# Multi-species Acoustic Information Networks:

# from Neurons to Predator-Prey Communities

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Version 1.1, 02.11.2021: Correction of factual errors in the Curriculum Vitae

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Habilitationsschrift zur Erlangung der *Venia Legendi* im Fach Zoologie

Vorgelegt an der Ludwig-Maximilians-Universität München,

Fakultät für Biologie, 10.09.2021

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In memory of PD Dr. Björn M. Siemers and Prof. Dr. Lutz Wiegrebe

To Nadine, Felix & Janne

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# Summary

Decisions and actions require appropriate information. In a nutshell, I strive to uncover the **functional and ecological principles of sensing and acting**. My research aims to understand how animals obtain, process and exchange sensory information, how this information informs their actions, and how evolution has shaped sensory-motor processes to match ecological needs. I apply an integrative and comparative approach that combines modelling, neurophysiological studies and behavioural experiments under controlled lab conditions and outside in the real world.

Sensing and acting are tightly intertwined processes within every individual. Beyond the individual, sensing and acting also connect different individuals of the same species, e.g., during communication and courtship, and of different species, e.g., during predator-prey-interactions. These mutual interactions generate diverse, complex and dynamic multi-species information networks (**Fig. 1**), which exist everywhere on the planet, are of large ecological as well as economic importance, yet are still little understood. In my research, I aim to understand the functional and ecological principles of sensing and acting in different behaviourally and ecologically relevant contexts, focusing on a complex multi-species acoustic information network. In four different interrelating research directions, I investigate ***Sensing and Perception in Individuals***; how sensing and acting are adapted to and shape ***Predator-Prey-Interactions***; how active sensing affects ***Communication and Interference in Dynamic Acoustic Information Networks***; and how sensing deals with continuous ***Environmental and Anthropogenic Change and Variation***.

I investigate **sound as the main carrier of information**, which mediates the complex and diverse acoustic information network in the community of echolocating bats and different eared and acoustically communicating insects. I investigate the auditory processing of sound in these taxa, their auditory-guided behaviours, and the ensuing organismal interactions. By comparing across species and sensory systems, I investigate fundamental principles of sensory physiology and behavioural ecology.

# 1 Introduction

We all interact in two main ways with our surroundings: we **collect information with our senses**, and **use our motor systems to act** (Dall et al., 2005). Within each animal, sensing and motor behaviour form a tightly integrated closed loop (Ahissar & Assa, 2016; Zweifel & Hartmann, 2020), to achieve fitness-relevant behavioural goals such as finding food, attracting mates for reproduction, and avoiding and escaping predators. In addition, these individual-level sensory and behavioural processes interact across individuals, shaping their organismic interactions, their ecology and evolution. This is evident in animal communication, but also applies to the framework of my research, the interactions of predators and prey (Dawkins & Krebs, 1979; Endler, 1991; Stevens, 2007; Ruxton, 2009). Within split-seconds, predators and prey have to collect information, evaluate it with their nervous systems, and react accordingly in an adaptive manner. The actions of one contestant change the situation, the sensory input and the required actions of the other contestant. Therefore, from genes over cells to the ecology of organismal interactions, evolution has tightly integrated sensing and acting. In a nutshell, in my here presented research, I strive to uncover the **functional and ecological principles of animal sensing and acting in ecologically relevant contexts**. Using neuroethological, bioacoustic and modelling approaches, I investigate passive and active auditory perception in echolocating bats and eared insects, intra- and interspecific information transfer, and the neuroethology and (co-)evolution of predator-prey-interactions.

## 1.1 Sensory-behavioural algorithms to simplify complexity

Natural selection has not only shaped the morphology of animals (e.g., Price et al., 1984; Schluter & McPhail, 1992), but also their sensory and behavioural properties (Humphries & Driver, 1970; Dominy et al., 2004; Goerlitz et al., 2010b; Giacomini et al., 2021; Hall et al., 2021). Sensory systems provide animals with information about their surroundings, which is processed by the nervous system and informs an animal's actions (Dall et al., 2005), including such crucial behaviours like foraging (Stephens & Krebs, 1986) and predator avoidance (Edmunds, 1974; Lima & Dill, 1990). Importantly, sensory information not only informs actions, but animals actively sample their environment to collect the sensory information they need (Schroeder et al., 2010). **Sensing and acting thus form a tightly integrated loop** (Ahissar & Assa, 2016; Zweifel & Hartmann, 2020). Animals constantly receive an overload of sensory input, where most behaviourally relevant information, e.g., about food, mates, and predators, is rare and noisy, i.e., it is occurring with relatively low probability within a background of unimportant information (Dukas, 2002; Krauzlis et al., 2014). Multiple processes, from peripheral spatio-temporal sampling (Yarbus, 1967) to cognitive attention (Dukas, 2002), filter this information, thereby simplifying sensory complexity for adaptive behavioural actions. **Behavioural algorithms** are the rules that map the sensory input to adaptive motor output (Marr, 1982; Krakauer et al., 2017; Hein et al., 2020). Sequences of behavioural algorithms are the basis for and combine into fitness-relevant natural behaviours, such as courtship, prey pursuit or predator evasion, thereby linking low-level physiological implementations to the coarse-level ecological outcomes of behaviour.

## 1.2 Sensory-behavioural strategies in predator-prey-interactions

Some of the most crucial behaviours for survival are **foraging** (Stephens & Krebs, 1986) and **predator avoidance** (Edmunds, 1974; Lima & Dill, 1990). Both behaviours depend on the adequate processing of sensory input to detect, find and evaluate potential food items (including prey) and potential predators, respectively, and on the appropriate action for consuming the food and escaping the predator. The relevance of both behaviours for survival renders them ideal to study behavioural adaptations in a functional and ecological context. Predator-prey-interactions occur everywhere in nature, pose a strong selection pressure on both predators and prey (Dawkins & Krebs, 1979; Lima & Dill, 1990; Endler, 1991; Lima, 2002), and require rapid reactions based on limited information (Catania & Remple, 2005; Bar et al., 2015; Hein & Martin, 2020). Besides morphological adaptations, **sensory and behavioural strategies are crucial for both predators and prey** (Kavaliers & Choleris, 2001) and are particularly well documented in the visual system, including camouflage and warning colouration (Stevens, 2007; Ruxton, 2009) and visually-guided pursuit and escape (e.g., Ewert, 1987; Mischiati et al., 2015; Temizer et al., 2015; Mills et al., 2018). Pursuit and evasion are great models to study the sensory-behavioural strategies of predators and prey (Hein et al., 2020). They serve a clearly identifiable and observable behavioural goal that can be experimentally tracked and mathematically described (e.g., Mischiati et al., 2015; Corcoran & Conner, 2016; Fujioka et al., 2016; Mills et al., 2018).

Echolocating bats and insects with bat-detecting ears (moths and bushcrickets) are ideal for research into sensory-behavioural strategies and predator-prey interactions. Both taxa are speciose, diverse and connected as predators and prey, where they functionally, ecologically and evolutionary interact with one another solely based on auditory information. I take advantage of this biodiversity, the active sensory system of bats, and the contrast between one of the simplest (only 1-4 auditory neurons in moths) and one of the most derived auditory systems (echolocating bats), to comparatively investigate the functional and ecological principles of sensing and acting in different behaviourally and ecologically relevant contexts. Importantly, my research encourages direct comparisons between sensory systems (both active and passive) and between unrelated taxa where the same traits evolved independently (vocalizations for spatial orientation in bats and toothed whales; ears in insects), to ultimately understand **fundamental principles of sensory processing, functional ecology and trait evolution in interacting organisms**. Such a **comparative approach** is crucial to advance our general understanding of sensory-behavioural algorithms including common principles as well as fundamental differences between sensory systems For example, sensory flow information is important during visual steering for flight control (Gibson, 1954; Krapp & Hengstenberg, 1996), but also exploited by acoustically-orienting bats (Müller & Schnitzler, 1999; Kugler et al., 2016). Likewise, looming cues are used by the visual system to detect an attack (Temizer et al., 2015), which might also be exploited by the auditory system (Ghazanfar et al., 2002). In contrast, despite similar performance in detecting spatial frequencies, the underlying sensory mechanisms differ between vision (Wiesel & Hubel, 1966) and echolocation (**Baier et al., 2019**), likely due to the low angular resolution of echolocation (Geberl et al., 2019)

## 1.3 Echolocation and sound-based environmental perception

My research focuses on **sound-based perception of the world**. Many animals, including insects, anurans, birds and mammals, use acoustic information for communication and species discrimination (Bradbury & Vehrencamp, 2011). Acoustic information is independent of illumination and spreads well through the environment (Marten & Marler, 1977; Marten et al., 1977; Wehner, 1997; Dominy et al., 2001; Dominy et al., 2004). Many animals from such diverse taxa as owls, bats and primates also use sound for hunting, by detecting and localizing their prey by listening for prey-generated calls and noises (Payne, 1971; Charles-Dominique, 1977; Arlettaz et al., 2001; Page & Ryan, 2005; Goerlitz & Siemers, 2007). Furthermore, bats (Chiroptera) are the taxa best known for their extensive reliance on sound for environmental perception and for hunting (Griffin, 1958; Neuweiler, 2000), by using a biological sonar termed echolocation.

**Echolocating bats** perceive their environment based on an active sampling of space with self-generated powerful calls (e.g., Schnitzler et al., 2003; Moss et al., 2011; Corcoran & Moss, 2017). They use various sensory strategies to find their prey, such as eavesdropping on prey sounds, simple detection of prey echoes in open space, and complex auditory analysis of wing-beat generated "flutter information" within vegetation (Denzinger & Schnitzler, 2013), with significant flexibility in their sensory-behavioural strategies (Ratcliffe & Dawson, 2003; Hackett et al., 2014; **Lattenkamp et al., 2018**). This well-studied sensory perception of bats provides the basis to study the sensory-motor control rules of prey pursuit (e.g., Ghose et al., 2006; Bar et al., 2015; Vanderelst & Peremans, 2018a). The term ***echolocation*** was coined by Donald Griffin (Griffin, 1944), highlighting the ability of bats (and other echolocators) to locate an object's spatial position based on returning sound echoes. However, bat echolocation is capable of more than just object localisation, which is better captured by the phrase ***echo-imaging***, meaning the ability to generate an internal representation of the environment. Importantly, the phrase *imaging* must not imply that this internal representation resembles a visual image as we experience it. More likely, echo-imaging generates its own kind of internal representation of the environment with its own characteristics; as is the case for any sensory system (von Uexküll, 1909; Nagel, 1974). The internal representation of the world based on echo-imaging has high acuity and resolution in distance (Simmons, 1971), but is "blurry" along elevation and azimuth (Geberl et al., 2019). It encodes the world likely along frequency and time (Wiegrebe, 2008; Simmons, 2012), possibly without conversion into spatial distance (Amichai & Yovel, 2021). The further neuronal representation of environmental features shows striking differences, e.g. in spatial encoding (Yartsev et al., 2011; Ginosar et al., 2021), as well as similarities, e.g. in sensory flow extraction (Müller & Schnitzler, 1999; Kugler et al., 2016) and spatial frequency perception (**Baier et al., 2019**), to visual systems.

Eared moths (Lepidoptera) have been intensively studied for their multiple evolution of ears and evasive flight behaviours against attacking bat predators (Roeder, 1998). **Eared moths possess the simplest auditory system on earth** (ter Hofstede & Ratcliffe, 2016) **with only 1-4 primary auditory afferents** depending on family (Yager, 1999; Yack, 2004), that directly connect to the tympanum. Echolocating bats and eared moths are engaged in predator-prey-interactions (ter Hofstede & Ratcliffe, 2016; Kawahara et al., 2019) that are exclusively based on auditory information (Conner & Corcoran, 2012) and often involve three-dimensional search, pursuit and evasive manoeuvres (Corcoran & Conner, 2016). The simple auditory system of eared moths makes them an ideal system to link sensory input, neuronal processing and evasive behavioural output. In general, the evasive manoeuvres of prey animals received a lot of theoretical (e.g., Howland, 1974; Domenici et al., 2011a; Goerlitz et al., 2020) and empirical interest (e.g., Webb, 1976; Domenici et al., 2011b; Corcoran & Conner, 2016). In eared moths, the evasive response to sounds was described already in the 1950ies and '60ies (Treat, 1955; Roeder, 1967), suggesting a two-staged response consisting of negative phonotaxis to quiet sounds (i.e., distant bat) and last-ditch responses such as loops, zig-zags and dropping to the ground to loud sounds (i.e., close bats). In parallel, the peripheral neural encoding of sound by the ears of moths has been well-studied in many different species of different families and with different ears (e.g., Fullard, 1998; ter Hofstede et al., 2013; ter Hofstede & Ratcliffe, 2016). In contrast to the neuronal basis, the suggested two-staged evasive flight is much less studied, lacks interspecific comparisons (summarized in **Hügel & Goerlitz, 2019**) and theoretical models (but see Corcoran & Conner, 2016; Goerlitz et al., 2020), hindering a mechanistic understanding of the sensory-motor link and the corresponding behavioural algorithms.

## 1.4 My research

My research aims to understand **information use, animal behaviour and organismal interactions in ecologically relevant contexts** on multiple levels from the informational input, to its neuronal and cognitive processing and to its adaptive functions. To this end, I study how animals obtain and process sensory information, how they adjust their actions in response to changing information, and how evolution has shaped sensory-motor strategies to match environmental conditions and ecological needs. I pursue these questions in the fitness-relevant context of predator-prey interactions, using echolocating bats and eared insects (moths and bushcrickets) as model systems. These taxa strongly rely on auditory information for communication and environmental perception, and functionally, ecologically and evolutionary interact with one another as predator and prey based on auditory information (**Fig. 1**). These mutual interactions generate diverse, complex and dynamic multi-species information networks, which exist everywhere on the planet, are of large ecological as well as economic importance, yet are still little understood (McGregor, 2005). I apply an integrative and comparative approach that combines state-of-the-art technology including acoustic virtual realities, 3D-flight tracking and biologging for behavioural experiments in controlled lab and natural field conditions with theoretical modelling and neurophysiological experiments. In my long-term vision, we will see the world from the animal's perspective – and understand the functional and ecological principles of its sensory-behavioural strategies: how and why they work the way they work.

- In individuals, I investigate the acquisition of auditory information to elucidate the **sensory strategies, behavioural algorithms and ecological drivers of sound-based sensing**. By comparing across sensory systems (Baier et al., 2019) and species (Egert-Berg et al., 2018; Hügel & Goerlitz, 2019), I address sensory-system- and species-specific mechanistic differences and ecological effects.
- Bats and eared insects **interact as predators and prey**. In eared moths, I investigate the prey's adaptive traits selected by bat predation, from neuronal processing (ter Hofstede et

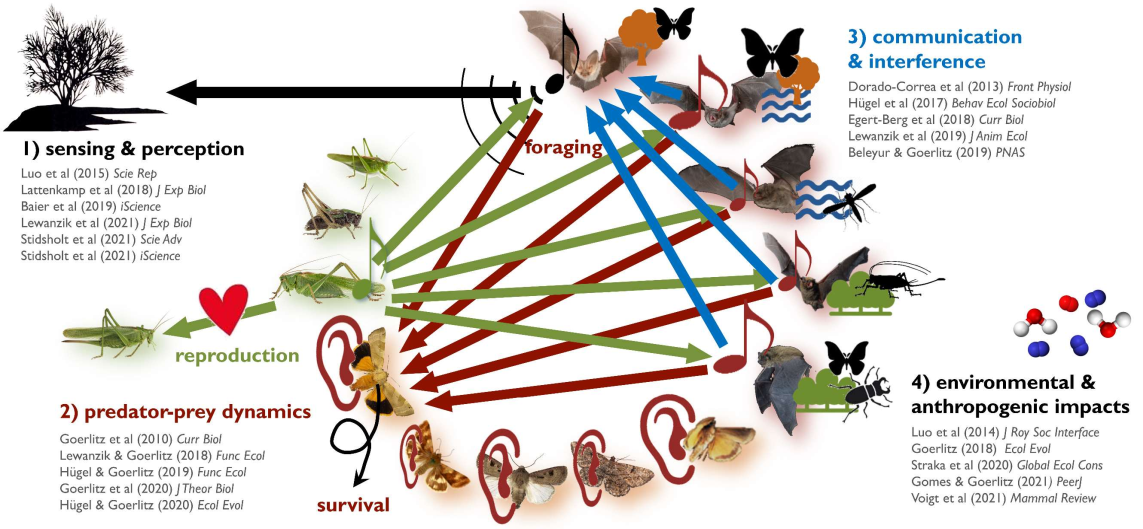

**Fig. 1: Complex multi-species acoustic information networks.** In the darkness of every night, the large diversity of echolocating bats, acoustically communicating and other ear-possessing insects form complex interspecific acoustic information networks.

**(1) Sensing & Perception:** echolocating bats employ self-generated sounds to perceive their surroundings, showing flexible, fast and task-specific sensory-motor integration to optimize information flow.

**(2) Predator-prey interactions:** echolocation drove the evolution of ears and anti-predator behaviours in many insects (e.g., moths, red arrows). Importantly, predators and prey differ in many functional traits (call parameters, prey preferences, flight & hearing ability, habitats, activity periods, etc.), resulting in a complex and diverse interspecific network with species-specific-connections and -interactions, which is virtually unexplored. Besides listening for predators, many insects use sound also for their own communication, e.g., bushcrickets attracting mates (green arrows). Because their courtship song also attracts predatory eavesdropping bats, these species require strategies to trade-off reproduction with survival.

**(3) Communication & interference:** echolocation evolved for the signaller's benefit, but the continuous and powerful calls are also audible to other bats (blue arrows), sustaining complex dynamic acoustic information networks between individuals of the same and different species. On the one hand, echolocation calls provide task- and species-specific information and may support community-level social structures and coordinated group flight. On the other hand, the calls of other bats may interfere with the perception of a bat's own faint echoes ("sonar cocktail party nightmare"), yet with increasing evidence contesting this idea.

**(4) Environmental and anthropogenic impacts.** Both natural variation (e.g., the daily and seasonal fluctuation in weather and thus sound attenuation) and anthropogenic change (e.g., noise and light pollution) are external factors that influence the biological processes described above, with direct consequences on the animals' perception and behaviour, and downstream consequences on their survival and reproduction, and finally on species interactions, ecological networks and ecosystem functioning.

**Overall, the objective of my research** is to understand the functional and ecological principles of animal sensing and acting, by investigating functional sensory-motor processes in relation to an animal's biotic and abiotic environment. I therefore study individual-level sensory-behavioural processes, the organismic interactions in this network, and community-wide network interactions.

al., 2013; Goerlitz et al., 2020) to the variability of anti-predator behaviour (Hügel & Goerlitz, 2019), as well as the predator's counter-measure (Goerlitz et al., 2010b; Lewanzik & Goerlitz, 2018) and its evolution. In bushcrickets, whose courtship song not only attracts mates but also predators, I investigate the adaptive decision-making strategies to trade-off reproduction and survival.

- Bats are **highly social and vocal**. Their vocalisations support complex, dynamic and three-dimensional interspecific communication networks that are virtually unexplored and both beneficial (intra- and interspecific information transfer: Egert-Berg et al., 2018; Lewanzik et al., 2019) and potentially costly (interference and jamming: Beleyur & Goerlitz, 2019). Using modelling and field experiments with flying groups of bats, I quantify the perceived sensory

scene and study the behavioural rules, inter-individual interactions and collective movements.
- Intersecting all my research topics is another question: **how does sensory processing deal with variation and change?** Sensory processing naturally copes with huge variation in physical input and dynamic changes of the environment, which is recently further challenged by anthropogenic changes (*light*: Hügel & Goerlitz (2020), Straka et al. (2020); *noise*: Luo et al. (2015), Gomes & Goerlitz (2020); *warming*: Luo et al. (2014)). Throughout my work, I investigate sensory-behavioural adaptations to cope with variation and change, ranging from fast task-dependent adjustments, over unpredictable organismic interactions to slow anthropogenic change.

To address these fundamental questions in sensory-behavioural ecology, I integrate various **methods** into my research, covering neuroethological experiments in the lab and field, custom-developed technical systems and software, and diverse modelling, placing my work at the forefront of state-of-the-art technology for **quantitative sensory-behavioural research in wild and free-flying animals**. Specifically, I include precisely computer-controlled behavioural observations and experiments in the lab and field; ground-based 3D-tracking of animal movement (acoustic and video); animal-borne tags to study primary sensory input, sensory sampling and movement in the field (bio-logging); auditory neurophysiology; varied bioacoustic analyses; and modelling of sensory input and movement trajectories. For example, my research group and I are at the forefront of developing semi-automated multi-microphone systems for precise sound-analysis and three-dimensional localization of freely moving vocalising animals. The acoustic properties of *recorded* (ultra-)sound is strongly affected by the distance to the vocalising animal (**Goerlitz, 2018**) and the recording methods (Ratcliffe & Jakobsen, 2018). In addition, echolocating bats constantly adjust their flight and call parameters **(Lewanzik & Goerlitz, 2018; Lewanzik & Goerlitz, 2021**). Analysing the *emitted* vocalisations and the flight behaviour of bats thus depends on precise calculation of their spatial positions and the *emitted* calls, which is even more challenging when done in the field – where however natural behaviour is happening. To achieve this, I develop (semi-)automated and precise tools for measuring the 3D-position and emitted call parameters of multiple free-flying bats in the lab and wild, based on my extensive experience in bioacoustic analysis (e.g., Goerlitz & Siemers, 2007; Goerlitz et al., 2008a; **Goerlitz et al., 2008b; Goerlitz et al., 2012; Luo et al., 2015; Goerlitz, 2018; Lattenkamp et al., 2018; Gomes & Goerlitz, 2020**) and flight path reconstruction (**Goerlitz et al., 2010b; Hügel et al., 2017; Lewanzik & Goerlitz, 2018; Lewanzik & Goerlitz, 2021**). To simplify the flexible use of large multi-microphone arrays in the field, I also contribute to methods for the automated measurement of microphone positions on arbitrary structures in natural settings (**Batstone et al., 2019**). As atmospheric parameters are crucial for these acoustic analyses, I provide information and tools for their calculations (**Goerlitz, 2018**). Lastly, in an earlier study aiming to test methods to protect expensive research equipment in the field, we found that informative and friendly labels significantly lowered how often passers-by touched, disturbed and destroyed the equipment (**Clarin et al., 2014**), highlighting the important role that mode of address and tone of the message play in science communication.

# 2 Sensing and perception of the environment

IT USED TO BE A COMMON MISCONCEPTION THAT BATS' USE OF SOUND PULSES TO NAVIGATE AND LOCATE PREY IS A CRUDE SYSTEM […].

Suga (1990)

**Sensory processing is generally dynamic** (Schroeder et al., 2010). This includes both the dynamic sampling of a constant environment as well as the perception of movement in a dynamic environment. For active sampling of (stationary) environments, the visual system uses saccadic eye-movements to selectively sample a visual scene (reviewed in Kowler, 2011), the olfactory system compares bilateral input to detect odour gradients (Rajan et al., 2006; Steck et al., 2010), active touch employs whisker movements to analyse objects (Anjum et al., 2006), and the auditory systems relies on its high computational power for auditory scene analysis and stream segregation (Bregman, 1990). When objects in the environment are moving, this creates spatio-temporally changing information. Sensory systems are very sensitive and specialised to extract such motion-related features, such as during foreground-background separation and the analysis of direction and velocity of motion in the visual system (Ewert, 1968) or the extraction of spectral and spatial motion in the auditory system (Bregman, 1990; Andoni & Pollak, 2011).

