaries. Furthermore, the acquisition of new information does not seem to be negatively influenced by daily torpor and the retention of newly acquired information is not affected by long-term hibernation over winter. Daily torpor and long-term hibernation are characterized by a very different physiological state than sleep. During sleep body temperature may drop slightly and animals usually are less responsive to external stimuli like light or sound. However, the transition to wakefulness happens quickly and does not come with increased energy demands. Sleep is generally thought to be important for memory consolidation (e.g., Van Dongen et al. 2003). In contrast, a larger drop in core body temperature accompanies torpor and hibernation. Responsiveness to external stimuli is further decreased and the transition to wakefulness may take some time (e.g., Luo et al. 2014) and require considerable amounts of energy. Torpor and hibernation lie on a continuum and differ in duration, magnitude of the decrease in body temperature, and metabolic rate. Hibernation is characterized by not only a larger drop of body temperature but also of metabolic rate and takes place over a longer duration. Both states, torpor and hibernation, have been associated with an impairment of memory consolidation and retention in other mammals (for a detailed description of the difference between sleep, torpor, and hibernation and a review on the negative impacts of torpor and hibernation on learning see Roth et al. 2010). As laid out in Chapter 2, bats are very long-lived mammals and the accumulation and preservation of information over many years is therefore vital to relocate roosts and foraging sites and to increase foraging success by learning new cues that might indicate prey.

Future Directions

We now understand more about the predictors of cognition in bats. We know that foraging ecology can be an indicator for learning performance and behavioral flexibility. However, it is important to expand the species range tested, to find out whether these results hold true also for distantly related species groups.

I have shown that mouse-eared bats can learn socially in the laboratory even across species boundaries, and that socially acquired information can be retained for at least a year. The next step would be to find out how common social learning is in the wild and whether it occurs at higher rates when less artificial cues are involved. The amount of information gathered by social learning, as compared to trial-and-error learning, and the duration of its retention would also be interesting to focus on. Additionally, it should be investigated, whether information transfer across species happens under natural conditions. Mouse-eared bats, like many other bat species, often form large mixed-species assemblages. The role of these mixed groups for the information transfer across species should be investigated. It would also be interesting to know whether mouse-eared bats can transfer information about potential predators or roost and foraging sites and what, if any, role echolocation plays in intra- and interspecific communication (Jones & Siemers 2011). The ecology of mouse-eared bats is relatively well studied. However, unlike for example Bechstein's bats, little is known about potential social groups within large colonies and information transfer within and among these groups.

We studied the influence of daily torpor on learning performance of relatively easy tasks and did not find a negative effect. It would therefore be interesting to know whether more complicated tasks would be more affected by daily torpor. Also, the physiological mechanisms bats use to avoid memory loss during daily torpor and hibernation should be investigated.

Last, I tested the effect of different light conditions on the foraging behavior of greater mouse-eared bats under controlled laboratory conditions. Such experiments need to be taken into the field, to assess how serious the negative effects of light pollution are on light-averse species in terms of foraging success, predation, or the ability to locate suitable roosts. For the development of bat-friendly lights, however, not only the direct effects on bats need to be studied. Additionally, the influence of lights on other species in direct or indirect contact with bats has to be considered. A great step in this direction has already been taken by the “Light on Nature” project by the Netherlands Institute of Ecology and the University of Wageningen (www.lichtopnatuur.org) and the “Loss of the Night Network” (www.verlustdernacht.de).

I feel that my work has advanced our understanding of bat cognition and behavior and provides important insight into the learning abilities of bats. It should also contribute to our knowledge about the ability of bats to adjust to changing environmental conditions. Additionally, it opens up new exciting paths for future research.

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Thank you for being my inspiration!

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LIST OF FIGURES

LIST OF TABLES

AUTHOR CONTRIBUTIONS

(where more than one author contributed to the same part of the project, authors are named in the order of their appearance on the authors list of the respective manuscript)

General Introduction

The general introduction was written by me with helpful comments from Bruno-Markus Clarin, Klemen Koselj, Rachel Page, and John Ratcliffe.