In addition to this dynamic and active sampling, **echolocation is an active sensory system in the more restrictive sense that it that actively emits energy into the environment**, which interacts with and is reflected by the environment, and which is then analysed by the nervous system (Nelson & MacIver, 2006; Zweifel & Hartmann, 2020) – like electrolocation, active touch and human-made radar and sonar. This active sensing is a highly dynamic process. Echolocation is very flexible and constantly adapts to the behavioural task and the local surrounding by adjusting the temporal, spectral and spatial features of the echolocation calls (reviewed in Moss & Surlykke, 2010). The most derived echolocation systems are found in bats (order Chiroptera, except for almost all Pteropodiae) and toothed whales (suborder Odontoceti). Both groups are only distantly related (e.g., Liu et al., 2010), yet they show a remarkable similarity in their echolocation behaviour, **pointing towards convergent evolution due to strong selective pressure on high-speed active sensing and auditory processing**.

**Echolocation evolved as the main remote sense for orientation and foraging under lightless conditions**. Bats, one of the most notable taxa using echolocation, fly and forage in complex 3D environments. In the 60 years since Griffin's seminal "Listening in the Dark" (Griffin, 1958), the number of published studies on echolocation has strongly grown, and yet, we do not fully understand how the auditory system solves the same tasks as the visual system with a fundamentally different sensory apparatus. Based on a standard mammalian auditory system, bats are experts in auditory processing (Neuweiler, 1990; Neuweiler & Schmidt, 1993; Simmons, 2014; Corcoran & Moss, 2017) and possess specialized auditory mechanisms to compute an echo-based internal representation of their outside world (Goerlitz et al., 2008b). Bats use their echo-based sensory input for multiple purposes, including orientation (Schnitzler et al., 2003), foraging (Neuweiler, 1989) and social interactions (Dechmann et al., 2009; Knörnschild et al., 2012;

Lewanzik et al., 2019) and are thus a perfect model system to study auditory processing and auditory-guided behaviour.

Yet, echolocation also suffers from several **limitations in comparison to other sensory systems**. The eye's two-dimensional retina supports high spatial acuity and resolution along the two dimensions of azimuth and elevation. Perception of the third dimension, depth, arises from computations in the visual cortex by comparing the images of the left and right eye. In contrast to vision, the ear does not possess a spatially oriented sensory epithelium, which results in an intrinsic lack of spatial information. Echolocation supports high acuity in depth perception but is poorly set up for representing azimuth and elevation: target range, i.e., depth, is explicitly encoded in the time delay between sound emission and echo return (Simmons, 1971; Simmons, 1973), while all incoming sounds —from all directions— are superimposed at one point, the eardrum, thereby destroying spatial information. Any spatial information except for distance must later be neurally computed, including the most basic information such as the direction of a single sound source (Rayleigh, 1907), also resulting in very low resolution along the dimensions of azimuth and elevation (Goerlitz et al., 2010a; Geberl et al., 2019). In vision, azimuth and elevation are topographically represented in the visual cortex (Zeki, 1978), while in echolocating bats, target range (= depth) is topographically represented in the auditory cortex (O'Neill & Suga, 1979; Hoffmann et al., 2008; Hagemann et al., 2010). Further limitations of echolocation, both in comparison to vision and passive hearing, are its relatively short range of only a few meters to maximally a few tens of meters, depending on frequency and object size (Boonman et al., 2013; Goerlitz, 2018), and the discrete nature of the emitted calls, which results in a rather scarce and stroboscopic information flow.

These limitations of echolocation, as well as sensory strategies to overcome them, are evident in the rapid task- and context-dependent biosonar changes. Bats constantly adapt individual vocalisations to the current requirements by changing the spectro-temporal structure (Kalko, 1995; Schnitzler et al., 2003), intensity (Brinkløv et al., 2010; **Lewanzik & Goerlitz, 2018**), beam width (Jakobsen & Surlykke, 2010) and beam direction (Ghose & Moss, 2006; Surlykke et al., 2009) of their echolocation calls, as well as their mouth gape width (Jakobsen & Surlykke, 2010; Jakobsen et al., 2012) and head direction (Ghose & Moss, 2006). Further changes occur on the level of complete call sequences, such as the changes of the spectro-temporal call features during prey pursuit, ending with a high-speed calling pattern that appears to be very stereotyped in both echolocating mammalian groups (e.g., Schnitzler & Kalko, 2001; DeRuiter et al., 2009; Elemans et al., 2011). Echolocation thus constitutes a **fast and flexible system of high-speed sensory-motor integration** (Valentine & Moss, 1998; Ulanovsky & Moss, 2008; Moss & Surlykke, 2010; **Stidsholt et al., 2021a**), exhibiting sensory strategies that match known strategies of other sensory systems, such as gaze control and focusing (Ghose & Moss, 2006; Wisniewska et al., 2012), and enabling navigation and prey pursuit in complex environments based on its own internal representation of space and use of behavioural algorithms (Yartsev et al., 2011; Vanderelst et al., 2015; Vanderelst et al., 2016; Eliav et al., 2018; Vanderelst & Peremans, 2018b; Ginosar et al., 2021). Investigating sensory strategies in echolocation in a comparative approach to other senses will provide insights into potential common sensory strategies as well as unique solutions to overcome the intrinsic limitations of a low-resolution, short-range and stroboscopic sensory system for sampling space. In this chapter, I address the sensory strategies of echolocating bats, investigating their flexibility to optimize information acquisition and their adaptations to overcome system-intrinsic limitations.

## 2.1 Adaptive flexibility in echolocation-based sensory sampling

Active sensing animals (e.g., bats) offer a great advantage for sensory research: we can easily observe their vocalisations to quantify how they adjust sensory processing to changing tasks and environments, in order to understand their sensory strategies (Moss & Surlykke, 2010; Corcoran & Moss, 2017). I use multi-microphone arrays (for localisation and sonar beam analysis), video (for localisation and behavioural analysis), real-time acoustic simulations and collaborative biologging in the field, to study adaptive, task-dependent vocalisation strategies under realistic situations in the lab and field and in comparison to other senses.

Because animals need to acquire adequate and sufficient information, but brain power is energetically costly, they face a **trade-off between gathering too little and too much information**. Echolocating bats are ideal to investigate active sensory adjustments through motor control in naturally behaving animals. All echolocating bats use echolocation to perceive their surroundings for orientation (Schnitzler et al., 2003). In addition, the majority of echolocating bats also use echolocation for foraging, e.g., by listening for the faint returning echoes of their prey (Neuweiler, 1989) or the specific echo-signatures of nectar-bearing flowers (Simon et al., 2011). Despite the large ecological variety of the more than 1200 bat species that echolocate (Wilson & Mittermeier, 2019), every bat needs to perform specific tasks on a daily basis, such as exiting the roost through an opening, drinking from a water body, capturing prey and landing on surfaces. Each of these tasks constitutes a very different sensory-motor challenge, which bats might solve by adaptively adjusting their biosonar parameters to optimize the rate and features of the acquired information. In **Lewanzik & Goerlitz (2021)**, we extended previous work on task-specific behavioural flexibility in echolocation to a systematic quantitative comparison of echolocation during four tasks of increasing sensory-motor complexity (emergence, drinking, landing, prey capture). We show that echolocating barbastelle bats (*Barbastella barbastellus*) optimized multiple parameters independently from each other and adjusted them to the current task. These task-specific differences existed from the onset of object approach, implying that bats plan their sensory-motor program for object approach before execution and exclusively based on information received from search call echoes. With call rates during final prey capture of more than 250 calls/s, we present some of the fastest sensory sampling in bats (Ratcliffe et al., 2013; Russo et al., 2016). Vocalising at such fast rates requires extraordinary performance of the laryngeal muscles, only achieved by specialised super-fast muscles (Elemans et al., 2011), which highlights the outstanding importance of fast sensory sampling during prey capture. Despite this importance, the function of the so-called “final buzz” during prey captures is unclear. Since high call rates improve the perception and evaluation of object movement (Goerlitz et al., 2010a; Baier et al., 2018; Baier & Wiegrebe, 2018), we suggest that barbastelle bat might perceive and track the wing beats of its prey. This would enable barbastelle bats to resolve moving prey from stationary backgrounds and possibly even to estimate prey size and thus profitability based on wing beat frequency. To date, this kind of sensory processing was only shown for high-duty cycle bats that emit very long and constant-frequency echolocation calls (Kober & Schnitzler, 1990; Koselj et al., 2011; Denzinger et al., 2018). Confirming this hypothesis would provide evidence for the convergent evolution of sensory processing of prey features for optimal foraging, yet based on very different sensory cues and underlying sensory-motor specialisations. Overall, we here provide insight into how echolocating animals deal with the constraints they face when sequentially sampling the world through sound by adjusting acoustic information flow from slow to extremely fast in a highly dynamic manner.

In **Lattenkamp et al. (2018)**, we investigated another species of echolocating bat, the highly-specialised greater horseshoe bat *Rhinolophus ferrumequinum*, and its use of passive-acoustic cues. Despite the extreme morphological and neuronal specialisations for echolocation (Ostwald, 1984; Vater et al., 1985; Suga, 1990; Schnitzler & Kalko, 2001), the horseshoe bats in our study were very attentive to various sounds presented from loudspeakers (c.f. Schnitzler, 1968), raising their vocalisation levels and steering their biosonar beam towards the sound source, presumably for further echo-based evaluation. Contrary to my predictions, the bats were equally attentive to prey-related acoustic cues and non-prey sounds. I suggest that the bats evaluate passive acoustic cues for general surveillance of their environment, and supplement echo-acoustic information with environmental acoustic cues to enlarge their perceived space beyond the sensory volume covered by biosonar. The fast orientation of the sonar beam towards passive acoustic cues suggests that the bats perceptually integrate the separate auditory streams of passive acoustic and echo-based information (Barber et al., 2003; Goerlitz et al., 2008b). More general, our findings suggest that even specialised echolocators exploit a wide range of environmental information, and that phylogenetically older sensory systems can support the evolution of sensory specialisations by compensating for their intrinsic limitations.

A key parameter in echolocation is **call intensity**, since it determines the spatial range and volume that a bat can sample (**Goerlitz et al., 2010b; Goerlitz et al., 2020; Stidsholt et al., 2021a; Stidsholt et al., 2021b**). Accordingly, bat calls are amongst the most powerful animal vocalisations to maximize sensory range, despite increasing metabolic costs (Currie et al., 2020). Together with directing their sonar beam towards the sound source, the horseshoe bats increased their call amplitude, probably to optimize signal-to-noise ratio (**Lattenkamp et al., 2018**). However, the *reduction* of call intensity is also an important sensory strategy, which *minimizes* sensory range and thus simplifies the sensory scene and perceptually releases small prey echoes from louder background echoes (**Stidsholt et al., 2021a**). Some species even constantly use a sensory strategy of **low-intensity "stealth" echolocation**, which I investigate. Low-intensity echolocation functions to counter insect hearing (**Goerlitz et al., 2010b; Lewanzik & Goerlitz, 2018**). This function, however, might be a secondary consequence of an original adaptation to dense habitats and a gleaning foraging style (**Clare et al., 2014; de Framond-Bénard et al., in prep-a; Lewanzik et al., in prep**). I discuss the function of low-intensity echolocation for predator-prey interactions and its potential evolution in the following chapter 3.

Overall, my work above shows pronounced behavioural flexibility in the sensory strategies of echolocating bats, including the joint use of phylogenetically older passive listening with derived sophisticated echolocation (**Lattenkamp et al., 2018**) and the independent adjustment of multiple call parameters and individual differences in adjustment strategies (**Lewanzik & Goerlitz, 2021**). Independent call parameter adjustments and inter-individual differences were also shown by another species, the lesser spear-nosed bat *Phyllostomus discolor*, in response to various acoustic challenges (**Luo et al., 2015; Gomes & Goerlitz, 2020**), which I will further discuss in chapter 5 on how sensory processing deals with change and variation. My results contribute to the increasing evidence of behavioural flexibility in the sensory and foraging strategies of echolocating bats (Ratcliffe & Dawson, 2003; Clare et al., 2014; Hackett et al., 2014; Stidsholt et al., in prep), suggesting that many if not all bat species will exploit many more cues and sensory information than classically assumed based on their foraging guilds (Schnitzler & Kalko, 2001).

However, the sensory-behavioural strategies of echolocating bats had mostly been investigated in flight rooms, like in my previously presented studies, or within small patches over rather short time spans in the field. The secret nocturnal life style of bats, their ability for powered flight over long distances and their low body weight made it very difficult to continuously investigate the physiology and ecology of their sensory strategies and behaviour where it really occurs, in complex natural habitats. However, over the past few years**, biologging tags** became sufficiently lightweight and suitable for small flying mammals (Stidsholt et al., 2019). I am collaborating with Prof. Yossi Yovel (Tel Aviv, IL) and Prof. Peter Teglberg Madsen (Aarhus, DK) to mount miniature tags on different bat species, recording GPS, accelerometer and highly sensitive audio data (**Egert-Berg et al., 2018; Stidsholt et al., 2021a; Stidsholt et al., 2021b; Stidsholt et al., in prep**). These tags give unprecedented direct access to the primary sensory stream, the flight behaviour and spatial position of wild free-flying animals, opening amazing possibilities in ecological research of individuals and groups. Our work delivered unprecedented insights into the sensory behaviour and organismal interactions from very detailed (**Stidsholt et al., 2021a; Stidsholt et al., 2021b; Stidsholt et al., in prep**) to large temporal and spatial scales (**Egert-Berg et al., 2018; Stidsholt et al., in prep**), including predator-prey-interactions taking place in split-seconds within less than a meter, to daily and seasonal foraging patterns over tens of kilometres. Our work on comparative foraging ecology and drivers of sociality in bats (**Egert-Berg et al., 2018**) is presented in Chapter 4. Here, I focus on our work on the greater mouse-eared bat *Myotis myotis*, one of the largest European species. It is one of the classical European gleaning bat species (Arlettaz et al., 2001; Siemers & Güttinger, 2006; Dietz et al., 2009), which is considered to forage for large beetles on meadows and open woodland by listening for their walking sounds (Siemers & Güttinger, 2006; Dietz et al., 2009), but actually also strongly relies on aerial hunting as foraging style (**Stidsholt et al., 2021a; Stidsholt et al., 2021b; Stidsholt et al., in prep**).

We caught bats emerging from the Orlova Chuka cave system close to my field station in Bulgaria and equipped them with biologging tags, which recorded GPS, 3D-accelerometer and acoustic data consisting of the outgoing calls and even the faint returning echoes. By combining accelerometer and acoustic data, we first investigated **biomechanical constraints on echolocation in flight and the consequences for bats' sensory strategies** (**Stidsholt et al., 2021b**). As in terrestrial mammals (Bramble, 2015), echolocating bats synchronize breathing to their locomotory strides (wingbeats), thereby saving energy because the exhalation for vocalizations is coupled to muscle contractions required for beating the wings (Speakman & Racey, 1991; Koblitz et al., 2010; Voigt & Lewanzik, 2012). However, depending on the behavioural task, bats can break this tight relationship between sound emission and wingbeats by emitting calls throughout the entire wingbeat cycle as observed in the laboratory (Lancaster et al., 1995; Moss et al., 2006) and field (Kalko & Schnitzler, 1989), but the precise relationship between call timings, call levels and the wingbeat phase remains to be understood and quantified, even more so in the field under natural flight conditions. Here, we first confirmed that bats couple their call emissions during search flight one-to-one to the end of the upstroke of the wingbeat, but that this coupling breaks down during prey capture. After prey detection, the bats increased their call rate while tracking and intercepting the prey (approach and buzz-phase). This increase was partly mediated by an increase in the wingbeat rate, reflecting the kinematic demand to orient towards the prey, but mainly by an increase in the number of calls emitted per wingbeat. During the final prey interception, the bats emitted on average 11 calls per wingbeat cycle, distributed throughout an entire wingbeat cycle, with a 100x lower (-20 dB) call energy summed over all calls during a wingbeat. We suggest that the need for fast sensory sampling during hunting causes bats to emit calls well outside of the optimal wingbeat phase, leading to reduced sound production efficiency. In contrast, during search flight, bats coupled call emission to wingbeats to minimize energy expenditure, but at the cost of low sensory update rates. Given their call rate, flight speed and body size, *M. myotis* receives about one sensory update per one meter flown, corresponding to one sensory update per 10 body lengths flown, which is an extremely low sensory update rate (Healy et al., 2013). **Thus, bats rely on very sparse sensory inputs to guide motor patterns and decision making when commuting and to detect and identify prey**. We posit that this sparse sensory input might be the result of the (bio-)physical constraints of a fast-flying echolocator in air that must couple call rates to a relatively low wingbeat rate to minimize the energy expenditure of echolocating. When periodic snapshots are sufficient (during travel and search), wild bats **prioritise energy efficiency over sensory flow**. In contrast, when high information update rates are critical during hunting periods, bats decouple call emission from wingbeats, and thus **prioritise sensory flow over energy efficiency**. Since these rapid calls are weaker and comprise less than 2% of all calls during a night of hunting, they add little to the bats' overall costs of sound production, despite the inefficiency of decoupling calls from wingbeats. Overall, we suggest that these biomechanical constraints, restricting cheap and powerful vocalizations to specific phases of the wingbeat cycle, have been a major driving force underlying the evolution of slow sensory sampling rates (Jones, 1999) in bats, in turn driving the evolution of complex call designs (Woodward, 1953) and movement patterns (Hedenström & Johansson, 2015) to maximise echo information while avoiding obstacles.

In **Stidsholt et al. (2021a)**, we quantified in detail the call design, movement patterns, and the perceived sensory scene of hunting *M. myotis* bats in the field. **Overall, we show how wild bats adjust their sensory strategies to their prey and natural environment**. The intense calls emitted while commuting and searching for prey maximize sensory volumes and thus extend the object detection range and the chances of detecting small prey. Despite these intense calls, the sensory volume for detecting prey items is short, which, combined with the bats' flight speed, results in low sensory-to-motor-range ratios (~5). In contrast to most other predators (Demšar et al., 2015; Wisniewska et al., 2016), **hunting bats thus operate in a highly reactive mode** (Snyder et al., 2007), meaning they have little time to react to sensory information returning from their prey, leaving them little time for movement planning. Despite this highly reactive mode, we found that bats do not use stereotyped approach movements, but approach their prey at variable speeds and flight patterns. To successfully hunt in a reactive mode over short time scales, bats must rely on efficient auditory stream segregation to guide their motor patterns. By visualising the bats' perceived sensory scenes as echograms based on the on-board sound recordings, we show how bats control the timing and intensity of their calls to simplify the auditory scene. While searching for prey, bats use intense calls with long intervals, resulting in clearly visible echoes of background structures ("clutter") at distances of up to 8 m. We argue that bats actively keep background echoes in their auditory stream for spatial orientation, but keep a distance to these background structures to maintain a clutter-echo-free window for prey detection within about 2 m, thereby temporally separating the prey echoes-of-interest from background echoes. Within 2 m of the prey, the bats deliberately and continuously lowered their call intensity, resulting in received prey echo intensities with a surprisingly narrow and low distribution just above the bats' hearing threshold. Our results show how wild bats adjust their sensory sampling and flight motor planning during foraging. These adjustments lead to very weak prey echoes that bats protect from interference by segregating clutter and prey sensory streams in time and space by using a combination of fast-acting sensory and motor strategies. Doing so may critically facilitate perceptual organization of their sensory inputs to inform echo-guided captures in less than 0.5 s. Counterintuitively, these weak sensory scenes allow echolocating bats to be efficient hunters close to background clutter, broadening the niches available to hunt for insects. **Echolocating bats are therefore extreme examples of predators that have evolved a flexible and rapid control over their dominant sensory system and motor actions to hunt fast, evasive prey efficiently in highly dynamic and complex scenes**.

Finally, in **Stidsholt et al. (in prep)**, we studied the foraging strategies of 30 female greater mouse-eared bats (*M. myotis*) to investigate the **drivers of foraging decisions in the wild**. Foraging success is paramount for the survival and reproduction of animals (Stephens & Krebs, 1986; Prat & Yovel, 2020), yet the drivers of successful foraging are poorly understood. Optimal foraging decisions need to incorporate immediate sensory cues, prior experience and memory, habitat types, resource availability, distribution and distance, capture success and handling times, etc. Here, we combine data on GPS-location, 3D-movement, echolocation, mastication sounds, and metabarcoding of bat faeces to understand how prey and habitat features influence foraging decisions in a wild predator. Besides resting in- and outside of the colony (43% of total night time) and commuting (17%), the ***M. myotis*** **bats used two different foraging strategies**, namely ground gleaning (30% of their time) and aerial hawking (10%). The foraging strategies strongly differed in their success rate (33% vs. 85% for gleaning vs. hawking) and the targeted prey species (larger prey vs. smaller prey). The bats used aerial hawking both during commuting flights and area-restricted foraging flights, with equally high success rates independent of the habitat or flight types. However, rather than targeting flying insects at high success rates, the bats spent 3x more time on targeting larger ground-dwelling prey at low success rates, yet restricted this ground-gleaning primarily to foraging flights, where they obtained the highest success rates above open fields. Since bats spent much more time on a habitat-specific foraging strategy with lower success rate (ground gleaning), we suggest that they actively chose this strategy, presumably to optimize their energy intake because of the much larger prey size. **Overall, our data show that prey size, availability and accessibility are important drivers of habitat choice during foraging**, but also that bats do not focus exclusively on one foraging strategy, habitat and prey type. Our high-resolution data further revealed strong variation across nights and individuals, indicating that foraging decisions are extremely varied between bats of the same species and colony and tied to immediate environmental factors. This huge variation in foraging success, strategy and energy intake is important for energy-efficiency models and conservation efforts where means of a population across one night often guide models and management, but may not be representative of the bat individuals. Further investigations need to link this flexibility in foraging behaviour to the spatio-temporal variation in habitat profitability, to investigate whether individuals adjust their foraging strategies to local prey conditions and profitability (Koselj et al., 2011).

## 2.2 Perception of space by echolocation

To advance our fundamental understanding of sensory processing, a comparative approach is crucial to identify common principles of sensory processing as well as fundamental differences between sensory systems. Some examples of common sensory processing include the perception of sensory flow information, which is used during visual steering for flight control (Gibson, 1954; Krapp & Hengstenberg, 1996) and by acoustically-orienting bats (Müller & Schnitzler, 1999; Kugler et al., 2016). Looming cues are used by the visual system to detect an attack (Temizer et al., 2015), and might likewise be exploited by the auditory system (Ghazanfar et al., 2002). Thirdly, both the visual system's colour constancy ("white balance") (Smithson, 2005) and the auditory system's timbral constancy (Risset & Wessel, 1982; Watkins, 1991; Goerlitz et al., 2008b) enable the perception of an object's spectral properties independent of variation in the environmental (light or sound) spectrum (cf. Chapter 5.1).

Given the fundamental differences in the sensory epithelium between vision (two-dimensional retina whose spatial activation pattern encodes light direction) and hearing (point-like tympanum and frequency-encoding basilar membrane), the sensory mechanisms for perceiving space must differ, too. However, both visually and echo-acoustically orienting animals require information about the spatial layout of their environment for orientation. In vision, spatial frequency analysis is central to the visual perception of the environment's spatial layout (Wiesel & Hubel, 1966). Nocturnal echolocating bats do not have access to this kind of sensory information, but their fast flight in complex three-dimensional habitats clearly shows that they process environmental spatial information, too. In **Baier et al. (2019)**, we trained the lesser spear-nosed bat *Phyllostomus discolor* and used formal psychophysics to quantify bats' perceptual sensitivity to sinusoidal wave patterns of different spatial frequencies, as they naturally occur on agitated water bodies. These wave patterns represent an echo-acoustic equivalent to a sinusoidal luminance-grating used in visual studies. **We demonstrate that bat echo-imaging processes spatial frequency with a high-pass characteristic directly comparable to vision**. This is remarkable because the auditory system lacks a sensor that directly encodes space and evaluates fundamentally different sensory cues for spatial frequency analysis. To investigate the sensory mechanism, we quantified the echo-acoustic parameters of the surface-wave patterns and modelled their spectro-temporal auditory representation, demonstrating that the spectro-temporal auditory representation of a wave pattern implicitly encodes its spatial frequency. We conclude that echo-imaging accesses spatial information by exploiting an inherent environmental high-pass filter for spatial frequency. The functional similarities yet mechanistic differences between visual and auditory system signify **convergent evolution of spatial-information processing**. Our findings challenge the notion that the auditory system's sensory constraints inevitably lead to inferior spatial performance.

For echolocating bats, waves of low spatial frequency and/or low height are perceptually indistinguishable from a flat smooth surface (**Baier et al., 2019**). Smooth surfaces possess mirror-like reflection properties, where the angle of incidence equals the angle of emergence. Thus, bats flying above smooth water only receive an echo from directly orthogonally below them, and no echoes from the forward direction (Siemers et al., 2005; Zsebok et al., 2013). Echolocating bats use this property as a simple and innate perceptual rule to classify horizontally extended smooth surfaces as water, even trying to drink from any artificial horizontal smooth surface (Greif & Siemers, 2010). In contrast, they regularly collide with vertically extended smooth surfaces (Greif et al., 2017). In contrast to water surfaces, which are naturally occurring horizontal echo-acoustic mirrors, no vertical echo-acoustic mirrors exist naturally. Therefore, bats likely interpret the lack of frontal echoes generated by vertical smooth surfaces as an opening in a vertical structure, causing them to collide with the smooth surface when attempting to fly through the perceived opening. Given these two fundamentally different perceptual interpretations of smooth surfaces, we asked how bats interpret angled smooth surfaces (**Rahman et al., in prep**). We presented a smooth metal plate at six different angles (0, 30, 37.5, 45, 60 and 90 degrees) parallel to the flight direction of 40 experimentally naïve, adult greater mouse-eared bats (*Myotis myotis*). With increasing angle of the metal plate, bats reduced their attempts to drink (up to 45°) and collided more often (from 37.5°). Our results show that **bats perceptually interpret the same type of stimulus (lacking frontal echoes in combination with an orthogonal echo) in a continuous way** that depends on the lateral elevation of the lacking frontal echoes and the single orthogonal echo. Natural horizontal surfaces are always water, whereas wall openings exist in all orientation angels, from cave openings on the ground to openings in vertical cliff walls. **A continuous interpretation, combined with spatial memory of water bodies and openings, thus seems ecologically plausible**. Over the past decades, however, the number of anthropogenic smooth surfaces has strongly increased, including vertical large glass facades and windows, horizontal roofs of cars, or solar panels at various orientation angles. These human-made structures pose a sensory trap to echolocating bats, since bats misinterpret the sensory cues of their environment and react with maladaptive responses (Davis & Barbour, 1965; McGuire & Fenton, 2010; Greif et al., 2017). In Chapter 5, I present and discuss further anthropogenic changes of our environments, ranging from sensory pollutants that interfere with sensory processing to wind turbines, yet another novel addition to our landscapes that is misinterpreted by echolocating bats.

# 3 Predator-prey interactions

> EVOLUTIONARILY SPEAKING, INSECTS HAVE RESPONDED TO SELECTIVE PRESSURE FROM BATS WITH NEW EVASIVE MECHANISMS, AND THESE VERY RESPONSES IN TURN PUT PRESSURE ON BATS TO "IMPROVE" THEIR TACTICS.
>
> Miller & Surlykke (2001)

Predators and prey are parts of the (biotic) environment of most animals, and their interactions are fundamental to their survival: predators need to eat, while prey need to survive (Barbosa & Castellanos, 2005). This reciprocal dynamic (Weber et al., 2021) poses a strong selection pressure on both predators and prey (Dawkins & Krebs, 1979; Endler, 1991) and lead to the diffuse (*sensu* Janzen, 1980) co-evolution of various adaptations in both predators and prey for optimized attack and escape (Brodie III & Brodie Jr, 1999; ter Hofstede & Ratcliffe, 2016; Wilson et al., 2018a). Besides structural, morphological and anatomical adaptations, like armour or muscle mass, **sensorial and behavioural strategies are key components for both predators and prey** (Kavaliers & Choleris, 2001; Gable et al., 2021). For example, predators first need to detect and identify potential prey (Endler, 1991), requiring sensory adaptations such as the highly resolved vision of raptorial birds, or the acute hearing and localization ability of barn owls. Likewise, also the prey's detection and identification abilities are critical to elicit adaptive behavioural anti-predator defences. In addition, both predators and prey us a variety of strategies to interfere with each other's sensory systems to prevent detection, identification and localization (Endler, 1991). Visual strategies are particularly well studied, such as camouflage, mimicry and warning colouration (Stevens, 2007; Ruxton, 2009) and visually-guided pursuit and escape (e.g., Ewert, 1987; Mischiati et al., 2015; Temizer et al., 2015; Mills et al., 2018). Prey regularly employ chemical defences, which might be combined with warning signals of another modality (aposematism), commonly in the visual domain (Guilford, 1988; Leavell et al., 2018), though also acoustic warnings exist (Brown et al., 2007). In general, however, acoustic predator and prey strategies are much less studied than visual ones (Ruxton, 2009; Bradbury & Vehrencamp, 2011; MacLeod et al., 2018; Brooker & Wong, 2020), though regularly extend our understanding of the function, ecology and evolution of auditory processing and predator-prey-interactions (Corcoran et al., 2009; **Goerlitz et al., 2010b**; Akre et al., 2011; Jensen et al., 2018; Rubin et al., 2018).

**Pursuit and evasion** are great models to study the sensory-behavioural strategies of predators and prey (Hein et al., 2020). They require rapid reactions based on limited information (Catania & Remple, 2005; Bar et al., 2015; Hein & Martin, 2020) and serve a clearly identifiable and observable behavioural goal that can be experimentally tracked and mathematically described (Mischiati et al., 2015; Corcoran & Conner, 2016; Fujioka et al., 2016; Mills et al., 2018). The ability to detect, identify and discriminate mates, prey, and predators, and to react with appropriate behaviour, are key selective forces acting on the performance of sensory systems and animal behaviour. In my previous and ongoing work, I investigate sensory strategies and behavioural algorithms (Marr, 1982; Hein et al., 2020) of echolocating bats to detect, select and pursuit elusive prey, and of eared insect to detect and escape from bats, as well as additional sensory anti-predator strategies.

## 3.1 The predator-prey-interactions of echolocating bats and eared insects

Echolocating bats and eared insects are an **ideal study system to investigate sensory-behavioural strategies that mediate predator-prey interactions in the acoustic domain** (Miller & Surlykke, 2001; Conner & Corcoran, 2012; ter Hofstede & Ratcliffe, 2016). The most-studied interaction is between echolocating bats (Chiroptera) and eared moths (Lepidoptera). Having originated ~150 million years ago (Misof et al., 2014), Lepidoptera (moths and butterflies) are much older than Chiroptera that originated around 60-95 mya (Bininda-Emonds et al., 2007). Once echolocation evolved in bats to perceive their surroundings, including their insect prey, they became the most significant predators on nocturnal Lepidoptera and other insects (e.g., Roeder, 1998; Miller & Surlykke, 2001; Ratcliffe, 2009). A sense of hearing evolved independently in at least six or seven insect orders (Hoy & Robert, 1996; Yack & Dawson, 2008) and at least six to nine times independently alone in Lepidoptera (Fullard, 1998; Yack, 2004; ter Hofstede & Ratcliffe, 2016; Kawahara et al., 2019), and significantly reduces the prey's risk of being eaten by a bat (Roeder, 1998). Consequently, it was classically thought that hearing in moths evolved in response to bat echolocation and has the single purpose of detecting and evading echolocating bats (Roeder, 1998; Yack, 2004).

Like the debate around the timing and sequence of the evolution of echolocation and powered flight (Jones & Teeling, 2006), the timing, sequence and number of independent origins of echolocation in bats is still debated (Teeling et al., 2000; Springer et al., 2001; Teeling et al., 2005; Veselka et al., 2010; Wang et al., 2017; Thiagavel et al., 2018; Jebb et al., 2020; Nojiri et al., 2021). This has important consequences for the (co?-)evolutionary relationship between bats and moths. In contrast to the classic assumption, Kawahara et al. (2019) recently dated the evolution of most moth ears to 78-92 million years ago, which is earlier than previously assumed and would thus be before the evolution of bat echolocation dated to ~50 mya (Simmons et al., 2008; Teeling, 2009; Veselka et al., 2010). This challenges the classic notion that echolocation drove the evolution of moth ears, suggesting that moth ears originally served a general auditory monitoring of the environment, for example to listen for sounds of moving animals (Jacobs et al., 2008; Fournier et al., 2013) – similar to our suggestion for the continued use of passive listening in a highly specialised echolocator (**Lattenkamp et al., 2018**, see Chapter 2). Furthermore, increasing evidence shows that several moth families use sound also for sexual communication (Spangler, 1988; Conner, 1999; Nakano et al., 2008). Despite these additional functions of ears and their potential pre-echolocation origin, the properties of moth hearing have clearly adapted to bat echolocation (ter Hofstede et al., 2013; ter Hofstede & Ratcliffe, 2016; Kawahara et al., 2019) and elicit a large diversity of acoustically-guided counter-measures such as acoustic jamming (Corcoran et al., 2009; Corcoran et al., 2011) and evasive flight (Roeder, 1967; Roeder, 1998).

Finally, the strong selection pressure exerted by echolocating predatory bats is also shown by a range of primary defences in moths, including decoys (Lee & Moss, 2016; Rubin et al., 2018), acoustic camouflage (Neil et al., 2020a; Neil et al., 2020b), acoustic mimicry (Barber & Conner, 2007; O'Reilly et al., 2019) and acoustic aposematism (Hristov & Conner, 2005; Brown et al., 2007), as well as by secondary auditory-guided defences in many other insect orders (crickets: Moiseff et al., 1978; mantids: Yager et al., 1990, Triblehorn et al., 2008; bushcrickets: Libersat & Hoy, 1991; beetles: Yager & Spangler, 1997; antlions: Holderied et al., 2018), whose ears either evolved as direct response to bat echolocation or which were secondarily co-opted for bat detection.

## 3.2 Hearing and evasive flight in eared moths

PERHAPS THERE IS SOME COMFORT IN THE THOUGHT THAT THIS UNPREDICTABILITY, WETHER DETERMINED INDIVIDUALLY OR SPECIFICALLY, IS PROBABLY AS CONFUSING TO THE BATS AS IT IS TO THE EXPERIMENTER [...]

Kenneth D. Roeder (1962)

Antipredator behaviours, like any antipredator defence, are classified as either primary or secondary defences (Edmunds, 1974). Primary antipredator defences aim to reduce encounters with predators and occur regardless of the presence and detection of a predator. Secondary defences aim to increase the survival of predator encounters, and are active responses after having detected a predator. They thus depend on the prey animal's sensory system being able to detect the predator.

**The evasive flight of eared moths** is a secondary anti-predator behaviour, which is elicited after auditory detection of bat echolocation calls (or any above-threshold sound, for that matter). The evasive flight response shows a graded, bimodal response pattern, consisting of two different evasive flight types with two different functions (Roeder, 1974). The first response type is **negative phonotaxis** in response to quiet sound (i.e., a distant bat), which aims to prevent detection by distant bats that have not yet detected the moth. The second response type is **last-ditch flight**, such as (power) dives, spirals, erratic manoeuvres etc., in response to loud sound (i.e., a close-by bat) which aims to prevent capture after being detected by the bat. Evasive flight is elicited by sound-evoked neuronal activity in the moth's auditory system. **Moths possess the simplest auditory system on earth** (ter Hofstede & Ratcliffe, 2016), **having only 1-4 primary auditory afferents** depending on family (Yager, 1999; Yack, 2004), that directly connect to the tympanum. In the well-studied family Noctuidae, the ear has two primary auditory afferents, termed A1 and A2. Both afferents are broadly tuned to ultrasonic frequencies, with the A2-cell being roughly 20 dB less sensitive than the A1-cell (**ter Hofstede et al., 2013**). The classic, yet untested hypothesis suggests that activity of the A1-cell elicits the first stage of evasive flight, negative phonotaxis, while activity of the A2-cell elicits the second stage, last-ditch flight (Roeder, 1974). However, the family Notodontidae has only one auditory neuron and still shows bimodal evasive flight (Surlykke, 1984); and in the dogbane tiger moth *Cycnia tenera*, the strength of anti-bat behaviour is proportional to the combined activity of A1 and A2 and does not depend on one specific neuron (Ratcliffe et al., 2009). In summary, the functional link from auditory neuronal activity to evasive flight is still mostly unknown, as is the exact function of the auditory neurons, and there are likely family-specific differences. An integrative and comparative research approach is thus timely and needed to address these longstanding questions.

Decades of research into the anti-predator adaptations of eared moths have well documented the peripheral auditory processing across many individuals and families, particularly the audiograms (i.e., frequency-threshold curves for pure tones) of the primary auditory neurons (e.g., Surlykke et al., 1999; **ter Hofstede et al., 2013**). In contrast to this neural basis, the escape behaviour elicited by the sound-evoked neuronal activity is much less understood and often anecdotal or experimentally limited to a few species (e.g., Roeder, 1962; Fullard, 1979; Skals & Surlykke, 2000), despite being the phenotype that is selected by bat-mediated predation. In general, the field is still largely limited to the peripheral neuronal processing of sound, and to comparatively few and disparate behavioural studies (reviewed in ter Hofstede & Ratcliffe, 2016). We lack a functional understanding of the sensory-motor processing from the sensory input to the behavioural reaction, a description of the diversity of three-dimensional flight and of the behavioural algorithms underlying it, and an adaptive explanation of the (variability of) evasive flight in individuals, in species, and in whole communities. In contrast, related neuroethological fields of visually-guided orientation (von Reyn et al., 2014) or acoustic communication (Schöneich et al., 2015) have achieved a much better integrated understanding of the physiological and behavioural processes (Long & Lee, 2012).

Therefore, my **ultimate objective is to understand the full sensory-motor-processing loop from auditory input over neural processing at different levels to behavioural output in flying moths, using bat predation as the fitness-relevant context driving neural and behavioural adaptations**. My own (failed and successful) experiences over the past years of studying moth evasive behaviour in tethered and free-flying individuals in the lab and field taught me the difficulty of studying moth flight behaviour, likely explaining why many researchers over the past decades have published individual studies, but no long-term research programme has developed. Challenges originate from the variable nature of evasive flight and the difficulty of tracking free-flying smalls animals over large spatial volumes in dark field settings.

My research focused mainly on the moth family Noctuidae with its tympanic ears and the two primary auditory afferents A1 and A2. Starting with the sound-evoked neuronal activity of the A1- and A2-afferents, we first validated the neurophysiological methods for recording neuronal activity. The established method to record A1- and A2-neuronal activity requires dissection of the moth thorax, which might affect the vibration of the tympanum. In **ter Hofstede et al. (2011)**, we combined neural recordings of the A1- and A2-cells with vibration measurements of the tympanum. We showed that the dissection does not affect the biomechanics of the tympanum close to the neuronal thresholds, validating for the first time that this method provides good estimates of what intact moths hear. Second, we showed that the key biophysical parameter for triggering action potentials in the sensory cells of noctuid moths is tympanum displacement, not velocity.

Next, I asked how the A-cells' sensitivity for sound translates into detection distances of bats by moths, which is the behaviourally and ecologically relevant trait. In the lab, we recorded the neural activity of moths in response to pure tones and bat calls, resulting in audiograms, which can be readily compared between species and studies, and in call detection thresholds. In the field, we recorded the neural activity in response to the calls of free-flying bats, while tracking the bats' 3D-position, resulting not only in call detection thresholds, but also in the distances over which moths can detect free-flying bats. Comparing across three moth species and five bat species, we show large differences in the detection distances (~5-30 m for A1, ~2-20 m for A2), highlighting the importance of studying bat-moth-interactions comparatively at the community

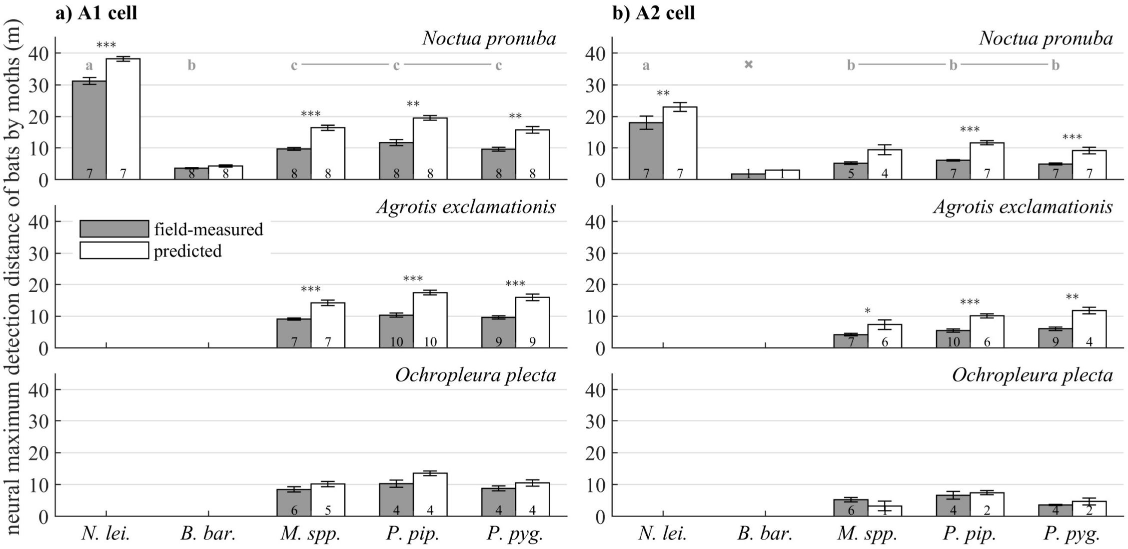

**Figure 2. Moths' detection distances for bats in the field differ between species and can be predicted based on basic lab-derived neuronal audiograms.**

Eared moths of three different species (top to bottom) in the field (grey bars) detect the echolocation calls of five different free-flying bat species (left to right) over distances of about 30 – 3 m with their A1-cell (**a**), and over distances of about 18 – 0 m with their A2-cell (**b**).

**Detection distances in the field** (grey bars) were measured as described in **Goerlitz et al. (2010b)** and are shown as means of individual means ± sem (N of individuals is given in the bars). For the moth *Noctua pronuba*, we had sufficient data to compare the field-measured detection distances between bat species (two ANOVAs, one for each sensory cell, with Tukey post-hoc tests). Lines connect species without significant differences between detection distances ($p>0.05$). Due to the small sample size, *B. barbastellus* was excluded from the A2 cell ANOVA (indicated by a cross).

**The predicted detection distances** (white bars) were calculated based on lab-measured neuronal audiograms (see **ter Hofstede et al. (2013)** for methods) and on average bat call parameters (**Goerlitz et al., 2020**). Asterisks indicate significant differences between field-measured and predicted detection distances (one-sample two-sided t-tests with sequential Bonferroni correction) with $\alpha = 0.05$ (*), $\alpha = 0.01$ (**) and $\alpha = 0.001$ (***). These differences can be compensated for by a correction factor, allowing to predict the distance over which eared moths can detect flying bats in the field (**Goerlitz et al., 2020**).

Unpublished data by **Goerlitz*, ter Hofstede* & Holderied**.

level (**Fig. 2**). Methodologically, together with **ter Hofstede et al. (2011)**, we show that lab-based neuronal audiograms can predict detection distances in the field. Neuronal audiograms are readily measured and are a tool to characterise the physiological properties of auditory systems. Detection distances, in contrast, are much more difficult to obtain, yet are the relevant parameter in an ecological and evolutionary context, which determines the distance and time available to a prey to escape from an attacking predator. **Our results validated lab-based audiograms for the first time with field-derived data, and show that behaviourally relevant detection distances can be predicted based on lab-derived audiograms and bat echolocation call characteristics**.

Having established the functional validity of neuronal audiograms and how they relate to detection distances, we investigated how audiograms are adapted to the moths' sympatric community of bat predators. Larger moths are more sensitive to sound (Surlykke et al., 1999): the A-cells' best threshold is negatively correlated with moth size. This might be an anti-predator adaptation because larger moths reflect more intense echoes, which bats can detect over larger distances. However, it could also be a simple allometric relationship, resulting from the larger tympany of larger moths. Distinguishing between both hypothesis was difficult, because the relationship between best threshold and moth size shown by Surlykke et al. (1999) is confounded by the concurrent relationship of best frequency with moth size. In **ter Hofstede et al. (2013)**, we thus tested the allometry hypothesis against the predator-adaptation hypothesis by analysing the threshold-size correlation at fixed sound frequencies. Based on the predator-adaptation hypothesis, we predicted that a negative threshold-size-correlation should exist at all and only those sound frequencies that are used by sympatric bats. This is exactly what we found, with community-specific differences in the pattern of those correlations across sound frequency. For example, in Denmark and Canada, the threshold-size-correlation disappeared with increasingly higher frequencies, indicating relaxed selection for size-dependent auditory sensitivity, matching the lack of bats echolocating at these high frequencies (>70 kHz). In contrast, in the UK, the threshold-size correlation became stronger again above ~50-70 kHz, likely due to the strong predation threat exerted by sympatric horseshoe bats, which strongly prey on moths and call at high frequencies (~80-100 kHz).

Following the analysis of the audiograms, I used a theoretical modelling approach as a first start to link the neuronal activity to the ecologically relevant outcome of the sound-triggered evasive flight behaviour: **the success of predator avoidance**. Using data on neuronal audiograms, bat flight and bat call parameters, I modelled moth escape flight in a community of 25 sympatric moth and bat species (**Goerlitz et al., 2020**). In general, most animals are at risk from multiple predators and can vary anti-predator behaviour based on the level of threat posed by each predator and perceived by their senses. Therefore, moth ears, despite their simplicity, must be adapted to multiple sympatric bat predators. First, I showed that bat call frequency is strongly correlated to bat threat level, since low-frequency bats experience lower atmospheric sound attenuation and emit calls of higher intensity (thus detecting moths over larger distances) and fly faster (thus reaching moths faster). Call frequency is thus a good predictor of predation threat level. This correlation turns the bats' (perceptible) call frequency into a proxy for its (imperceptible) predation threat. I thus predicted that the frequency-dependent tuning of moth auditory cells is a functional adaptation exploiting this correlation, i.e. a matched filter (Wehner, 1987; Römer, 2016; von der Emde & Warrant, 2016), allowing moths to respond to different sympatric bat species at appropriate distances. Second, I tested this prediction for the A1- and A2-cell, testing different cell-specific hypotheses about their function, by modelling presumed moth behaviour in response to A1-cell activity (negative phonotaxis) and A2-cell activity (onset of last-ditch flight). Despite a more than 10-fold difference in the A1-cells' detection distances for different bat species by different moth species, negative phonotaxis allowed moths to escape detection by all sympatric bats with similar safety margin distances, confirming the constant buffer hypothesis. In contrast, the less sensitive A2-cell usually responded to bat echolocation calls at a similar distance across all moth species for a given bat species. If this neuron triggers last-ditch evasive flight, this suggests that there is an ideal reaction distance for each bat species, regardless of moth size (fixed onset hypothesis). Together with **ter Hofstede et al. (2013)**, this study shows that even a very simple sensory system can adapt to deliver information suitable for triggering appropriate defensive reactions to each predator in a multiple predator community.