Chapter 1 (Foraging ecology predicts learning performance in insectivorous bats)

The plastic maze as a set up for learning experiments in shrews and bats was invented by RAP and Sophie von Merten (Page et al. 2012). The idea to compare learning and re-learning performance of bat species with different ecological background in the maze was proposed by RAP and BMS. Details of the experimental protocol were developed by me and IR. Experiments, video- and data- analysis were conducted by me. I wrote a first draft of the manuscript, which was refined with much help from IR, RAP, and BMS.

Chapter 2 (Social learning within and across species: information transfer in mouse-eared bats)

The idea to this experiment and the general experimental protocol were proposed by me. Details of the experimental procedure were refined together with RAP, JMR, and BMS. Experiments were mostly conducted by me. IB took over some experimental nights. I analyzed the videos and data and wrote a first draft of the manuscript, which was refined with much help from RAP and JMR.

Chapter 3 (Do bats experience a trade-off between energy conservation and learning?)

This experiment was the idea of IR and BMS. Details of the experimental protocol were developed by IR and me. The experiments and video analysis were conducted by IR. Statistical analysis was performed by IR and me. IR wrote the first draft of the manuscript, which was refined together with me.

Chapter 4 (Effect of different light conditions on *Myotis myotis* foraging behavior)

This project was conducted in collaboration with Philips Lighting. The idea was proposed by MD. The general experimental procedure was planned by BMS and refined by me and BMC. The experiments were conducted by me and BMC. I also performed sound analysis and most of the video analysis. Statistical analysis was conducted by me, BMC, and SZ. I wrote the first draft of the manuscript which was refined together with BMC and SZ.

General Discussion

The general discussion was written by me with helpful comments from Bruno-Markus Clarin, Klemen Koselj, Sophie von Merten, and John Ratcliffe.

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LIST OF PUBLICATIONS

Part of this thesis

Clarin TMA, Ruczyński I, Page RA, Siemers BM (2013). Foraging ecology predicts learning performance in insectivorous bats. PLoS ONE 8(6): e64823.

Clarin TMA, Borissov I, Page RA, Ratcliffe JM, Siemers BM: Social learning within and across species: information transfer in mouse-eared bats. Canadian Journal of Zoology 92, p. 129-139

Under Review for the Journal of Experimental Biology

Ruczyński I, Clarin TMA, Siemers BM: Do bats experience a trade-off between energy conservation and learning?

In Preparation

Clarin TMA, Clarin BM, Zsebök S, Donners M, Siemers BM: Effect of different light conditions on *Myotis myotis* foraging behavior

Not part of this thesis

Clarin T, Sandhu S, Apfelbach R (2010). Odor detection and odor discrimination in subadult and adult rats for two enantiomeric odorants supported by c-fos data. Behavioural Brain Research 206 (2), p. 229-235

LIST OF CONFERENCE CONTRIBUTIONS

Oral Presentations

2011

"Flexible bats in two-dimensional space": Treffen der Fledermausforscher in Deutschland (German Bat Researchers Meeting) (20.01.-22.01.2011 Loccum bei Hannover; Germany)

"Flexible bats in two-dimensional space": MPIO Retreat (03.02.-05.02.2011 Lindau; Germany)

2012

"Social learning in bats": MPIO Retreat (26.01.-28.01.2012 Biberach; Germany)

2013

„Social Learning in Mouse-Eared Bats": Treffen der Fledermausforscher in Deutschland (German Bat Researchers Meeting) (11.01.-13.01.2013 Rottenburg-Ergenzingen; Germany)

"Social learning in the mouse-eared bats, *Myotis myotis* and *Myotis oxygnathus*": 106th Annual Meeting of the German Zoological Society (13.09.-16.09.2013 München; Germany)

"Social Learning Within and Across Species: Information Transfer in Mouse-Eared Bats": 16th International Bat Research Conference; 43rd North American Symposium on Bat Research (11.08.-15.08.2013 San Jose; Costa Rica)

Poster

2010

"Can bats count?": 15th International Bat Research Conference (23.08.-27.08.2010 Praha; Czech Republic)