These theoretical results still require empirical confirmation. However, a systematic and comparative quantification of moth evasive flight is mostly lacking. Starting such a research program, I focused on last-ditch flight, which is better traceable than the negative phonotaxis which spatially extends over many tens of meters. Last-ditch flight comprises different behaviours, including passive dives, power dives, sudden turns or random manoeuvres, resulting in a large variability of escape trajectories (Roeder, 1962). This variability of last-ditch flight is supposed to make flight trajectories hard to predict and thus should reduce the moth's likelihood of being caught by an attacking bat. This is a classic example of so-called **protean behaviour, i.e., the erratic and unpredictable movement** seen in many animal species as anti-predator adaptation (Chance & Russell, 1959; Humphries & Driver, 1970; Domenici et al., 2011b).

Previous observations of erratic flight were unable to assess the individual and species identity of the observed moths (Roeder, 1962). It is thus unclear at which level the variability of last-ditch flight arises – between repeated executions of last-ditch flight in the same individual, between individuals, or even between species. This raises the remarkable possibility that the variability required for an efficient protean display occurs not within individuals or species, but between multiple sympatric species. This called for a comparative approach measuring evasive flight repeatedly across individuals and different species.

My initial work based on 3D-video-tracking of bat-moth-interactions and moth evasive flight in the real-world suggested a rather high degree of stereotypy in the erratic flight of two moth species (**Fig. 3**; **Goerlitz et al., 2009**). Both species showed spiralling behaviour with ~1.5 rotations per second around an approximately horizontal axis (**Fig. 3E**), making the evasive behaviour somewhat predictable. Despite this stereotypy, these flight paths still seemed effective to escape from attacking bats. It is unclear how much variability is needed for a successful escape, and whether this variability originates from any remaining variability in trajectory parameters, from variable onset timing, or due to the overall community-level variability that bats encounter when attacking different individuals and species. In the two species studied here, despite the stereotypy in shape, evasive flight was faster and more variable during the last-ditch flight than before (**Fig. 3 C,D**), and started at different times before the bat attacked (**Fig. 3 F**). Overall, however, experimental manipulation, data collection and trajectory analysis proved to be very time-consuming and difficult, and resulted in trajectory parameters with unclear variability, making the identification of general patterns in the data (both about absence or presence of variability) inconclusive.

Therefore, to investigate moth evasive flight in a better controlled, systematic and comparative way, I developed a system for measuring flight activity in tethered flight. We exposed eight moth species caught in the same habitat and thus exposed to the same bat predators to a simple bat-like ultrasonic stimulus (**Hügel & Goerlitz, 2019**), resulting in the first comparative quantification and comparison of (tethered) flight to test the escape-tactic diversity hypothesis (Schall & Pianka, 1980). This hypothesis postulates that species-specific differences in evasive behaviour will increase the overall unpredictability experienced by predators within a predator–prey community. Our results showed species- and (in some species) individual-specific differences in evasive flight strategies, leading to community-level variability that is larger than within each species. This increases the community-level unpredictability experienced by hunting bats, supports the escape-tactic diversity hypothesis, and will likely lead to increased predator

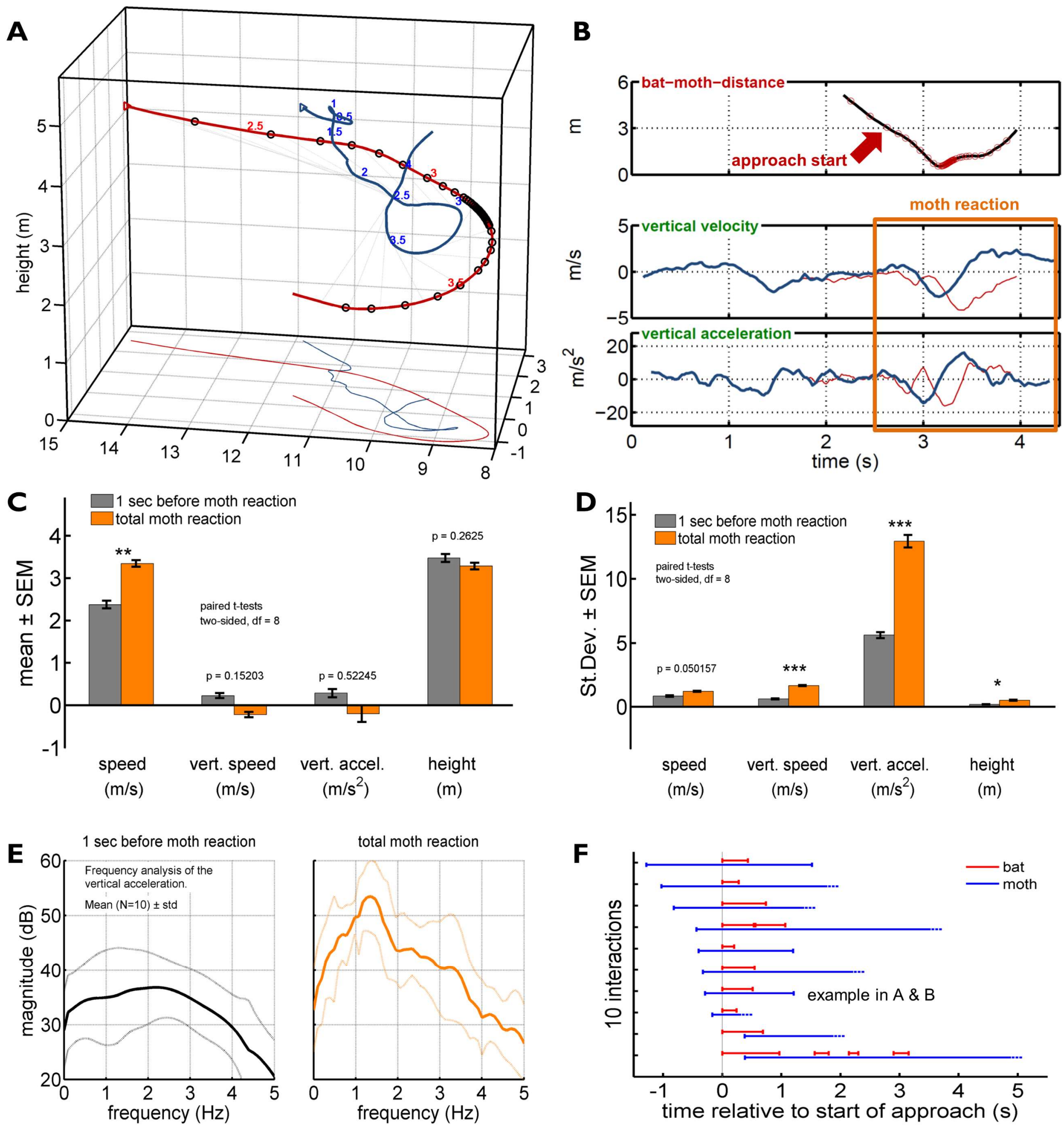

**Figure 3. Bat-moth-interactions in the field.** Naturally interacting bats (*Pipistrellus kuhlii*) and moths (*Heliothis peltigera* and *H. nubigera*) in the field were video-recorded with two calibrated cameras to obtain three-dimensional flight trajectories, and the bat's echolocation calls were recorded with a synchronised audio system.

**A)** One example of the three-dimensional flight trajectories of a bat (red; circles indicate position of call emission) attacking a moth (blue), which reacts with an evasive spiralling flight. Small numbers indicate time (sec).

**B)** Trajectory parameters of the trajectories shown in A). The start of the bat's approach was estimated based on call-intervals (red arrow). The evasive flight reaction of the moth was estimated based on changes in the kinematic parameters (orange box).

**C, D)** I compared trajectory parameters of 10 moth trajectories before the evasive flight reaction (grey) to during the reaction (orange). **C)** The means of the trajectory means only differed for flight speed, showing that moths increased flight speed during the reaction. **D)** The means of the trajectories' standard deviation differed, showing that the moths' flight speed, acceleration and flight height was more variable during the reaction than before.

**E)** The vertical acceleration during the reaction had a prominent peak around 1.5 Hz, suggesting that moth's flew spirals with about 1.5 rotations per second around a roughly horizontal axis.

**F)** 8 out of 10 moth reactions started before the onset of the bat's approach, and continued after the bat aborted its attack. Unpublished data by **Goerlitz*, ter Hofstede* & Holderied**.

protection. This increased predator protection is an emergent benefit of mixed-species prey groups and might counteract potential negative effects such as resource competition. Methodologically, we advanced the field by having established a basic lab-derived measure (flight strength of tethered fight) that provides **systematic and comparative insights into the function and ecology of predator-prey interactions**.

Having established an objective method to quantify evasive flight, I next focused on one species to address mechanistic sensory-motor properties of evasive flight (**Hügel & Goerlitz, in prep**). We studied the moth *N. janthe*, because it exhibits a clear behavioural reaction (increase of flight strength) in response to supra-threshold sound (**Hügel & Goerlitz, 2019**). We recorded the flight strength of 51 individuals, first in response to pulse trains consisting of 1-20 short pulses, to quantify **temporal properties of evasive flight**, and second in response to single pulses of different frequencies and increasing intensity to measure **behavioural audiograms**.

The time-course of any dynamic system is defined by (multiple) time constants. A system's time constant is the time that it would take the system to reach its minimum or maximum value if the initial rate of change had been maintained. For example, temporal integration describes the duration over which a system is summating incoming energy, and which affects how quickly a system is changing its state in response to input. The temporal properties of an auditory system are central to its function (Michelsen, 1985). When considering auditory-guided behaviour such as the evasive flight of moths, multiple integrative processes determine its time course, from the temporal integration of tympanum vibration, over the intrinsic time constant of the auditory receptor cells and the summation of detection probabilities, to the higher-level auditory processes and the time constants of muscle activity.

The moth ear integrates acoustic energy (Surlykke et al., 1988; Tougaard, 1996) with measured time constants around 10-70 ms (Surlykke et al., 1988; Tougaard, 1998; Waters and Jones, 1996). We first show that **the moths' evasive flight strength tightly followed the temporal pattern of the acoustic stimulus**: flight strength increased already within the first 100 ms after stimulus onset, reached its maximum after 300 ms, remained high throughout the stimulus, and decreased again after stimulus offset within 100-300 ms. With a median value of 74 ms (quartiles: 51-107 ms), the measured behavioural time constant of flight onset is similar to the neuronal time constants. In contrast, the time constant of stopping flight was 389 ms (quartiles 122-636 ms), showing that moths stop their evasive flight slower than they started it. This longer time constant of flight offset might prevent moths from stopping evasive flight too quickly when the received sound fluctuates due to their own erratic movements and the varying shadowing of the sound by their own wings (Fullard et al., 2003). Despite this, the relatively fast stopping of evasive flight after sound offset shows that last-ditch flight is not a fixed action pattern, in contrast to the evasive and anti-predator behaviours of some fish (Giaquinto and Hoffmann, 2010; Law and Blake, 1996), molluscs (Willows et al., 1973), and crustaceans (Reichert, 1988). By quickly adjusting their evasive flight to the sensory input and thereby to the actual predation threat, moths might reduce risks associated with evasive flight (Guignion and Fullard, 2004) and save time and energy to spent on other activities like foraging and mating (Candolin, 1997; Ryer and Olla, 1998; Sih, 1980; Travers and Sih, 1991).

Second, we obtained complete **behavioural audiograms**, which, in contrast to the neuronal audiograms, are largely missing or yielded rather high threshold curves with shapes differing from neural audiograms (Fullard, 1979). In contrast, our results revealed consistency between neuronal and behavioural threshold curves for acoustic stimuli in *N. janthe*. Specifically, the shape and threshold of the behavioural threshold matched the shape and threshold of the neuronal threshold curve of the A2-neurons. This does not imply, however, that the observed behaviour (increase in flight strength) was triggered by A2-activity, since the functional link from neuronal activity of the two auditory cells to the two types of evasive flight is still unclear. The increased flight strength could have been triggered by the activity of the more sensitive A1 cell (Surlykke, 1984), the less sensitive A2-cell (Roeder, 1964, 1974a), or a combination of both (Ratcliffe et al., 2009). Despite this, our data does show that the frequency tuning of evasive behaviour matches the frequency tuning of auditory neurons, and that evasive flight is triggered at maximally 20 dB higher intensities than the underlying neuronal activity (of the more sensitive A1-cell). This matches previous studies showing a difference of ~10-20 dB between neuronal and behavioural thresholds (reviewed in **Lewanzik & Goerlitz, 2018**), and explains why the barbastelle bat can successfully hunt eared moths with sound levels reaching the moth that are ~10 dB higher than the moths' neuronal threshold (**Lewanzik & Goerlitz, 2018**). Lastly, we showed that light reduced the flight strength both during normal flight prior to acoustic stimulation as well as during evasive flight, demonstrating multisensory integration of auditory and visual information. This lab-data confirms the suppressive effect of artificial light on both negative phonotaxis and last-ditch flight shown by **Hügel & Goerlitz (2020)** in a natural setting (cf. Chapter 5).

## 3.3 Function and evolution of low-intensity echolocation

While there is clear evidence that sensory processing in eared moths is shaped by bat predation, it was unclear whether the many species of predatory bats responded in any way to the diversity of sensory anti-predator strategies of moths (ter Hofstede & Ratcliffe, 2016). Examples of predators prevailing over their prey, such as the toxin resistance in garter snakes (Geffeney et al., 2005), are generally rare, possibly due to the lower selection pressure on predators compared to their prey ("life/dinner-principle", Dawkins, 1999) or more general asymmetries in selection pressures and evolutionary responses of predators and prey (Abrams, 1986). For bats and their insect prey, the allotonic frequency hypothesis proposes that some bat species responded to hearing prey by calling at frequencies outside the range of the prey's greatest auditory sensitivity (Fullard, 1998). Despite much support for this hypothesis (Fullard, 1998; Waters, 2003), other benefits could have initially driven selection for these changes, such as increased sensory range at low frequencies or improved spatial resolution at high frequencies (Rydell et al., 1995). Another recent hypothesis suggests that the call properties during the final stage of the aerial prey attacks (the "final buzz") might be a counter-adaptation to the evasive flight manoeuvres of prey. Because call frequency during the final buzz drops by an octave, the widths of the sonar beam doubles (Jakobsen & Surlykke, 2010; Jakobsen et al., 2013). This widening of the sonar "field of view" might help to better track evading insects (Ratcliffe et al., 2013; Hulgard & Ratcliffe, 2016; ter Hofstede & Ratcliffe, 2016).

In **Goerlitz et al. (2010b)**, we tested yet another hypothesis, which predicts that a sensory strategy based on low-intensity calls can exploit the relative differences in hearing thresholds between bats and moths to counter moth hearing (Fenton & Fullard, 1979; Surlykke, 1988). We combined comparative acoustic flight path tracking, field neurophysiology in eared moths, faecal DNA analysis and perceptual modelling, to show that one European bat, the woodland species *Barbastella barbastellus*, preys almost exclusively on ear-possessing moths by emitting low-intensity calls while searching for prey. Because these calls are about ~20-30 dB fainter than the calls of other aerial-hawking bats, they are inaudible for distant moths and therefore enable the bat to approach the moth without being detected. Subsequently, **Lewanzik & Goerlitz (2018)** extended this result to the attack flight, by showing that the barbastelle bat lowers its call level further during an attack, thus remaining below or just above the hearing threshold of most moths, preventing evasive flight manoeuvres. In addition, Corcoran & Conner (2017) showed that the closely related species *Corynorhinus townsendii* also emits low-intensity calls, and that these calls prevent most evasive flight manoeuvres of attacked moths. These studies clearly established the function of low-intensity “stealth echolocation”: enabling echolocating bats to sneak up on eared prey, thereby exploiting a food resource that is difficult to catch for other aerial-hawking bats emitting calls of higher intensity.

Low intensity “stealth echolocation” imposes the cost of strongly reduced detection distances to the bat and has no compensating benefits other than making the calls inconspicuous to eared prey (**Goerlitz et al., 2010b; Lewanzik & Goerlitz, 2018**). **Low-intensity echolocation thus became the first unambiguous example of a co-evolutionary sensory counteradaptation by echolocating bats to the evolution of hearing in moths** – apparently finally supporting this text-book example of (diffuse; Janzen, 1980) coevolution (ter Hofstede & Ratcliffe, 2016). Recently, however, I doubted my own conclusions and suggested an alternative evolutionary scenario, proposing that low-intensity calls are an adaptation to the foraging habitat, thereby falling in the broadest sense under the acoustic adaptation (Morton, 1975; Rothstein & Fleischer, 1987) and the sensory drive (Endler, 1992; Cummings & Endler, 2018) hypotheses. Under this scenario, the use of low-intensity calls for the aerial hawking of (eared) prey only evolved secondarily, while primarily low-intensity echolocation evolved as adaptation to forage for insects just in front of vegetation ("gleaning", **Lewanzik & Goerlitz, 2018**). Gleaning poses a special sensorial challenge to echolocating bats, since they need to avoid the masking of the faint rustling sounds or echoes of their prey by the loud echoes reflecting off the vegetation (Siemers & Schnitzler, 2004; Geipel et al., 2013; Clare & Holderied, 2015). The same sensorial challenge is experienced by bats with a very different foraging niche: nectarivorous species also fly close to vegetation and drink nectar from flowers, which they find by echolocation (Simon et al., 2011). They typically emit calls that are short, broadband, of high-frequency and low intensity as an adaptation to foraging in dense tropical forests. In **Clare et al. (2014)**, we show that these call characteristics render the nectarivorous neotropical species *Glossophaga soricina* also inaudible to eared insects, and that at least 20% of *G. soricina* individuals, if not more, also consumed eared moths and other insects that they catch in the air.

The low-intensity species *B. barbastellus* and *C. townsendii* are closely related to other low-intensity bats (de Framond-Bénard et al., in prep-a) from the genera *Plecotus*, *Corynorhinus*, *Otonycteris*, and *Idionycteris* (Shi & Rabosky, 2015). In contrast to barbastelle bats, however, these low-intensity species predominantly glean prey from terrestrial surfaces such as vegetation or the ground. In addition to low-intensity echolocation, *B. barbastellus* also shares several other traits with (a subset of) these species, such as large pinnae, broad wing shape with low aspect ratio, slow flight, and (combined) nasal and oral sound emission. In **Lewanzik et al. (in prep)**, we are performing ancestral state reconstructions of these traits to infer the putative foraging modes, echolocation strategies, and morphology of the common ancestor of barbastelle bats and their gleaning relatives. The results of these phylogenetic reconstructions suggest that low-intensity echolocation in barbastelle bats rather reflects a co-option of ancestral gleaning traits, and not a counter-measure to circumvent moth hearing. Our results thus ***challenge*****, rather than support, the barbastelle bat as the supposed unambiguous example of a bat counter-measure** in the putative evolutionary predator-prey arms-race of bats and moths.

## 3.4 Trading-off predator avoidance with reproduction

While echolocating bats and eared moths “just” interact as predators and prey based on sound, another level of complexity is added by prey that use sound also for communication. Acoustic communication is widespread throughout the animal kingdom and used by many species to attract mating partners (Bradbury & Vehrencamp, 2011). Like foraging and predator avoidance, **attracting mates for reproduction** is a third directly fitness-relevant behaviour. Very often, however, non-intended receivers such as parasitoids and predators also exploit communication sounds (Zuk & Kolluru, 1998; Halfwerk et al., 2014). Acoustically courting individuals are thus in a conflict between sexual and natural selection and need to trade off mate attraction for reproduction with predator avoidance for survival (Zuk & Kolluru, 1998; Falk et al., 2015). Thus, defence mechanisms evolved in many communicating animals, including primary defences such as inconspicuous song (Belwood & Morris, 1987) and secondary defences such as evasive flight (Libersat & Hoy, 1991; Schulze & Schul, 2001) or stopping to sing when detecting a predator (Faure & Hoy, 2000; ter Hofstede et al., 2008). To address the conflict between mate attraction and predator avoidance, I recently started to investigate the **acoustic communication and anti-predator behaviour in singing bushcrickets** (=katydids; Tettigonidae), complementing my work on the anti-predator traits of eared moths. Bushcrickets are distributed globally with a primarily nocturnal lifestyle and a diverse acoustic communication system for attracting females (Gwynne, 2001), are regularly attacked by bats (Jones et al., 2011; Falk et al., 2015; ter Hofstede et al., 2017), and possess behavioural defences against bat attacks (Belwood & Morris, 1987; Libersat & Hoy, 1991; Faure & Hoy, 2000; Schulze & Schul, 2001; ter Hofstede et al., 2008)

**A common secondary antipredator behaviour is song cessation** (Faure & Hoy, 2000; ter Hofstede et al., 2008): upon hearing a bat-like sound, the singing males stop to sing – **the acoustic equivalent of hiding in a burrow against visually orienting predator**s (Ruxton, 2009; Brooker & Wong, 2020). Ceasing courtship signals, however, is costly because it reduces the likelihood of attracting a mate and thus reduces a signaller's fitness (Zuk & Kolluru, 1998). Therefore, the **threat sensitivity hypothesis** postulates that prey animals adjust the magnitude of their anti-predator behaviour to the level of the predation risk, to trade-off predator avoidance with other fitness-relevant behaviours (Helfman, 1989). In addition to avoiding predators, prey

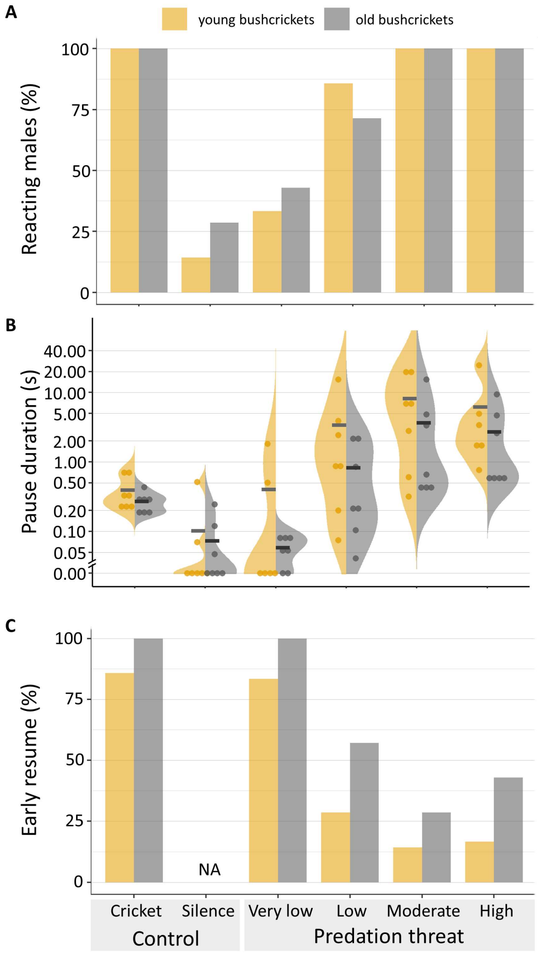

**Figure 4: Singing male bushcrickets adjust their anti-predator defence to predation threat level and age.**

We played different sound stimuli to individual male *Tettigonia viridissima* bushcrickets while they were singing their courtship song. Each sound was 960 ms long, was presented once, and belonged to one of six treatments:

- **2 control sounds**: ***cricket*** = similar to the song of the sympatric innocuous cricket *Modicogryllus frontalis* (88 dB SPL RMS re. 20 µPA); and ***silence***.
- **4 levels of predation threat** (from very low to high), consisting of sequences of bat-like sweeps with increasing received sound pressure levels (57, 67, 77 and 87 dB SPL).

Each individual was tested twice, once early in the reproductive season (***young***, N=7, yellow), and once late (***old***, N=7, grey).

**A)** The percentage of all males that paused singing increased with increasing predation threat level, but was independent of age.

**B)** In those males that paused singing, the duration of the song pause increased with increasing predation threat, and was longer in young than in old males. Split violin plots show raw data, mean values and density curves (Kernel density estimation with 0.9 smoothing bandwidth).

**C)** In those males that paused singing, the percentage of singing males that resumed singing before the end of the simulated bat attack decreased with increasing predation threat, and was lower in young than in old males.

Figure from **Hubancheva et al. (in prep-b)**.

animals also need to consider their own life expectancy, which limits the total time available for mating. **Life history theory** predicts that animals adjust their reproductive effort and other behaviours over their life time to maximize their fitness (Roff, 1993). Specifically, older individuals towards the end of their life should invest more into reproduction and less into anti-predator behaviours than younger individuals (Clutton-Brock, 1984). Taken together, prey species with conspicuous courtship signals should adjust their courtship both to short-term changes in predation threat (threat sensitivity hypothesis) and to their own age (life history theory). In **Hubancheva et al. (in prep-b)**, we tested these two hypotheses in the European bushcricket *Tettigonia viridissima*. We measured song cessation of male *T. viridissima* at the beginning and towards the end of their 3-month long life in response to bat-like playbacks at different sound levels, thus simulating bats at different distances and thus of different threat levels (**Fig. 4**). With increasing predation threat, the bushcrickets paused their song more often and for longer, thereby reducing their predation risk at the cost of reduced mate attraction. Of those males that stopped singing, the pauses of old males were on average 40% shorter than those of young males. Our results support the threat sensitivity hypothesis and life history theory, showing that acoustically courting male bushcrickets adjust their courtship display both to threat level and their age, presumably to optimize their life time reproductive success. Additional recordings of the neuronal audiograms of old bushcrickets and detailed comparison of the behavioural responses furthermore showed that (i) the reduced response of old males is not caused by reduced auditory sensitivity and that (ii) individuals of all ages initially paused briefly (200-400 ms) in response to all threat levels and only subsequently resumed singing in a threat-level- and age-dependent manner. Mechanistically, this suggests that any sound of sufficient intensity elicits an initial brief pause, during which the bushcrickets assess the threat level of the received sound and trade-off predation risk (as indicated by the sound) with their age-dependent importance of courtship.

While the song of *T. viridissima* and many other bushcrickets contains regular pauses, enabling the singing males to listen for bat calls, other song types also exist. The loud and continuous ("high-duty cycle") song of other bushcricket species and of other prey insects such as chorusing cicadas, poses a conundrum. **These acoustically communicating prey species seem to be maladapted to the predation threat posed by eavesdropping predators:** their song is well perceptible for predators, and they do not stop singing in response to bat attacks,  most likely due to inhibition of the auditory neurons during sound production (Poulet & Hedwig, 2002). **Thus, continuously singing species must use other primary or secondary defence strategies to prevent capture by bats**.

In **Hubancheva et al. (in prep-a)**, we tested the **acoustic jamming hypothesis**, which posits that the high-repetition rate and high duty-cycle of the courtship song interferes with echolocation – like the jamming clicks of some Arctiinae tiger moths (Fullard et al., 1994; Corcoran et al., 2009) and the jamming social calls of *Tadarida brasiliensis* bats during intraspecific food competition (Corcoran & Conner, 2014) interfere with echo processing and cause bats to miss aerial prey. The short and broadband spectro-temporal properties of the high-duty cycle song of some bushcrickets resemble these jamming moth clicks and bat calls, suggesting that the song's acoustic properties can act as a primary anti-bat defence, ultimately proposing a **dual function of courtship songs**. We investigated the bushcricket *Ruspolia nitidula* to test for acoustic jamming of predatory bats by courtship songs. *R. nitidula* is a very common species in Southern Europe. Despite this, our results show that it lacks from the diet of sympatric bats (meta-barcoding of bat faces), despite being palatable (feeding trials with bats) and singing a highly attractive song (behavioural tests with bats) from exposed locations without stopping when presented with bat echolocation calls (behavioural tests with singing males). To understand why *R. nitidula* is not consumed by bats, we brought wild-caught greater mouse-eared bats *Myotis myotis* into a flight room, where they could hunt tethered mealworms, while playing courtship song and control sounds from 1, 4 or 8 loudspeakers. *R. nitidula* courtship song reduced the bats' foraging success by 36% (quartiles 26-50%) compared to silence and cricket song, independent of the number of loudspeakers (**Fig. 5**). *R. nitidula* courtship song thus indeed has a dual function, whose anti-bat function relies on the same mechanism of acoustic interference that has independently evolved in tiger moths (Fullard et al., 1994; Corcoran et al., 2009) and competing foraging bats (Corcoran & Conner, 2014). *R. nitidula* song thus interferes with the echo-processing of echolocating bats, hampering their aerial-hawking of prey and their spatial orientation in cluttered habitats. However, since *R. nitidula* is not flying while singing, but sitting within and on top of dense shrub vegetation, I propose that the protective function of its song for itself is based on reducing the bat's ability to navigate within and close to vegetation. I had planned further tests on the effect of *R. nitidula* song on bat navigation, which I had to postpone

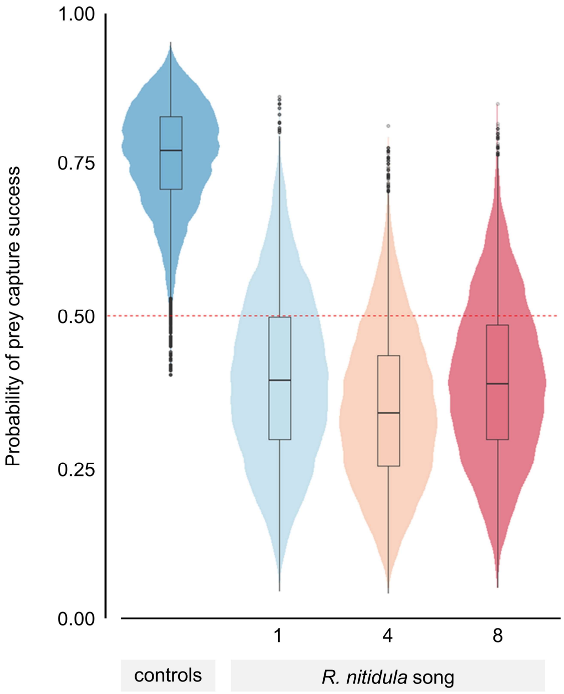

**Figure 5: A courtship song acting as anti-predator defence.**

We quantified the prey capture success of greater mouse-eared bats, *Myotis myotis*, in the presence of control sounds and bushcricket courtship song.

The courtship song of the bushcricket *Ruspolia nitidula* reduced the probability of prey capture success by 36% compared to the controls (silence, courtship song of the cricket *Oecanthus pellucens*).

The number of sound sources presenting the song (1, 4, or 8 loudspeakers) did not affect prey capture success.

Violin plots show the posterior predictive distribution of prey capture success according to a Bayesian model (Bernoulli-logit regression implemented in STAN). Boxplots show median, quartiles, 95% of the probability mass, and outliers shown as dots.

From **Hubancheva et al. (in prep-a)**.

due to the SARS-CoV2 pandemic. It also remains to be tested whether sexual or predator-mediated natural selection was the prime selective factor on the acoustic features of this song.

This jamming effect of the continuous song of *R. nitidula* on aerial-hawking bats suggests a fascinating consequence and opportunity for other prey species. My **acoustic umbrella hypothesis** posits that the jamming effect also protects other nearby flying (earless) insects by putting up an “acoustic umbrella” within a few meters around singing males. This hypothesis postulates a yet undescribed consequence of a jamming signal, where the defence strategy of one prey species also provides benefits to other prey species, resulting in a short-term commensal relationship. It remains to be tested whether this umbrella exists, how far it ranges, and whether other insects actively seek out singing *R. nitidula* (and other similar sound sources).

*R. nitidula* males regularly sing together in groups with interindividual distances of approximately ≤1 m (own data). This may provide another advantage predicted by the **acoustic safety-in-numbers hypothesis**, which posits that the combined high-duty cycle song of multiple males interferes with the sensory perception of the predator, preventing the localization of single males for capture. This is related to the confusion effect of prey groups that is mostly studied in the visual system, yet based on a different sensory mechanism. The mammalian auditory system cannot separately identify and localize auditory events that are separated by only a few milliseconds, leading to the precedence effect (Wallach et al., 1949) and summing localization (“stereo effect”; Litovsky et al., 1999) of multiple sounds. Multiple males singing together at high duty cycle could exploit these effects to obtain safety in numbers by a sort of sensory exploitation, leading to failed or wrong localisation of individual males by hunting bats. Because I had to cancel field work in 2020 due to SARS-CoV2, we could not yet test this hypothesis.

# 4 Communication and interference

NO MAN IS AN ISLAND
ENTIRE TO ITSELF

John Donne (1624)
Devotions upon emergent occasions

To paraphrase John Donne, also no animal is an island entire of itself. **All animals interact with other animals**, from random encounters, over parasitic and predatory interactions, to small social family groups and large herds and to mating and raising offspring (Krause & Ruxton, 2002). From a sensory and behavioural perspective, inter-individual interactions have major effects on the sensory information available to individuals and on the actions that they take. Generally speaking, the actions of one individual directly change the sensory scene of another animal. This is directly obvious for the intentional communication between sender and receiver during courtship, territorial signalling or threat displays, but also during the predator-prey-interactions discussed in the previous chapter.

In contrast to the personal information that animals acquire themselves about their physical environment, information that they obtain from the behaviours of other animals is called **social information** (Danchin et al., 2004). Social information is a rich source of environmental information (Danchin et al., 2004), which can originate both from con- and heterospecifics (Seppänen et al., 2007; Goodale & Kotagama, 2008; Ruczyński et al., 2009; Dawson & Chittka, 2012) and both from signals that were selected for information transmission, as well as from inadvertently produced cues. Eavesdropping on the cues inadvertently produced by other animals can be beneficial in a variety of ecological contexts (Valone & Templeton, 2002; Goodale et al., 2010) and has evolved in various taxa (Gil et al., 2018). In the case of bat echolocation, the echolocation calls are signals adapted for sensing the sender's surroundings. At the same time, the calls are also a life-saving cue for the bats' prey (see Chapter 3), can be a cue for other bats (Fenton, 2003; Jones & Siemers, 2010), but thirdly can also be a major sensory problem for other bats due to interference (Matsubara & Heiligenberg, 1978; Ulanovsky & Moss, 2008).

In this chapter, I investigate potential communication and interference in the highly dynamic acoustic information networks that are formed by echolocating and swiftly moving bats. **Echolocating bats are highly social and vocal**. They are ideal to study the functional ecology of sensing and movement in groups, because of their very diverse ecology, the occurrence of small (<10 individuals) to very large (millions of bats) groups, and their active sound emission. Each individual echolocating bat constantly (~10 times/sec) emits calls of very high intensity (louder than a jackhammer) for its own benefit of sensing its environment. Because these calls can encode crucial information, including the caller's current behavioural task (Kalko, 1995; Lewanzik & Goerlitz, 2021), habitat (Denzinger & Schnitzler, 2013; Denzinger et al., 2018), species identity (Schuchmann & Siemers, 2010b; Voigt-Heucke et al., 2010), group affiliation (Voigt-Heucke et al., 2010), sex (Kazial & Masters, 2004; Knörnschild et al., 2012; Schuchmann et al., 2012) and even individual identity (Yovel et al., 2009; Voigt-Heucke et al., 2010), bats might exploit this social information for their own benefit (Fenton, 2003; Jones & Siemers, 2010). At the same time, this continuous high rate of intense calls has the potential to mask the faint echoes of interest, to interfere with sensory processing, and thus to jam an individual's perception, particularly in groups of multiple actively sensing animals (Matsubara & Heiligenberg, 1978; Ulanovsky & Moss, 2008). Echolocating bats are thus an ideal system to address the costs and benefits of dynamic sensory information networks. In this chapter, I present my work on echolocation in the context of communication and interference, which advances the field by community-scale analyses of free-flying bats, multi-sensor datasets, and the first quantification of the perceived auditory scene during collective movement.

## 4.1 Eavesdropping on echolocation calls reveals interspecific community-level social structures

Echolocating bats are a great model system to study social information transfer due to their constant emission of high-intensity acoustic energy, which contains information on species, habitat and current task (Jones & Siemers, 2010). A particular focus had been on eavesdropping during foraging (Gager, 2019). Echolocating bats emit a typical rapid call sequence just prior to prey capture ("feeding buzz"), which reveals their prey attack rate (Racey & Swift, 1985; Kalko, 1995). The subsequent echolocation behaviour reveals whether an attack was successful or not (Surlykke et al., 2003). A bat's echolocation behaviour thus informs about its foraging behaviour, foraging success and in consequence the profitability of its foraging patch. By eavesdropping on this rich information, other bats can extend the sensory range for prey several times beyond the range of their own echolocation (Dechmann et al., 2009; Jones & Siemers, 2010; Gager, 2019; Prat & Yovel, 2020). Many bat species use this information and approach playbacks of conspecific feeding buzzes in the field (Barclay, 1982; Fenton, 2003; Gillam, 2007; Dechmann et al., 2009). In the lab, some bat species are also able to recognize and distinguish the echolocation calls of different sympatric species (Schuchmann & Siemers, 2010a; Voigt-Heucke et al., 2010). However, it is still unknown if and how acoustic species recognition mediates interspecific interactions in the field. Thus, I investigated eavesdropping in different species during foraging in the field, to test whether bats recognize species identity from echolocation calls, and how this informs their behavioural decisions under natural conditions (**Dorado-Correa et al., 2013; Hügel et al., 2017; Lewanzik et al., 2019**). Generally, I hypothesize that bats evaluate the profitability of a foraging patch based on the information contained in the echolocation of other close-by bats. Since profitability is indicated by feeding buzzes and depends on a species' foraging ecology, the bats' reactions should depend both on the call-type and the species identity of the calling species.

In **Dorado-Correa et al. (2013)**, we started by presenting playbacks of search calls and of feeding buzzes of both conspecific and heterospecific bat species to four different species of bats in the field. In general, the bats were more attracted by feeding buzzes than search calls and more by the calls of their conspecifics than their heterospecifics. Furthermore, bats showed differential reactions to the calls of their heterospecifics. In particular, *Myotis capaccinii* reacted equally to the feeding buzzes of conspecifics and of the ecologically somewhat similar heterospecific *Hypsugo savii*. Our results thus confirmed **eavesdropping on feeding buzzes at the intraspecific**

**level in wild bats** and provided the first experimental quantification of **potential eavesdropping in European bats at the interspecific level**. Despite this, we did not find a general and unequivocal evidence for interspecific eavesdropping. While attraction to ecologically dissimilar species was generally lacking, in line with our predictions, we found the matching attraction to ecologically similar species only in *M. capaccinii*, but not in the open-space species *N. noctula* and *P. nathusii* to each other. The attraction of *M. capaccinii* to *H. savii* could have been mediated by species recognition, followed by an approach to a species with partially overlapping foraging ecology (foraging similarity hypothesis). Another possibility, however, is that the positive reaction of *M. capaccinii* to *H. savii* is due to the acoustic similarity of their echolocation calls (acoustic similarity hypothesis; Balcombe & Fenton, 1988; Übernickel et al., 2013), particularly in case of the feeding buzz calls. Because the species-specificity of echolocation calls is more pronounced in search calls than in feeding buzzes, it is possible that the bats were not able to identify species based on feeding buzzes alone.

In **Hügel et al. (2017)**, I specifically tested the **acoustic similarity hypothesis** versus the **foraging similarity hypothesis** with three linked playback experiments. Focusing on *M. capaccinii*, we tested in the flight room and the field if foraging *Myotis* bats approached the foraging call sequences of conspecifics and four heterospecifics that were similar in acoustic call structure only (acoustic similarity hypothesis), in foraging ecology only (foraging similarity hypothesis), both, or none. As stimuli, we used this time full capture sequences consisting of search, approach, and buzz phase, presented at high repetition rate. In this way, we presented both the species-specific as well as the foraging-related information, and simulated highly attractive above-average bat activity and prey capture rates. In the lab, *M. capaccinii* only approached call sequences of conspecifics and of the heterospecific *M. daubentonii* with similar acoustics and foraging ecology, but did not approach the other species. In the field, we analysed the total acoustic activity of free-flying bats and additionally 128 acoustically tracked three-dimensional flight trajectories of individual bats in response to the same playbacks. Although the bats were largely not attracted to any of the playbacks, they showed slight tendencies to approach *M. capaccinii* and *M. daubentonii* calls, indicated by increased group activity and altered individual flight trajectories. Overall, and in contrast to my original predictions, the bats did not approach the species only similar in acoustic call structure or foraging ecology, thus **neither supporting the acoustic similarity nor the foraging similarity hypothesis**. The most likely reason for the unexpected result is that classifying the similarity of co-occurring is problematic. Co-occurring species need to differ to avoid competition (Schluter & McPhail, 1992). The species that we classified as similar in call design and foraging ecology will still possess differences that might be relevant and perceptible to wild bats. In addition, other factors such as behavioural context, local environment, current prey availability, or interspecific competition will modulate the reaction to acoustic cues. For example, the benefits of reacting to heterospecific information is likely higher when detecting predators, which hunt multiple prey species (Shriner, 1998; Vitousek et al., 2007; Magrath et al., 2009; Fallow & Magrath, 2010; Fallow et al., 2011; Magrath & Bennett, 2012; Getschow et al., 2013; Haff & Magrath, 2013; Fuong et al., 2014), compared to a foraging context, where foraging ecologies are non-identical and inter-individual competition lowers the benefits. In the field, the natural prey availability was uncontrolled and unknown in relation to our simulated prey attack rate. Likewise, the natural bat activity was uncontrolled and unknown, potentially diluting the effect of our playbacks. In summary, our study highlights the complex influences on information transfer within and between species. It supports, together with previous studies (Dorado-Correa et al., 2013; Übernickel et al., 2013), the general idea that interindividual information transfer based on echolocation calls is possible in bats, both within and across species boundaries. Bats use both conspecific as well as heterospecific cues as a source of information to guide their own decision making.

Having established the potential of interspecific information transfer, as well as the multitude of additional factors influencing it, I designed a study to explicitly test and tease apart those factors. Besides the scarce literature on responses towards heterospecific cues, showing variable responses, previous studies are also difficult to compare and ignored relevant biological parameters. Previous playback studies presented very different stimuli, e.g., by using single call types only (search calls, feeding buzzes) and very different rates of feeding buzzes, thus simulating low to unrealistically high patch profitability, which will likely affect the bats' responses. The actual natural bat activity prior to experimental playbacks has rarely been considered, although it strongly varies over time and space and affects eavesdropping (Roeleke et al., 2018). In **Lewanzik et al. (2019)**, we systematically tested the effect of feeding buzz rate (= patch profitability) on interspecific eavesdropping behaviour in a free-ranging bat ensemble while at the same time controlling for actual bat activity. We performed a large-scale field experiment at 12 field sites, presenting 1-min-long playbacks of echolocation capture sequences of six different bat species with different acoustics and foraging ecologies, and observed the natural and experimentally manipulated activity of four free-flying response species. Playbacks contained 0 to 96 feeding buzzes per minute, simulating very low to very high prey capture rates, and thus very low to very high prey density and patch profitability. For all treatments, we analysed how focal bat activity changed during the 1-min playback compared to the preceding minute. Overall, our results show a **complex pattern of interacting effects of natural bat activity level, prey density and species identity on bat species-species-interactions**. (i) *Natural conspecific bat activity* was strongly negatively correlated with activity change: at low natural bat activity, echolocation call playbacks attracted bats, but repelled them at high natural bat activity. This indicates a strong density-dependent attractive-to-repellent effect of bat echolocation calls, likely due to intra- as well as interspecific competition. (ii) *Feeding buzz rate*, a sensory cue for prey density and patch profitability, had species-specific effects on bat activity changes. Increasing the feeding buzz rate lead both to increased and decreased bat activity, often in a non-linear fashion, and depending on the specific species pairs. (iii) *Species identity* of both the playback and the focal species affected the response pattern. This is likely driven by various similarities and differences in behavioural and ecological traits including prey spectrum, prey handling capabilities, hunting style, territoriality, competitive ability etc, leading to species-pair-specific interaction patterns. Our study shows that bats in the field integrate social information from vocalisations about conspecific activity, prey abundance and species identity. It furthermore illustrates the diversity and complexity of interspecific interactions in bat communities, highlighting that inferences from single species studies are not sufficient to understand population dynamics and space use, and provides "**rare experimental evidence for the existence of interspecific community-level social structures**" (Culina & Garroway, 2019).

The studies above investigated echolocation call-based information transmission during foraging in bats with short, frequency-modulated calls. In **Chang et al. (in prep)**, we turned towards another group of species, horseshoe bats (Rhinolophidae), which emit long, whistle-like constant-frequency calls. Horseshoe bats are, to date, the only taxa known that can discriminate calls of their own species from other species, and as well between different congeneric species (Schuchmann & Siemers, 2010a). First, we demonstrated a very strong sexual dimorphism in the echolocation call frequencies in acuminate horseshoe bats (*Rhinolophus acuminatus*), an understudied species of southeast Asia. After controlling for body size, we found a large effect of sex on call frequency, with the (larger) males calling about 5 kHz lower than the (smaller) females. Sexual dimorphism in bat echolocation calls had been described in only 16 species, all except for one emitting constant-frequency calls (Rhinolophidae and Hipposideridae), with a maximum difference of 1 kHz. Given that bat echolocation is typically adapted to orientation and foraging in darkness and rarely shows sexual dimorphism, **we hypothesized that the strong intersexual difference of 5 kHz in *R. acuminatus* might have evolved under sexual selection to serve a communicative function** (Punzalan & Hosken, 2010). We presented unaltered and frequency-shifted male and female calls to roosting males and females and quantified their ear movements and calling behaviour as a measure for their interest in the playback. Individuals of both sexes clearly reacted to the playbacks, shown by 5x more ear movements, 3x higher call duty cycle, and by directing their calls towards the playback. Despite the bats' interest in echolocation calls and some trends of females reacting less to male playbacks and males reacting more to female playback, we failed to find any clear sex- or frequency-specific pattern, possibly due to large interindividual variation and small sample sizes. Overall, we report **the strongest example of sexual dimorphism in echolocation call frequency**, but can neither confirm a communicative function of this dimorphism nor sexual selection as its driving force.