2013

"Effect of different light conditions on *M. myotis* foraging behavior": 3rd International Berlin Bat Meeting: Bats in the Anthropocene (01.03.-03.03.2013 Berlin; Germany)

Conference Participation without Contribution

2009

DZG Fachgruppe Verhaltensbiologie: Graduiertentreffen Verhaltensbiologie (11.11.-13.11.2009 Seewiesen; Germany)

2014

Mini-symposium "Ecological Effects of Light Pollution" (08.01.2014 Seewiesen; Germany)

9th Topical Meeting of the Ethologische Gesellschaft: Function and Mechanisms of Animal Behaviour (06.02.-08.02.2014 Tutzing; Germany)

PARTICIPATION IN THE IMPRS-OB CURRICULUM

Courses

2010

“Coping with the Challenges of a PhD” (04.10-06.10.2010 Seewiesen; Germany)
“Introduction of Basic Statistics with R” (06.10.-08.10.2010 Seewiesen; Germany)
“Linear models and linear mixed models with R” (23.11.-25.11.2010 Radolfzell; Germany)

2011

“Generalized linear models (GLM) and generalized linear mixed models (GLMM) with R” (28.03.-31.03.2011 Radolfzell; Germany)

2012

“Scientific Integrity” (09.10.2012 Seewiesen; Germany)
“First Aid during field work” (18.10.-21.10.2012 Radolfzell; Germany)
“Introduction to scientific paper-writing” (15.11.-21.11.2012 Balmaha; Scotland)

2013

“Scientific Writing” (06.05.-07.05.2013 Seewiesen; Germany)
“Conference Presentation” (27.11.-29.11.2013 Seewiesen; Germany)

Other IMPRS-OB events

2010

Symposium Grand Challenges in Ecology and Evolution (01.10.-03.10.2010 Seewiesen; Germany)
Students Retreat: What do you expect from the IMPRS? (15.10.-17.10.2010 Überlingen; Germany)

2011

2nd IMPRS Selection Symposium (14.03.-18.03.2011 Radolfzell, Konstanz, Seewiesen; Germany)

2012

Students Retreat: Career options after the PhD (29.11.-01.12.2012 Lindau; Germany)

2013

Evaluation of the IMPRS for Organismal Biology (24.09.-25.09.2013 Seewiesen; Germany)
Symposium Grand Challenges in Communication in Social Communities (25.09.-26.09.2013 Seewiesen; Germany)
Students Retreat: Academic Communication and Leadership skills (17.11.-19.11.2013 Hitzenlinde in Leutkirch; Germany)

EXTRA-CURRICULAR OUTREACH AND OTHER ACTIVITIES

2011

"A PhD-thesis: Learning and Cognition in Bats": Talk given as part of the First-Semester-Students Retreat organized by the "Fachschaft Biologie" of the Ludwigs-Maximilian-Universität Munich (11.10.2011 Grafrath; Germany)

2012

Organisation of the MPIO Retreat 2012 at the Jugendherberge Biberach (26.01.-28.01.2012) together with Daniela Schmieder, Susanne Seltmann, Jaap van Schaik

"Foraging ecology predicts learning performance in insectivorous bats": Talk given at the Smithsonian Tropical Research Institute as part of the Behavioral Seminar (10.04.2012 Panama City; Panama)

"A PhD-thesis: Learning and Cognition in Bats": Talk given as part of the First-Semester-Students Retreat organized by the "Fachschaft Biologie" of the Ludwigs-Maximilian-Universität Munich (10.10.2012 Grafrath; Germany)

2013

"Generalized Linear Modelling" Course by Prof. Michael Crawley taken at the Imperial College London (04.02.-22.02.2013 Silwood Park; UK)

"A PhD-thesis: Learning and Cognition in Bats": Talk given as part of the First-Semester-Students Retreat organized by the "Fachschaft Biologie" of the Ludwigs-Maximilian-Universität Munich (09.10.2013 Grafrath; Germany)

"Experiments on Cognition in Bats": Talk given at the Tierärztliche Hochschule Hannover as part of the Zoological Colloquium (11.11.2013 Hannover; Germany)