Finally, returning to a foraging context, we addressed the driving force of sociality and the use of social cues during foraging (**Egert-Berg et al., 2018**). Using GPS- and acoustic data from bat-borne data loggers, we compared the foraging movements and the social environment of five free-ranging bat species, showing that **resource distribution and ephemerality drives social foraging in bats**. Two of the tested species forage on ephemeral resources: the greater mouse-tailed bat *Rhinopoma microphyllum*, an open-space bat hunting ephemeral insect swarms, and the Mexican fish-eating bat *Myotis vivesi*, which hunts ephemeral fish swarms at the surface of marine waters. The three other tested species forage on spatially and temporally predictable resources, namely on cactus nectar and pollen (the lesser long-nosed bat *Leptonycteris yerbabuenae*), tree fruit (the Egyptian fruit bat *Rousettus aegyptiacus*), and on terrestrial insects that predictably occur on open forest floors (the greater mouse-eared bat *Myotis myotis*). The species that forage on ephemeral resources changed their foraging sites nightly, showed large variation in the time spent foraging, commuted together with conspecifics as evidenced by regular on-board recordings of conspecific echolocation calls, and were highly attracted to playbacks of conspecific echolocation calls. In contrast, the species that forage on predictable resources revisited the same foraging spot over multiple nights, spent similar amounts of time foraging each night, flew alone (no conspecific calls recorded) and were not attracted to call playbacks. In addition to the competitive interactions shown by **Lewanzik et al. (2019)**, our results here show **how resource (un)predictability influences the costs and benefits of social foraging**.

## 4.2 Echolocation and flight in collectives

As presented above, the constantly broadcast energy of active sensing animals has great potential for information transmission, both within and across species boundaries. The active emission of energy, however, can also pose a **costly sensory challenge in groups, termed the "cocktail party nightmare"** (Ulanovsky & Moss, 2008). In humans, the cocktail party effect describes how we (i.e., our auditory systems) analyse auditory scenes and segregate auditory streams to focus on and listen to a single speaking person, ignoring a multitude of surrounding sounds (Bregman, 1990). For bats, it is postulated that this problem of auditory scene analysis is much more complex (Moss & Surlykke, 2001; Ulanovsky & Moss, 2008; Moss & Surlykke, 2010). Each emitted call can result in many echoes reflecting off all the objects around the bat, which is repeating about 10 times a second, while the bat flies at a speed of 5-10 m/s and possibly searches for the rather faint echoes of insect prey. When other bats fly close-by, their intense calls can mask the faint echoes of interest. In addition, the echoes to the calls of those close-by bats will make identifying the correct echo increasingly difficult with increasing numbers of neighbouring bats (Ulanovsky & Moss, 2008; **Beleyur & Goerlitz, 2019**). In the bat echolocation literature, this problem is generally summarized as "jamming" (Jones & Conner, 2019), and consequently, potential "jamming avoidance responses" (JAR) of echolocating bats to various kinds of acoustic disturbances had been intensively studied (e.g., Griffin et al., 1963; Habersetzer, 1981; Møhl & Surlykke, 1989; Jones et al., 1994; Ratcliffe et al., 2004; Bartonicka et al., 2007; Gillam et al., 2007; Ulanovsky et al., 2007; Bates et al., 2008; Chiu et al., 2008; Tressler & Smotherman, 2009; Gillam et al., 2010; Jarvis et al., 2013; Amichai et al., 2015; Cvikel et al., 2015a; Lin & Abaid, 2015; **Luo et al., 2015**; Gillam & Montero, 2016; Götze et al., 2016; Adams et al., 2017; Mazar & Yovel, 2020; Beetz et al., 2021). Across all these studies, the high flexibility of bats to adjust to various sensory situations is evident. However, the support for a jamming avoidance response is mixed, depending on various species-, context- and call-dependent parameters, and the severity of potential jamming is getting increasingly challenged (Amichai et al., 2015; Cvikel et al., 2015b; Götze et al., 2016; Mazar & Yovel, 2020).

Despite this ongoing debate about the existence of jamming and the sender's potential sensory anti-jamming strategies, very little work addressed **jamming from the receiver's perspective strategies** (Lin & Abaid, 2015; Perkins et al., 2017) and never quantified the severity of it for bat echolocation. In **Beleyur & Goerlitz (2019)**, we present the first model describing the sensory perception in small to large groups of active sensing animals. Incorporating properties of echolocation, psychoacoustics, acoustics, and group flight geometry, we show that echo perception is unaffected in small groups (N<10), and that even in large groups (N~100), regular perceptual "glimpses" of a local neighbour are possible. This suggests that the typical behaviours performed in small and large groups, namely foraging and emergence, are not hampered by group echolocation. Even more, we show that echo perception in large groups is spatially limited to close-by and frontal neighbours. This spatial filter is likely even supporting group flight by limiting the perception to the closest frontal neighbours. Furthermore, our analyses provide theoretical predictions for potential sensory strategies that reduce interference in group flight.

We complement this theoretical work on active sensing in groups (**Beleyur & Goerlitz, 2019**) by a large empirical data set, termed the Ushichka dataset (Beleyur & Goerlitz, in prep), the Bulgarian diminutive for something with multiple ears. This dataset encompasses multi-microphone-multi-camera-data of the vocal and spatial behaviour of many individuals of free-flying bats of different species (Beleyur & Goerlitz, in prep; Mysuru et al., in prep) and the three-dimensional geospatial model of their cave environment (**Kamburov et al., 2018**). Our ongoing analyses address central questions in collective behaviour, such as which parameter space could (modelling) and do (empirically) bats use to optimize sensory information in dynamic social environments; which and how many neighbours can they perceive in groups; how does the spatial restriction of information lead to limited interactions between group members; and how do these interactions control leader-follower-dynamics and group structure in different behavioural contexts (emergence, swarming, foraging).

In a first small study (**Mysuru et al., in prep**), we analysed a subset of the data to investigate **jamming avoidance behaviour in high-duty cycle bats** of the genus *Rhinolophus*. To date, most studies on jamming investigated low duty-cycle bats that emit short frequency-modulated (FM) calls with long pauses. In contrast, high duty-cycle bats that emit long constant-frequency (CF) calls with short pauses are understudied, despite their higher chances of spectro-temporal call-call and call-echo overlap during group echolocation. This potential for spectro-temporal overlap, however, also complicates the analysis, likely explaining the lack of studies. We thus developed new approaches for analysing single calls and for analysing average call parameters. Comparing between bats flying alone and in small groups ($N \leq 4$), we found no difference in call duration and frequency parameters, neither for the central long constant-frequency component of the calls nor for the flanking short frequency-modulated components. We thus show that horseshoe bats, despite their long calls that are prone to spectro-temporal overlap, do not alter their calls when flying in groups of up to four bats in a complex echoic cave environment. Our results thus match the increasing evidence that jamming does not pose a problem for FM-bats (Amichai et al., 2015; Cvikel et al., 2015b; Götze et al., 2016; Beleyur & Goerlitz, 2019; Mazar & Yovel, 2020), now extending this to high-duty cycle CF-bats.

Finally, in another ongoing project in collaboration with Prof. Gloriana Chaverri (University of Costa Rica) and Dr. Damien Farine (University of Zürich), we investigate **vocal information transfer to coordinate group movement**. Efficient group coordination is essential for a number of reasons, but ultimately it may allow group members to reduce the costs and increase the benefits of group living. For example, many species of fish form schools and birds form flocks that allow individuals to reduce the costs of locomotion (Marras et al., 2015), improve navigation (Tamm, 1980), and reduce the risk of predation (Krause & Ruxton, 2002); these goals are achieved with synchronized speed and directionality of group members (Lissaman & Shollenberger, 1970; Dell'Ariccia et al., 2008; Pavlov & Kasumyan, 2020). When individuals are unable to synchronize their movement with others in the group, they face a greater risk of predation (Demsar & Bajec, 2014). Identifying the mechanisms that aid group coordination is thus critical for understating social aggregations. For example, we know that acoustic signals are used by several terrestrial and arboreal mammals for group coordination (Langbauer, 2000; Bousquet et al., 2011), which is particularly beneficial in light-deprived and visually cluttered habitats. Yet, we lack information on how sounds enhance collective behaviour for many species and particularly during flight, which, compared to terrestrial locomotion, may impose significant challenges for coordinating groups in three dimensions. We study the neotropical bat *Thyroptera tricolor* that forms small groups (<10 individuals) and roosts in furled developing leaves of banana-like plants. Because the leaves are only available for 5-31 hours, the group must regularly search for new roosts during day and night, coordinating their joint individual movements. Here, we analyse how in-flight vocalisation and specific individuals (leaders) contribute to group coordination in flying bats during critical roost finding events. In addition to echolocation calls, which had been the focus of my previously described work, the study here extends my research to **social calls**. Social calls are not adapted to individual perception, but **are used for 'real' communication between individuals**. Our study will represent one of the first studies to **provide evidence on the role of acoustic communication during coordination and decision making for groups on the wing**.

**Our current knowledge is just scratching the surface of how bats interact with one another in different social situations**. These situations differ along many ecologically relevant dimensions, such as each species' social system, typical habitat and foraging ecology, as well as the behavioural context, group size and group structure. All these dimensions affect the costs and benefits of specific behaviours in groups. As a simple example, the "optimal" behaviour in groups will likely depend on the context: emergence flight will show smaller inter-individual distances and less variable movement direction than foraging flight. During emergence, individuals share a (more or less) common goal, while foraging flight is affected by the external and unpredictable appearance of prey echoes and competitive interactions. Future research directions need to address whether these different contexts are governed by the same sensory mechanisms and behavioural algorithms, yet with context-dependent parameters, or whether different contexts require fundamentally different sensory-behavioural rules. Likewise, comparisons between sensory systems are needed to understand whether the same sensory-behavioural rules can be informed by fundamentally different sensory information, such as those provided by vision (long-range, directional, occlusion) and echolocation (short-range, less to omni-directional, less to no occlusion).

# 5 Environmental variation and anthropogenic change

> […] THE SPECIES THAT SURVIVES IS THE ONE THAT IS ABLE BEST TO ADAPT AND ADJUST TO THE CHANGING ENVIRONMENT IN WHICH IT FINDS ITSELF.
>
> Megginson (1963)

A central common theme of all my research is the question of **how animals deal with variation and change**. First, sensory systems constantly adjust to the fluctuating intensities of their physical input over orders of magnitudes. Second, predator attacks change the surrounding of prey animals within split seconds and require rapid adaptive reactions. In turn, predators react to the anti-predator actions of their prey. Thirdly, all social interactions take place in a highly dynamic environment that varies with the (inter-)actions of its group members. In addition to this natural variation, sensory systems are recently further challenged by anthropogenic sensory pollutants that cause downstream effects on survival, reproduction and species interactions (Dominoni et al., 2020; Senzaki et al., 2020).

In the previously presented empirical and modelling projects, I investigated how bats dynamically adjust biosonar parameters to different tasks and over fast timescales to optimize information transfer, how free-flying bats in the wild react to changes in their social (acoustic) environment, and how biophysical parameters enable perception of individuals and groups and potentially underlie collective movement. In parallel, I have a strong desire to understand how animals react to natural variation in their environments and to anthropogenic changes that occur on slower time scales, and to derive recommended actions (**Goerlitz, 2018; Voigt et al., 2021**). Specifically, combining modelling and field studies, I address how daily, seasonal and anthropogenic changes of temperature limit the sensory range of sound-based perception (**Luo et al., 2014; Goerlitz, 2018**), and if echolocating bats adjust call parameters to cope with this in European (**de Framond-Bénard et al., in prep-b**) and neotropical habitats (PhD research of P Iturralde-Pólit). Similarly, I address the impact of noise (**Luo et al., 2014; Gomes & Goerlitz, 2020**) and light (**Hügel & Goerlitz, 2020; Straka et al., 2020**) on sound-based perception and the underlying sensory mechanisms and individual coping strategies.

## 5.1 Natural variation of the environment

Sensing and acting takes place in an abiotic environment. The physico-chemical properties of the environment determine, enable and constrain organismal biology on all levels – which is the topic of ecology, the study of the interrelationship between organisms and their environment (Begon & Townsend, 2021). Animal signalling and sensing adapts and adjusts to environmental conditions over long evolutionary (Marten & Marler, 1977; Marten et al., 1977; Wiley & Richards, 1978; Endler, 1992; Wehner, 1997) and short behavioural time scales (Brumm, 2004; Hotchkin & Parks, 2013).

**Environmental conditions, however, are not constant, but dynamically change**. This includes daily and seasonal changes in the intensity and spectral composition of light; fluctuations in temperature, humidity and precipitation; yet also long-term climatic changes. Mechanisms to deal with natural variation in the environment evolved across sensory system. The colour constancy ("white balance") of the visual system enables to perceive the colour of an object independently of the spectral variation of the illuminating light which causes spectral variation in the object's reflected light (Smithson, 2005). In the auditory system, convergent evolution lead to the analogue phenomenon of timbral constancy (Risset & Wessel, 1982). Timbral constancy enables to perceive the spectral shape of a sound, i.e., its timbre or acoustic colour (Watkins, 1991), despite spectral changes caused by environmental frequency-dependent filtering (Wiley & Richards, 1978; Lawrence & Simmons, 1982; **Goerlitz, 2018**). Since a sound's spectral shape is of major importance to identify, segregate and group auditory signals (Bregman, 1990; Griffiths & Warren, 2004), timbral constancy was shown both for humans (Zwicker, 1964; Summerfield et al., 1987; Watkins, 1991) and bats (Goerlitz et al., 2008b) when listening to experimentally manipulated sounds.

Sound is a vibration that propagates through a medium (usually air, water or a solid), whose physical properties determine sound propagation. In air, sound propagation is mainly influenced by three factors: the sound's frequency and the air's temperature and relative humidity, which together determine the sound's attenuation (Lawrence & Simmons, 1982; Stilz & Schnitzler, 2012; **Goerlitz, 2018**). These factors interact non-linearly. Depending on the species- and habitat-specific starting conditions, any change of these parameters can either increase or decrease the sensory range and volume of auditory perception (**Luo et al., 2014; Goerlitz, 2018**). These inevitable physical properties have ecological consequences. First of all, a bat's call frequency strongly determines and limits its maximum detection distance for objects in its environment, including for its prey (and likewise, it limits the distance over which the bat can be detected by its prey; Goerlitz et al., 2020). Second, any unidirectional change, such as the global increase of average temperature (IPCC, 2021), leads to a unidirectional change in average sound attenuation and thus average object detection distance (**Luo et al., 2014**). Crucially, the direction of this unidirectional effect depends on call frequency: species calling above a climate zone-specific sound frequency will lose prey detection volume, while species calling below that sound frequency will gain prey detection volume. The sound frequency (~20-100 kHz) and the effect size of the gain and loss (±10-20%) depend on the local climatic conditions. Hence, the prey detection ability, and thus possibly the foraging efficiency, of echolocating bats is susceptible to rising temperatures through climate change. Within local species assemblages, this may change bat community composition and affect the predator-prey-interactions of echolocating bats and their eared prey. Third, daily and seasonal variation in air temperature and humidity causes variation in sound attenuation and thus in the bats' object detection distance (**Goerlitz, 2018**). In many climate zones, this daily and seasonal variation is much larger than the average change in temperature caused by global warming. It remains to be studied how the large natural variation and the smaller yet unidirectional change interact and how this affects the prey detection ability of individual bats and their interspecific interactions with competitors and prey.

Compared to vision, echolocation in air is a rather short-range sense. Depending on call frequency and object size, echolocating bats have detection distances of only a few meters to a few tens of meters (Jones & Siemers, 2010; Safi & Siemers, 2010; **Goerlitz et al., 2020; Stidsholt et al., 2021a**). In combination with their fast flight speeds, this means that hunting bats have a very small ratio between their sensory and motor volumes (**Stidsholt et al., 2021a**), i.e., they are acting within a highly reactive mode while hunting (Snyder et al., 2007). Any reduction in sensory range and volume caused by (natural and anthropogenic) environmental variation could be costly. Correspondingly, the call frequency of different species of the genus *Rhinolophus* (Heller & von Helversen, 1989) as well as some geographically disjunctive populations of single species (Guillen et al., 2000; Snell-Rood, 2012; Mutumi et al., 2016; Jacobs et al., 2017; Maluleke et al., 2017) were correlated with local climatic conditions. This suggests long-term evolutionary adaptation of bat echolocation to the acoustic properties of the environment to optimize object detection, in line with the acoustic adaptation (Morton, 1975; Rothstein & Fleischer, 1987) and sensory drive (Endler, 1992; Cummings & Endler, 2018) hypotheses. In contrast, short-term behavioural plasticity of bat echolocation in response to weather-dependent changes was to date only reported for the neotropical genus *Molossus* (Chaverri & Quiros, 2017). In two studies in temperate and tropical habitats, we are thus testing whether flying bats in the wild (**de Framond-Bénard et al., in prep-b**) and in large enclosures (PhD research of P Iturralde-Pólit) adjust their call properties to environmental conditions and thus maintain constant detection distances. I predict that bats compensate for weather-induced reduction of sensory range by lowering call frequency, increasing call intensity, and/or increasing call duration (**Luo et al., 2014**) – as they do when their perception is challenged in other ways, such as by noise (**Luo et al., 2015**). In **de Framond-Bénard et al. (in prep-b)**, we reconstructed the 3D-flight trajectories and echolocation call parameters (frequency, duration, source level & intensity) of three European species (groups) of free-flying bats in their local habitat over 30 nights across two years. Analysing >28.000 calls of >2.300 flight trajectories, we found weather-correlated changes only in the species group *Pipistrellus nathusii/kuhlii*, which lowered call frequency (as predicted) and lowered call energy (against our prediction) with increasing atmospheric attenuation. In contrast, we found no changes in the species *Pipistrellus pipistrellus* and *Myotis daubentonii*, although the effect size of call energy reduction was as strong as in *P. nathusii/kuhlii* yet with 95% confidence intervals that just overlapped with Zero. Although bat echolocation adjusts very fast and flexibly to the task (**Lewanzik & Goerlitz, 2021; Stidsholt et al., 2021a**), the evidence of behavioural plasticity in response to changing atmospheric conditions remains ambiguous. Crucially, physiological and physical limits might prevent the bats from showing the hypothesized changes in call parameters. In search flight, bats might already emit calls at their physiological limit (Currie et al., 2020), thus preventing a further increase of intensity. Reducing call frequency would reduce atmospheric attenuation, but it would also reduce the echo intensity of small insects in a size-dependent manner (Safi & Siemers, 2010), which might impose species-specific limits on the lower call frequency for different bat species depending on their diet. Finally, the potential sensory mechanisms and their precision that would allow bats to perceive current atmospheric conditions or their current sensory range are unclear (**de Framond-Bénard et al., in prep-b**).

## 5.2 Anthropogenic variation of the environment

Over the past decades, by now termed the Anthropocene (Steffen et al., 2007), we increasingly changed, and are still changing, the Earth's physico-chemical conditions and thus the environment of all living organisms (Vitousek et al., 1997). With respect to the sensory biology of acoustically orienting nocturnal animals, the increasing sensory pollution caused by noise (Barber et al., 2010; Slabbekoorn et al., 2010) and artificial light (Hölker et al., 2010; Falchi et al., 2016) is of major concern.

With more than 1.400 species, 1.100 of which echolocate (Wilson & Mittermeier, 2019; Simmons & Cirranello, 2020), bats form about one quarter of all mammals. They are of major ecological importance as top-level predators (Kalka et al., 2008; Williams-Guillen et al., 2008), pollinators (Hodgkison et al., 2003; Fleming et al., 2009) and seed disperses (Hodgkison et al., 2003; van Toor et al., 2019), thereby also providing invaluable ecosystem services (Jones et al., 2009; Kunz et al., 2011) of great economic value to humans (Cleveland et al., 2006; Boyles et al., 2011). Likewise, the ~160.000 species of Lepidoptera (moths and butterflies, Kawahara et al., 2019) have crucial ecological importance as pollinators, prey, and herbivores (Ehrlich & Raven, 1964; Mitter et al., 2017). About three quarter of all Lepidopteran are nocturnal moths (Kawahara et al., 2018), which are engaged with echolocating bats in an exclusively sound-based predator-prey-interaction (Conner & Corcoran, 2012; ter Hofstede & Ratcliffe, 2016). Their adaptations to a nocturnal life-style together with their sound-based perception makes them particularly susceptible to **anthropogenic noise and light pollution**.

**Anthropogenic noise pollution** is a widespread pollutant of increasing concern for wildlife, both in terrestrial (Pijanowski et al., 2011) and marine habitats (Duarte et al., 2021), with multiple adverse effects on all animals including arthropods, birds, fish and humans (Barber et al., 2010; McClure et al., 2013; Ware et al., 2015; Senzaki et al., 2020; Christensen et al., 2021; Classen-Rodríguez et al., 2021; Gomes et al., 2021b; Osbrink et al., 2021; van der Knaap et al., 2021). Due to their strong reliance on sound for sensory perception (Corcoran & Moss, 2017), bats are likely affected by noise pollution in multiple ways. This is evident for gleaning bats, i.e., those species that hunt by listening for the sounds generated by their prey. The frequency range of prey sounds is relatively low (Goerlitz et al., 2008a) and overlapped by anthropogenic noise (Schaub et al., 2008; Gomes et al., 2021a). Thus, gleaning bats suffer from noise by increased foraging time, reduced foraging success and subsequent degradation of their habitats (Schaub et al., 2008; Siemers & Schaub, 2011; Allen et al., 2021).

In contrast to the consequences on gleaning, we have limited understanding of the effects of noise on higher-frequency echolocation, and more generally of the **perceptual mechanisms of noise disturbance**. Likewise, **individual differences** in response to noise are likely widespread, but lacking in empirical data (Harding et al., 2019). In **Gomes & Goerlitz (2020)**, we explicitly tested perceptual mechanisms of noise disturbance. We challenged echolocating *Phyllostomus discolor* bats with three different types of noise while they performed an object discrimination task. Measuring their psychometric discrimination function, decision behaviour, and spectro-temporal call characteristics, we demonstrated evidence for multiple perceptual mechanisms of noise disturbance and high individual variability in susceptibility to and coping ability with noise. Two bats were able to cope with all three noise types, as their discrimination performance in noise was unaffected compared to silence. Two other bats, in contrast, were not able to cope with the noise, yet in different ways. All bats showed changes in their echolocation behaviour during noise playback. Most prominent was an increase in call level shown by all bats (Lombard effect), with additional changes in call frequency (without a clear pattern) and increased call duration, which was stronger for the coping bats than the non-coping bats. Given the presence of the Lombard effect, all bats were likely affected by the perceptual mechanism of masking. However, only some bats were able to maintain discrimination performance in noise. It is thus likely that other perceptual mechanisms, such as distraction, affected signal perception in at least one of the individuals tested.

In contrast to the perceptual mechanisms on the side of the receiver, mechanisms to deal with noise on the sender's side are better understood. The Lombard-effect, the (involuntary) increase of vocalization level in noisy conditions (Lombard, 1911; Brumm & Zollinger, 2011; Hotchkin & Parks, 2013), is a basic mechanisms for maintaining communication in noise in many vertebrates, including fish, frogs, birds and mammals including humans (Luo et al., 2018). The Lombard effect is often accompanied by additional changes in signal parameters, but it is generally unclear **how multiple changes in signal parameters combine to contribute to signal perception in noise**. In **Luo et al. (2015)**, we quantified how *P. discolor* bats change their echolocation calls under different noise treatments and used auditory modelling to investigate the effect of those changes on signal perception. As in **Gomes & Goerlitz (2020)**, the increase of call amplitude was most prominent. In addition, we found individual- and noise-specific increases in call duration and signal redundancy (signal repetition). The combined effect of these parameters determines signal detectability, because the auditory system integrates signal energy over time (Viemeister & Wakefield, 1991; Heil & Neubauer, 2003). Our results show that the Lombard effect contributed most strongly to signal detectability in noise, yet also signal duration and redundancy had marked effects on signal detectability. Our findings demonstrate that (changes of) signalling parameters are adjusted to the properties of the receiver's sensory system, to maintain signal transmission in noisy and fluctuating environments.

Together, both studies show a high degree of behavioural flexibility in the signalling behaviour of echolocating bats. Bats' behavioural flexibility in signalling in response to different tasks is well-known (cf. **Lewanzik & Goerlitz, 2021**), and here we extend it to short-term fluctuations in the environment, show how signalling flexibility exploits or is driven by receiver physiology, and we highlight the importance of individual differences in sensory strategies.

Nocturnal **light pollution** caused by human activity (ALAN: artificial night at light) has substantially increased over the last decades all over the globe (Hölker et al., 2010; Falchi et al., 2016; Kyba et al., 2017), with negative effects on many different animals (Longcore & Rich, 2004; Hölker et al., 2010; Knop et al., 2017; Davies & Smyth, 2018). Bats are highly adapted to a life in darkness (Fenton et al., 1995; Maor et al., 2017) and thus are a particularly relevant taxon for studying the effect of ALAN. Given the large ecological diversity of bats, it is not surprising that there is considerable species-specific variation in the reaction of bats to artificial light: while some species exploit prey accumulated at light (Rydell, 1992; Blake et al., 1994; Gaisler et al., 1998; Cravens et al., 2018), other species are severely disturbed in different behavioural contexts including foraging, commuting, and roosting (Stone et al., 2009; Mathews et al., 2015; Stone et al., 2015a), with intensity-, light-type, colour- and context-dependent effects (Stone et al., 2015a; Stone et al., 2015b; Lewanzik & Voigt, 2017; Spoelstra et al., 2017). Like bats, insects are strongly affected by ALAN (Stewart, 2021), with moths as nocturnal animals being particularly susceptible (Boyes et al., 2021). Moths are regularly attracted to light sources, which shortens foraging time (Macgregor et al., 2017; van Langevelde et al., 2017), disrupts navigation (Owens & Lewis, 2018), reduces pollination (Macgregor et al., 2017), increases predation risk (Wakefield et al., 2015) and causes population decline (van Langevelde et al., 2017; Wilson et al., 2018b). Given this large and still unexplored variation, as well as cross-modal effects of light on auditory-guided behaviours, we require additional species-, context- and colour-specific data on the effect of light on nocturnal wildlife to inform mitigation measures.

In **Straka et al. (2020)**, we tested four different bat species in the to date unstudied context of roosting. Testing both natural and simulated cave situations, we show species- and light colour-specific effects of artificial lighting on the bats' emergence behaviour and flight activity. In a choice experiment, two species, *Myotis capaccinii* and *Miniopterus schreibersii*, preferred red over white light, but showed no preference for red over amber, nor amber over white light. During natural emergence from caves, all light colours reduced the activity, with least negative effects observed for the red colour. The two tested *Rhinolophus* species showed the strongest reduction in flight activity in response to any light colour. In conclusion, the clear effects of red and amber lights question their use as bat-friendly lighting. The sensitivity of all four species, and particularly of *Rhinolophus* spp., calls for **utmost caution when illumining natural (roosting) habitats**.

In **Hügel & Goerlitz (2020)**, we tested the effect of light on the sound-evoked anti-predator behaviour of a community of eared moths in their natural environment. Except for the modelling results of Minnaar et al. (2015), previous results either included only (Svensson & Rydell, 1998; Wakefield et al., 2015) or can be sufficiently explained by (Treat, 1962; Agee & Webb, 1969) effects of light on last-ditch manoeuvres alone. Thus, we aimed to test the effect of artificial lighting on both the first (negative phonotaxis) and second (last-ditch) stage of sound-induced evasive flight. We found that the capture performance of light traps was not reduced when playing bat-like ultrasonic calls, suggesting that the **light interferes with and abolishes the sound-induced evasive flight**. This community-level field data is supported by experimental data during controlled tethered flight in the Noctuid moth *Noctua janthe* (**Hügel & Goerlitz, in prep**): artificial light lowered the flight strength both during normal flights as well as during evasive flight in response to bat-like acoustic stimuli. This cross-model suppression of flight makes eared moths easier prey for hunting bats under increasing levels of artificial light at night. Our data adds to the growing evidence showing that light severely interferes with flight in moths, and extends this evidence to negative phonotaxis. Negative phonotaxis is the first line of defence in evasive flight and activated over a much larger distance than last-ditch manoeuvres. The effect of ALAN as a sensory pollutant thus extends over an even larger spatial volume, implying even larger negative consequences for eared moths.

The anthropogenic changes of noise, light and temperature have, to some extent, their natural analogues in the daily and seasonal fluctuations of these environmental parameters. In contrast, **wind turbines** are completely novel additions to our landscapes. Energy production with wind turbines is a central component of our strategy to mitigate the global climate crisis and is globally increasing (GWEC, 2020). However, wind energy production has severe consequences for biodiversity. It requires large areas for establishing wind turbines, and large numbers of birds and bats are regularly killed, resulting in the so-called green-green dilemma (Northrup & Wittemyer, 2013; Voigt et al., 2015). To mitigate this dilemma, many countries mandate environmental impact assessments to assess the impact of newly constructed wind turbines on wildlife. The most common tool to assess bat activity around wind turbines is acoustic monitoring, using a microphone installed at the bottom of the wind turbine's nacelle and an autonomous recording unit. The acoustically recorded bat activity is then correlated with concurrent environmental factors, including date, time, wind speed, and others, to identify conditions of high bat activity, at which the wind turbine will in future be shut off. The validity of this approach thus directly depends on how well the recorded acoustic activity matches the presence of bats within the risk zone of the rotating blades. In **Voigt et al. (2021),** we argue that this match between recorded acoustic activity and real bat presence in the risk zone is much worse than generally assumed. This severely constraints acoustic monitoring in its current form. Three main factors underly this constraint: (i) Due to physical limits on microphone sensitivity, signal-to-noise-ratio and sound absorption in air, acoustic monitoring can detect bats only in a (very) small fraction of the total risk zone. Depending on call frequency and rotor diameter, this fraction covers maximally ~20% to less than 5% of the total rotor-swept area. (ii) Under the non-optimal conditions of the real world, this small fraction is further reduced because the directional sonar beam of bats is mostly not oriented exactly towards the microphone. (iii) Bats are not equally distributed within the rotor swept zone. Different species fly at different altitudes (Roeleke et al., 2016; Wellig et al., 2018); flight altitude differs between migration and non-migration period (Roeleke et al., 2016; O'Mara et al., 2019) and seasons (Goldenberg et al., 2021); and the wind turbines themselves might attract bats and influence their spatial distribution and flight behaviour for various reasons (Kunz et al., 2007; Cryan et al., 2014; Rydell et al., 2016; Voigt et al., 2017). In combination, **these physical and biological constraints mean that the acoustic activity recorded close to and below the nacelle is not well correlated with the total bat activity within the full rotor-swept risk zone**. This severely limits the predictive power of acoustic monitoring in its current form. We therefore call for methodological improvements, including placing multiple microphones at different places of a wind turbine and using additional monitoring techniques such as radar, cameras and thermal imaging.

The investigation of **sensory mechanisms** is scientifically rewarding and opened the doors to many "magic wells" of animal sensory and behavioural physiology and ecology (von Frisch, 1971; Griffin, 1995; de Waal, 2016). However, in the midst of the anthropogenic climate crisis (Ripple et al., 2021), the sixth mass extinction (Ceballos et al., 2015; Ceballos et al., 2017) and the collapse of the Earth's biodiversity (Laurance et al., 2012; Bradshaw et al., 2021), understanding sensory mechanisms that underlie ecological relationships such as predator-prey interactions, is not just a matter of scientific curiosity (Goymann, 2019), but is fundamental to mitigating, if not reversing these catastrophic trends (Dominoni et al., 2020).

# 6 Conclusions

HABE NUN, ACH! PHILOSOPHIE,
JURISTEREI UND MEDIZIN,
UND LEIDER AUCH THEOLOGIE
DURCHAUS STUDIERT, MIT HEIßEM BEMÜHN,
DA STEH ICH NUN, ICH ARMER TOR!
UND BIN SO KLUG ALS WIE ZUVOR

J. W. Goethe (1808)
Faust. Der Tragödie erster Teil

My research investigates **multi-species acoustic information networks from the neuronal processing to community-wide organismal interactions**. As a central theme, I investigate the sensory strategies and behavioural algorithms that link sensory information to motor output. My research is thus positioned between low-level physiological implementations and the coarse-level ecological outcomes and contributes both to uncovering the functional mechanisms as well as the ecological implications of natural behaviour.

By addressing **auditory processing**, I investigate a sensory system less studied than the visual system, yet I draw from insights of visual research, to ultimately unravel common traits of sensory-motor processing. For example, comparing across sensory systems and species, I address general principles that had previously been studied mostly in the visual system, such as (acoustic) camouflage and hiding and spatial frequency perception, and move from individuals to animal communities. My work showed that echolocation supports community-level social structures in the field, interferes little with echo perception in small groups and may even support coordinated group flight. Each example studies functional processes in a different ecological setting; yet all share my common goal of quantifying the sensory and behavioural mechanisms and the ecology and evolution of organismic interactions in complex, diverse and dynamically changing environments.

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# Curriculum vitae

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07.01.1978 in Stuttgart, Germany

Relationship, 2 children (*2014, *2016)

## Work Experience

**Research Group Leader** • *Max Planck Institute for Ornithology, Seewiesen (DE)* **3/2014 – present**

- **Management** of international teams (5-10 members), research projects & a research station in Bulgaria
- Acquisition of **third-party funding** (**Emmy Noether** 2014: ~1.5 MM €; **Heisenberg** 2021: ~1.1 MM €; and others)

- **Research** about the sensory ecology and physiology of multispecies acoustic communication networks
- **Teaching**: Development and teaching of various BSc, MSc & PhD courses (LMU München)

- **Deputy Spokesperson**, Int Max Planck Research School for Organismal Biology (*IMPRS-OB*), 2019 – present
- **Member of the Steering Board** of the *IMPRS-OB* (2015 – 2017, 2019 – present)
- **Faculty Member** of two graduate programs: *IMPRS-OB* (since 2014), Munich Graduate School for Evolution, Ecology & Systematics (since 2015)

**Senior Scientist** • *Max Planck Institute for Ornithology, Seewiesen (DE)* **3/2012 – 2/2014**

- Ad-hoc management of a research team (5 members) following the decease of the former team leader
- Re-focusing the ERC-funded project from 5 to 2 yrs, re-applying for and managing of the budget (400 k€)

**DFG Research Fellow** • *University of Bristol (UK)* **6/2011 – 2/2012**

- Research & Teaching about dynamic three-dimensional acoustic communication networks
- Acquisition of a DFG postdoctoral fellowship and third-party research grants

**Postdoctoral Research Assistant** • *University of Bristol (UK)* **4/2008 – 5/2011**

- Research & Teaching in bioacoustics, neurobiology, predator-prey-interaction
- Single-photon detection in locusts (Centre for Nanoscience & Quantum Information, 3 months)

**Research Assistant** • *Eberhard Karls University Tübingen (DE)* **12/2004 – 2/2005**

- Programming of signal processing & sound analysis / Teaching of various courses

**Community Service (*Zivildienst*)** • *White stork rearing station Schwarzach (DE)* **8/1997 – 8/1998**

- Animal care & nature conservation / Guided tours & public outreach / Documentation

## Education

**Dissertation** • *Neurobiology, Ludwig-Maximilians-University München (DE)* **3/2005 – 3/2008**

- "Perceptual strategies in active and passive hearing of neotropical bats"
- Psychoacoustics / Quantitative behavioural neurobiology / Real-time digital signal processing (MATLAB)
- Advisors: L Wiegrebe & B Grothe

**Studies of Biology and Chemistry** • *Eberhard Karls University Tübingen (DE)* **10/1998 – 11/2004**

- ***Erstes Staatsexamen* in Biology and Chemistry** (30.11.2004)
- ***Diplom* (MSc) in Biology** (16.4.2004), subject areas: Animal Physiology, Zoology, Biochemistry
- **Diploma thesis** (6/2003 – 4/2004, four months of field work in Madagascar); BM Siemers & HU Schnitzler

**Abitur** • *Otto Hahn Gymnasium Nagold (DE)* **1997**

## Appointment procedures for faculty positions

| | |
|---|---|
| **2021** | • **Interview invitation for the W3 professorship "Sensory Physiology and Behaviour", Carl von Ossietzky University Oldenburg** (declined for professional reasons) |
| **2021** | • **Interview invitation for the W2 professorship "Auditory Neuroscience", Carl von Ossietzky University Oldenburg** (declined for professional reasons) |
| **2020** | • **Short-listed for the W2/W3 professorship "Neural basis of Vocal Communication", FU Berlin** (appointment procedure stopped due to procedural errors before compiling the final list) |

## Funding and Awards

| | | | |
|---|---|---|---|
| **2021** | • **Heisenberg program** (5 years), Deutsche Forchungsgemeinschaft (DFG) | € | ~800,000 |
| **2021** | • **Sachbeihilfe** (for 2 PhD researchers), DFG | € | 303,000 |
| **2019** | • **Extended Emmy Noether Research Grant** (1 year), DFG | € | 186,000 |
| **2019** | • **Collaborative CONARE-MPG grant**, with Prof. G Chaverri (University of Costa Rica, CR) und Prof. D Farine (University of Zürich, CH) | € | 40,000 |
| **2014** | • **Emmy Noether Research Grant** (5 years), DFG | € | 1.314,000 |
| **2012** | • **Grant to continue a refocused version of an ERC-Starting Grant** after the decease of the original grantee (26 months), ERC | € | 405,600 |
| **2011** | • **Postdoctoral Research Fellowship** (2 years), DFG | € | 55,700 |
| **2011** | • **Research Grant**, Association for the Study of Animal Behaviour (£ 2,275) | € | 2,650 |
| **2011** | • **Research Grant**, The Royal Society (£ 10,000) | € | 11,700 |
| **2010** | • **Public Engagement Grant**, Research Councils UK (Co-Applicant; £ 1,300) | € | 1,500 |
| **2008** | • **Research Travel Grant**, Minerva Foundation (Max-Planck-Society) | € | 1,860 |
| | • **Research Grant**, Jacob Blaustein Institutes for Desert Research, Israel (EU Dryland Specific Support Action) (£ 1,750) | € | 2,500 |
| **2005** | • **Doctoral Scholarship** (3 years), DFG Graduate program 1091 "*Orientation and Motion in Space*", LMU Munich | € | 47,000 |
| **2003 – 07** | • **6 Awards, Research and Travel Grants** | € | 4,267 |

***37 grants and awards for my team members**, whom I actively encourage and support to apply for research grants and prizes. Where possible, I contribute to writing and act as Co-PI:*

**2020**

- Beleyur & Goerlitz (2020) PNAS: **Best student paper award**, IMPRS for Organismal Biology.
- Lewanzik et al (2019) J Anim Ecol: **short-listed for the 2019 Elton Prize of the British Ecological Society** as one of the top ten papers by an early career author in J Animal Ecology.
- Thejasvi Beleyur: **IMPRS Fellowship**, 6-month salary.
- Antoniya Hubancheva: **British Ecological Society**, conference travel grant.
- Paula Iturralde-Pólit: **Journal of Experimental Biology**, 3-month fellowship to visit my group.
- Paula Iturralde-Pólit: **The Rufford Foundation**, Rufford small grant.
- Paula Iturralde-Pólit: **Bat Conservation Trust**, Kate Barlow Award.
- Paula Iturralde-Pólit: **Organization for Tropical Studies**, graduate research fellowship.

**2019**

- Thejasvi Beleyur: **DAAD**, 6-month PhD stipend.
- Thejasvi Beleyur: **Google Cloud Platform** ($ 1000), to simulate sound propagation.
- Paula Iturralde-Pólit: **DAAD**, 5-month travel grant for visiting my group.
- Paula Iturralde-Pólit: **British Ecological Society**, travel grant.
- Paula Iturralde-Pólit: **American Society for Mammalogists**, Student Field Research Award.
- Paula Iturralde-Pólit: **Organization for Tropical Studies**, graduate research fellowship.

**2018**

- Leonie Baier: **IMPRS Fellowship**, 6-month salary.
- Leonie Baier: **German Academic Exchange Service (DAAD)**, travel grant.
- Thejasvi Beleyur: **DAAD**, 1-year PhD stipend.
- Antoniya Hubancheva: **DAAD**, 3-month travel grant for visiting my group.
- Theresa Hügel: **IMPRS Fellowship**, 6-month salary.
- Paula Iturralde-Pólit: **National Geographic Society**, early career grant.
- Paula Iturralde-Pólit: **Bat Conservation International**, student research grant.
- Paula Iturralde-Pólit: **Organization for Tropical Studies**, graduate research fellowship.
- Aiqing Lin: **China Scholarship Council**, 1-year scholarship for visiting my group.

**2017**

- Leonie Baier: **Smithsonian Society**, A. Stanley-Rand-Fellowship.
- Thejasvi Beleyur: **IMPRS Travel grant** for the Acoustic Communication Course Odense.
- Antoniya Hubancheva: **ERASMUS+**, 6-month training grant for visiting my group.
- Antoniya Hubancheva: **Bulgarian Academy of Sciences**, Outstanding Young Scientist Grant.
- Theresa Hügel: **IMPRS Fellowship**, 6-month salary.

**2016**

- Theresa Hügel: **IMPRS Research grant**, to work with Prof. Hannah ter Hofstede, Dartmouth College.
- Daniel Lewanzik: **DAAD travel stipend** for the 17th Int. Bat Research Conference in Durban (ZA).
- Ekaterina Morozova: **LEHRE@LMU Award** to visit Prof. Yossi Yovel, Tel Aviv University (IL).

**2015**

- Thejasvi Beleyur: **3-year PhD stipend (DAAD)** to study group flight and echolocation in bats.
- Theresa Hügel: **IMPRS Travel grant** for the Acoustic Communication Course Odense.
- Dylan Gomes: **1-year Fulbright scholarship** to study the effect of noise on bats.
- Ella Lattenkamp: **Runners-up poster prize** at the International Bioacoustic Congress 2015.

**2014**

- Theresa Hügel: **Price for an Outstanding Master Thesis**, University of Würzburg.
- Luo et al (2014) J Roy Soc Interface: **Best student paper award**, IMPRS for Organismal Biology.

## International Research Experience

| | |
|---|---|
| Bulgaria | • Managing of an international field research station in Tabachka, NE-Bulgaria, in collaboration with the Rusenski Lom Nature Park, since 2014<br>• Field research on sensory and behavioural ecology, since 2013 |
| UK | • PostDoc, lab and field research, 2008 - 2012 |
| USA | • Field research: bat-moth-interactions, in collaboration with Prof. Hannah ter Hofstede, Dartmouth College, Hanover, USA, 07/2016 |
| Israel | • Field research: bat-moth and bat-bat interactions, in collaboration with Prof. Berry Pinshow and Dr. Kami Corine, Ben-Gurion University of the Negev, 2008, 2009, 2011 |
| Belize | • Field research: task-dependent echolocation, 03/2010 |
| Trinidad | • Field research: echo-acoustic object perception, 12/2007 |
| Madagascar | • Field research: foraging ecology of Grey Mouse Lemurs, 04/2003 & 09-12/2003. |

## Collaborations

- **Hannah ter Hofstede**, Dartmouth College, Hanover (US): A*uditory neurobiology of moths.*
- **Peter Teglberg Madsen**, Aarhus University (DK) and **Yossi Yovel**, Tel-Aviv University (IL): *Bio-logging (GPS, sound, accelerometer,…) of sensing, foraging and navigation in flying bats in the wild.*
- **Manuela Nowotny**, University of Jena (DE): *Auditory neurobiology of bushcrickets.*
- **Gloriana Chaverri**, Universidad de Costa Rica (CR): *The effect of climate change on insectivorous bat communities in Neotropical montane forests* (Co-supervision of PA Iturralde-Pólit).
- **Gloriana Chaverri**, Universidad de Costa Rica (CR), and **Damien Farine**, University of Zürich (CH) & MPI for Animal Behaviour, Radolfzell (DE): *Acoustic communication for in-flight group coordination.*
- **Klaus Hochradel**, UMIT Hall (AT): *3D video tracking of bats and sound sources.*
- **Dragan Chobanov**, Bulgarian Academy of Science (BG): *Predator-prey interactions in a multiple predator-multiple prey community* (Co-supervisor of A Hubancheva).
- **Jens Koblitz**, MPI-AB Konstanz (DE) & **Peter Stilz**: *3D acoustic tracking of vocalizing moving animals.*
- **Lasse Jakobsen**, Syddansk University Odense (DK): *Spatio-temporal sensing in barbastelle bats.*
- **John Ratcliffe**, University of Toronta (CA): *Phylogenetic reconstruction of bat traits.*
- **Christian Voigt**, IZW Berlin (DE): *Human impacts on different bat species.*
- **Rusenski Lom Nature Park**, Ruse (BG): *Biology and ecology of bats in Northern Bulgaria*

## Visiting Researchers

- **Dr. Aiqing Lin**, Northeast Normal University, Changchun (CN). Visiting researcher, 11/2018 – 11/2019. *Behavioural flexibility in echolocation calls under environmental change.*
- **Prof. Erin Gillam**, North Dakota State University, Fargo (USA). Sabbatical, 09/2016 – 08/2017. *Ecological and behavioural drivers of jamming avoidance in echolocating bats.*

## Professional Activities

**Reviewer for Journals:** Acta Chiropterologica • Animal Behaviour • Behavioural Ecology and Sociobiology • Biology Letters • Canadian Journal of Zoology • Current Biology • Ethology • Evolution • Frontiers in Zoology • Journal of Animal Ecology • Journal of Comparative Physiology A • Journal of Experimental Biology • Journal of Experimental Zoology A • Journal of Mammalogy • Journal of Urban Ecology • Methods in Ecology and Evolution • Movement Ecology • Physiology & Behavior • PLoS Biology • PLoS Computational Biology • PLoS ONE • Proceedings of the Royal Society B • Royal Society Interface • Royal Society Open Science • Scientific Reports
(see my Publons review record, complete since 2017)

**Reviewer for Research Agencies:** German Research Foundation (DFG), National Geographic, South Africa National Research Foundation, National Fund for Scientific and Technological Development (FONDECYT) Chile, Carl Zeiss Foundation

**Deputy Spokesperson** and **Member of the Steering Board (since 2019):** International Max Planck Research School for Organismal Biology (joint graduate program of the MPI for Ornithology, MPI for Animal Behavior, and the University of Konstanz)

**Member of the Steering Board (2015-2017)**: IMPRS for Organismal Biology (joint graduate program of the MPI for Ornithology and the University of Konstanz)

**Organizer**
- German Bat Research Meeting 2020, Frauenchiemsee (DE; www.orn.mpg.de/TDFF)
- Symposium at the 17th International Bat Research Conference 2016, Durban (ZA)
- Organizing Committee, Topical Meeting of the German Society for Ethology 2014, Tutzing (DE)
- Two symposia at the 16th International Bat Research Conference 2013, San Josè (CR)
- Discussion Group on Senses and Behaviour (2010-12), University of Bristol (UK)

**Development of a professional online training course on animal experiments with bats for LAS interactive**, according to the requirements of German and European animal protection laws, with L Wiegrebe (LMU Munich) and U Firzlaff (TU Munich)

**Scientific Memberships**: Association for the Study of Animal Behaviour (ASAB), German Society for Zoology (DZG), German Society for Ethology, Int. Society for Neuroethology (ISN), Int. Primatological Society (IPS), Int. Society for Behavioral Ecology (ISBE), Gesellschaft für Primatology (GfP)

## Invited Seminars

**10/2020**
- **Nature of Life Seminars, Dept of Ecological Science, VU Amsterdam (NL)**
  invited by Prof. Wouter Halfwerk

**10/2020**
- **Annual Meeting of the Biology and Medicine Section, Max Planck Society (DE)**
  invited by the Perspectives Committee of the MPS Biology and Medicine Section

**03/2020**
- **Active Sensing: From Animals to Robots. International Conference Tel Aviv (IL)**
  invited by Nachum Ulanovsky, Yossi Yovel, Cynthia Moss, Ehud Assadir (postponed)

**02/2020**
- **Institute for Neurobiology, University of Ulm (DE)**
  invited by Prof. Harald Wolf

**07/2019**
- **Emmy Noether Lecture, Yearly Emmy Noether Meeting, Potsdam (DE)**
  invited by the Deutsche Forschungsgemeinschaft (DFG)

**07/2019**
- **Public lecture at the Open Day of Castle Ringberg, Max Planck Society (DE)**
  invited by Castle Ringberg, conference venue of the Max Planck Society, Kreuth (DE)

**05/2019**
- **Zoological Colloquium, University of Bonn (DE)**
  invited by Prof. Gerhard von der Emde

**05/2019**
- **Zoological Colloquium, University of Würzburg (DE)**
  invited by Dr. Jerome Beetz and Dr. Basil el Jundi

| | |
|---|---|
| **04/2019** | • **Collective Behaviour, University of Konstanz and MPI for Ornithology (DE)**<br>invited by Prof. Iain Couzin |
| **10/2018** | • **Aarhus Institute of Advanced Studies, University of Aarhus (DK)**<br>invited by Prof. Peter Madsen Teglberg |
| **01/2018** | • **Zoological Colloquium, University of Tübingen (DE)**<br>invited by Prof. Jan Benda |
| **01/2018** | • **Invited plenary speaker, German Bat Research Meeting 2018, Berlin (DE)**<br>invited by the organisation committee |
| **06/2016** | • **School of Biological Sciences, Dartmouth College, Hanover (USA)**<br>invited by Prof. Hannah ter Hofstede |
| **03/2016** | • **Institute seminar, Max Planck Institute for Ornithology, Seewiesen (DE)**<br>invited by the Managing Director |
| **07/2015** | • **EES Seminar, Ludwig-Maximilians-University Munich (DE)**<br>invited by Prof. Niels Dingemanse |
| **01/2015** | • **University of Bielefeld (DE)**<br>invited by Prof. Jacob Engelmann |
| **10/2015** | • **EUREKA Symposium, University of Würzburg (DE)**<br>invited by Dr. Sonja Lorenz and student organizers |
| **06/2015** | • **Zoological Colloquium, University of Graz (AT)**<br>invited by Prof. Heinrich Römer |
| **09/2014** | • **Main Symposium Speaker, 107th Annual Meeting of the DZG, Göttingen (DE)**<br>Invited by the DZG section Behavioural Biology |
| **12/2014** | • **Seminar Series in Behavioural and Evolutionary Ecology, Uni of Bern (CH)**<br>invited by the research group of Prof. Michael Taborsky |
| **06/2014** | • **Chair of Zoology, Technical University of Munich (DE)**<br>invited by Prof. Harald Luksch |
| **12/2012** | • **Alumni Day of the DFG Graduate Program "Orientation and Motion in Space"**<br>invited by the organisers, LMU Munich (DE) |
| **08/2012** | • **Gerhard Neuweiler Memorial Symposium, 15th Int. Bat Research Conference, Prague (CZ)**<br>invited by Prof. Gareth Jones & Dr. Björn Siemers |

## Selected Professional Training Courses

**Leadership and people management** (15 h personal coaching & "Leading awesome" course) **2021**

- Leadership Style / Effective Communication / Motivation / Feedback / Conflict management

**Management: Building and leading high-performance teams** (2 × 20 h) **2019**

- Strategic project management / Stakeholder management / Negotiation
- Building, motivating and leading high-performance teams / Performance management

**Effective proposal writing** (20 h) **2018**

- Principles, design, tools and methods of successful proposals

**Communication, didactics and rhetoric** (21 h, 18 h) **2015, 2016**

- Principles of didactics for university teaching
- Body language, standing & voice / Presentation and communication skills for large audiences

**Leadership: Leadership roles and self-assessment** (20 h) **2015**

- Personality and leadership types / Building and leading teams / Effective communication

## Public Engagement

| | |
|---|---|
| **regularly** | • interviews for print, radio and TV. |
| **2020** | • Research covered in the MaxPlanckResearch Science Magazine (issue 2/2020). |
| **2020** | • National Geographic documentary "Nature's secret language" (6-part series), 3 weeks filming at my field station for the episode "hunters (and hunted) – predator-prey interactions". |
| **2020** | • Documentaries about bat-prey interactions and scientific research, for ARTE and ZDF (French-German / German TV broadcaster), by Blue Paw Artists (DE). |
| **2020** | • Podcast (25:52 min onwards) about our research by Detector.fm and the Max Planck Society. |
| **2019** | • Public lecture at the Open Day of Castle Ringberg of the Max Planck Society. |
| **2019** | • Selected for the Scientific Highlights of the Max-Planck Yearbook 2018 (p. 9). |
| **2019** | • BBC 4 documentary "Inside the bat cave" (90 min), 3-day filming at my field station. |
| **2017** | • *GEO Tag der Natur*, Bund Naturschutz Tutzing: bat & moth inventory with the public. |
| **2017** | • Open Day, Max Planck Institute for Ornithology: public talks, tours and displays. |
| **2013** | • Open Day, Max Planck Institute for Ornithology: public talks, tours and displays. |
| **2012, 2009** | • Annual Research Seminar, Field Study Centre and National Nature Reserve, Slapton, UK. |
| **2011** | • Annual Conference of the *Arbeitskreis Fledermausschutz* and the Landesreferenzstelle für Fledermausschutz am Biosphärenreservat Sachsen-Anhalt, Roßla (DE). |
| **2010** | • Discover / National Science and Engineering Week, Bristol (UK). |
| **2009** | • Science Café, Festival of Nature, Bristol (UK). |
| **2009** | • Science Picnic, Botanical Garden, University of Bristol (UK). |

# Teaching and Supervision

***I possess broad training and experience in teaching and student supervision****: I hold a University degree as secondary school teacher, participated in professional didactical training for higher education, and I regularly design and teach lectures and practical courses at BSc and MSc level (mostly at LMU Munich).*

## University Teaching

### Lectures

| | |
|---|---|
| 2020 | **Perception in the Anthropocene** (1 x 45 min; within seminar **Urban Ecology**)<br>MSc Biology, LMU |
| 2021, ’19, ’19 | **Animal Communication** (2 x 90 min; in the terms of 2018/19, 2019/20, and 2020/21)<br>MSc Biology, LMU |
| 2020, ’19, ’18, ’17, ’16 | **Vision** (1 x 90 min)<br>BSc Biology, LMU |
| 2021, ’20, ’19, ’18, ’17, ’16 | **Sensory Ecology** (1 x 90 min, part of lecture series **Evolutionary Ecology**).<br>MSc Biology, LMU |
| 2016, ’15, ’14 | **Auditory-guided predator-prey interactions** (1 x 90 min)<br>Part of practical course **Current Topics in Behavioural Ecology**, MSc Biology, LMU |
| 2019, ’15, ’14 | **Introduction to Bioacoustics** (1 x 90 min)<br>MSc Biology, LMU & PhD, IMPRS for Organismal Biology |

### Practical Courses

| | |
|---|---|
| 2020, ’19, ’18, ’17, ’16 | **Animal Physiology** (7 or 9 groups per semester, 4 h per group)<br>BSc Biology, LMU |
| 2016, ’15, ’14 | **Current Topics in Behavioural Ecology** (1 day)<br>MSc Biology, LMU |
| 2019, ’15, ’14 | **Introduction to Bioacoustics and Sound Analysis** (2 days)<br>MSc Biology, LMU & PhD, IMPRS for Organismal Biology |
| 2010 | **Bio-Imaging** (1 day)<br>BSc Biology, University of Bristol |
| 2007 | **Multimodal Orientation and Learning in Rodents** (2 weeks)<br>Diploma (MSc) Biology, LMU Munich |
| 2005 | **Hearing Physiology and Psychoacoustics** (1 day, Teaching Assistant)<br>Diploma (MSc) Biology, LMU Munich |
| 2005, ’04, ’03, ’02 | Teaching Assistant in various courses on **Animal Physiology, Physiological Ecology, Behavioural Ecology** (1-2 weeks per course)<br>Diploma (MSc) & State Examination Biology, Uni Tübingen |

### Field Courses

| | |
|---|---|
| 2008 | **Biology of desert-dwelling bats** (2 weeks)<br>BSc Biology, University of Bristol (UK) and Ben-Gurion-University of the Negev (IL) |
| 2010, ’09 | **Bat Biology** (1 week)<br>Diploma (MSc) and State Examination Biology, LMU Munich |

### Additional Teaching Experience

| | |
|---|---|
| 2004, ’02 | **Personal Tutor in Animal Physiology** for an exchange student from Tufts University (US), Eberhard Karls University Tübingen (DE) |
| 1999 | **Teaching Internship as grammar school teacher in Biology and Chemistry** (4 weeks), Wildermuth Gymnasium Tübingen (DE) |

## Supervision Activity

*Since leading my research group in 2012, I supervised 10 MSc theses, 11 mandatory and 10 voluntary research internships at MSc level, 6 PhD students and 4 PostDocs. I help group members to design and perform experiments on various topics (see below) and train them in the use of our technologies, data analysis and programming. I aim to be approachable and interact closely with group members to know and help with their needs and requirements.*

### PostDocs:

- Beleyur T (2021 – present): *Active sensing and flight in free-flying bat groups*. Collaboration with I. Couzin.
- Baier L (2020 – 2021): *Echolocation and flight behaviour in normal-hearing and hearing-impaired bats* ► now PostDoc, funded by the Marie Skłodowska-Curie Actions and the Alexander von Humboldt Foundation, at the Smithsonian Tropical Research Institute (PA) with Dr. R Page (Smithsonian Tropical Research Institute) and Prof. M Ryan (Austin (TX), USA), and at Aarhus University with Prof. PT Madsen
- Lewanzik D (2014 – 2019): *Dynamic sensory perception in echolocating bats.* ► now Research Scientist at the Institute for Zoo and Wildlife Research, Berlin (DE)
- van Meir V (2013 – 2014): *Heterospecific species recognition and 3D-trajectory reconstruction of foraging bats in the wild.* ► now Research Scientist at the MPI for Ornithology, Seewiesen (DE), previously Research Scientist, Bio-Imaging lab, University of Antwerp (BE)

### PhD theses:

- Hubancheva A (2017 – present; Main supervisor; Co-supervisor: D Chobanov): *Predator-prey interactions in a multiple predator-multiple prey community: Myotis bats and katydids* (MPIO & Bulgarian Academy of Sciences)
- Iturralde-Pólit PA (2017 – present; Co-supervisor with G Chaverri): *The effect of climate change on insectivorous bat communities in Neotropical montane forests* (Universidad de Costa Rica & MPIO)
- Beleyur T (2015 – 2021): *Flight and vocal strategies for physical and sensory collision avoidance in moving animal groups* (MPIO & IMPRS-OB) ► now PostDoc with Prof. I Couzin (MPI for Animal Behavior & Uni Konstanz) and me
- Hügel T (2014 – 2020): *Behavioural variability as anti-predator adaptation in the evasive flight of moths* (MPIO & IMPRS-OB) ► now PhD program Manager at Vienna BioCenter (AT)
- Baier L (2014 – 2019; Co-supervisor, with L Wiegrebe): *Biosonar encoding of surface waves* (MPIO, IMPRS-OB & LMU) ► after PostDoc with me and Dr. U Firzlaff (TU Munich), now PostDoc, funded by the Marie Skłodowska-Curie Actions and the Alexander von Humboldt Foundation, at the Smithsonian Tropical Research Institute (PA) with Dr. R Page (Smithsonian Tropical Research Institute) and Prof. M Ryan (Austin (TX), USA), and at Aarhus University with Prof. PT Madsen
- Luo J (2012 – 2015; Co-supervisor): *Bats and ambient noise: from chatty neighbours to disturbing humans* (MPIO & IMPRS-OB) ► now Professor at Central China Normal University (Wuhan, CN), previously PostDoc with Prof. C Moss, Johns Hopkins University, Baltimore (MD), US
- Hackett T (2011 – 2012; Co-supervising collaborator): *Jamming avoidance in bats* (University of Bristol, UK). ► now PostDoc at the Department of Zoology, University of Oxford (UK)
- Drapeau V (2008 – 2011; Co-supervising collaborator): *Flight behaviour, call design and directional hearing in the echolocating nectar-feeding bat (*Glossophaga soricina*, Pallas 1766)* (University of Bristol, UK)

### MSc theses:

- Krishna A (2019-20; Co-supervisor): *Call adjustments in free-flying groups of horseshoe bats* (IISER Mohali, IN) ► now PhD researcher with C Moss, Johns Hopkins University, Baltimore (MD), US
- de Framond-Bénard L (2019-20): *Behavioural flexibility in echolocation parameters to maximize detection range under changing weather conditions* (EES LMU Munich) ► now scientific assistant with Dr. H Brumm, MPI for Ornithology, Seewiesen (DE)
- Chang Y (2018-19): *Function of the distinct sexual dimorphism in echolocation call frequency in acuminate horseshoe bats* (EES LMU Munich) ► now PhD researcher with Dr C Hoskin, James Cook Uni, Townsville (AU)

- Reininger V (2017-18): *Species-specific influences of weather condition and global warming on bat echolocation parameters for maximised prey detection distances* (University of Potsdam)
- Kaiser S (2016-17): *Temperature discrimination performance for fruit detection and evaluation in a frugivorous bat species* (University of Stuttgart)
- Morozova E (2016): *Calls in context – Dominance hierarchy recognition by lesser spear-nosed bats (*Phyllostomus discolor*) based on aggression calls* (EES LMU Munich)
- Lattenkamp E (2015): *Passive listening in* Rhinolophus ferrumequinum: *Do horseshoe bats complement their echolocation with listening for prey-generated sounds?* (MEME LMU Munich) ► completed PhD with Dr. S Vernes (MPI for Psycholinguistics, Nijmegen, NL) and Prof. L Wiegrebe (LMU Munich, DE)
- Ramakers J (2014): *Bats in a noisy landscape: ecological and behavioural effects of anthropogenic noise disturbance* (University of Utrecht, The Netherlands) ► now PostDoc, Biometris, Wageningen University (NL)
- Hügel T (2013): *Information gain from heterospecific echolocation calls: testing species-specific reactions in wild* Myotis capaccinii (University of Würzburg) ► after her PhD with me now PhD program Manager
- Dorado-Correa A (2013; Co-supervisor): *Interspecific acoustic recognition in bat communities* (EES LMU Munich) ► now Clinical Project Manager, Bioclinica Munich (DE) after her PhD with Dr H Brumm (MPI for Ornithology, Seewiesen, DE)

- Lin K-K (2012; Co-supervisor): *Automated flight-path reconstruction from bat calls* (University of Bristol, UK)
- Leigh J (2012; Co-supervisor): *Real-time reconstruction of bat flight trajectories* (University of Bristol, UK)
- Robsomanitrandrasana E (2003; Field advisor): *Prey detection and optimal foraging in Grey Mouse Lemurs* (University of Antananarivo, Madagascar)

BSc theses:

- Gray I and Cannon L (2010-11): *Hearing in the Noctuid moth* Noctua pronuba: *from tympanal recordings to behavioural responses* (University of Bristol, UK; joined BSc theses)
- Co-supervisor of 6 BSc theses (2008 – 2010), University of Bristol, UK

Mandatory MSc research projects:

- Mardus E (2020): Echolocation and flight behaviour in normal-hearing and hearing-impaired bats (Graduate School for Neuroscience, LMU Munich)
- de Framond-Bénard L (2018-19): Grant proposal: *Behavioural flexibility in echolocation parameters to maximize detection range under changing weather conditions* (EES LMU Munich)
- Chang Y (2017-18): Grant proposal: *Behavioural response of acuminate horseshoe bats to sexually dimorphic echolocation calls* (EES LMU Munich)
- Reininger V (2017): *Individual behavioural changes in echolocation call parameters of bats under the impact of climate change* (University of Potsdam)
- Großmann M (2016-17): *Dynamic sensory perception in echolocating bats* (EES LMU Munich)
- Guérin C (2016): *Modelling temporal sonar jamming confusion in bat aggregations* (MEME LMU Munich) ► now PhD student with Dr. Laurent Lehmann, University of Lausanne (CH)
- Sáenz-Soto I (2016): Influence of bat calls intensity on the *evasive flight of noctuid moths* (EES LMU Munich)
- Morozova E (2015-16): *Calls in context: individual recognition by lesser spear-nosed bats (*Phyllostomus discolor*) based on aggression calls* (EES LMU Munich)
- Muñoz Menese A (2015): *Eavesdropping and interspecific acoustic recognition in* Myotis capaccinii *and* Myotis daubentonii *(Mammalia: Chiroptera) in Northern Bulgaria* (EES LMU Munich)
- Zagkle E (2014-15): *To buzz or not to buzz? Behavioural flexibility in the approach phase of bats* (EES LMU Munich)
- Bitzilekis E (2013): *Polite messages reduce vandalism of unattended scientific equipment* (EES LMU Munich)

- Supervisor of 4 research interns for data analysis (2009, 2010), University of Bristol (UK)

Voluntary research internships and projects at MSc level and above:

- Mysuru N (2018-19): *Adaptive variation in echolocation calls in horseshoe bat groups* (research assistant) ► now PhD researcher with Dr. D Vallentin, MPI for Ornithology (DE)
- Hermans C (2018): *Calibration of sound-based animal 3D-localisation accuracy* (research internship) ► now PhD researcher with Dr. K Spoelstra, Netherlands Institute of Ecology, Wageningen (NL)
- Krishna A (2018): *Video- and sound-based 3D-tracking of bat groups* (research assistant) ► after MSc thesis with me, now PhD researcher with C Moss, Johns Hopkins University, Baltimore (MD), US
- Sundaramurthy A (2017): *Acoustic analysis of bat activity* (research assistant) ► now PhD researcher with Prof. K Helin, University of Copenhagen (DK)
- Großmann M (2016): *Dynamic sensory perception in echolocation* (research assistant for data analysis)
- Gomes D (2015-16): *Impact of noise on biosonar-based object analysis* (1-year Fulbright-funded research student) ► now PostDoc, Oregon State University, US, after this PhD with Prof J Barber, Boise State (ID), US
- Kaiser S (2015-16): *Passive listening and behavioural flexibility in biosonar* (internship, Uni of Stuttgart, DE)
- Kaučič R (2015): *Passive listening and behavioural flexibility in biosonar* (internship, University of Ljubljana, SI) ► now Project Leader, Dept for Water and Air, Eurofins ERICo Slovenija, University of Lublјana, SI
- Kugler K (2013): *Temporal analysis of prey-generated rustling sounds* (short-term research scientist) ► now Engineer at Mathworks, after her PhD with Prof Lutz Wiegrebe (LMU Munich)
- Busse U (2012): *Sensory niche partitioning and prey search images in related but ecologically dissimilar species* (research internship)

PhD-thesis advisory committee member:

- Hutfluss A (2017 – present): *Effects of environmental factors, human disturbance and behavioural syndromes on the singing behaviour of great tits* (LMU Munich)
- Mouchet A (2017 – present): *Effects of food availability on reproduction and population dynamics in great tits* (LMU Munich)

Member of PhD-thesis evaluation committees:

- Wechuli D: *Variation of echolocation pulse source levels and detection distances for bat assemblages across an environmental gradient in South Africa* (University of Cape Town, ZA)
- Olsen M: *Source parameters and its implications for group navigation in echolocating bats* (University of Southern Denmark, Odense, DK)
- Mutumi G: *Geographic variation in the phenotypes of two sibling horseshoe bats* Rhinolophus simulator *and* R. swinnyi (University of Cape Town, ZAF)
- Salvarina I: *Lakes as food resources for bats: evidence from stable isotopes and acoustic monitoring* (University of Konstanz, DE)
- Heinrich M: *Aspects of spatiotemporal integration in bat sonar* (Graduate School of Systemic Neurosciences, LMU Munich, DE)

## Academic self-organisation and management of teaching and supervision

| | |
|---|---|
| 2019 – present | **Deputy Spokesperson** of the *Int. Max Planck Research School for Organismal Biology*<br>MPI Ornithology Seewiesen, MPI Animal Behavior Konstanz, and University of Konstanz (DE) |
| 2019 – present | **Member of the Steering Board** of the *Int. Max Planck Research School for Organismal Biology*<br>MPI Ornithology Seewiesen, MPI Animal Behavior Konstanz, and University of Konstanz (DE) |
| 2015 – 2017 | **Member of the Steering Board** of the *Int. Max Planck Research School for Organismal Biology*<br>MPI for Ornithology, Seewiesen, and University of Konstanz (DE) |
| 2015 – present | **Faculty member** of the *Munich Graduate School for Evolution, Ecology & Systematics*<br>Ludwig-Maximilians-University Munich (DE) |
| 2014 – present | **Faculty member** of the *International Max Planck Research School for Organismal Biology*<br>MPI for Ornithology and University of Konstanz (DE) |

## Didactical and Leadership Training

**Leadership and team management** (15 h personal coaching; “Leading awesome” course) **2021**

- Leadership style / Effective communication / Motivation / Feedback / Conflict management

**Management: Building and leading high-performance teams** (2 × 20 h) **2019**

- Strategic project management / Stakeholder management / Negotiation
- Building, motivating and leading high-performance teams / Performance management

**Communication, didactics and rhetoric** (21 h, 18 h) **2015, 2016**

- Principles of didactics for university teaching
- Body language, standing & voice / Presentation and communication skills for large audiences

**Leadership: Leadership roles and self-assessment** (20 h) **2015**

- Personality and leadership types / Building and leading teams / Effective communication

**Studies of Biology and Chemistry as High School Teacher** (*Erstes Staatsexamen*), **1998 - 2004**
Eberhard Karls University Tübingen (DE)

## Publications

### Peer-reviewed Journal Articles [* indicates joint authorships]

**2021** (33) Stidsholt L, Johnson M, **Goerlitz HR**, Madsen PT: Wild bats briefly decouple sound production from wingbeats to increase sensory flow during prey capture. ***iScience*** 24(8), 102896.

(32) Stidsholt L, Greif S, **Goerlitz HR**, Beedholm K, Macaulay J, Johnson M & Madsen PT (2021): Hunting bats adjust their echolocation to receive weak prey echoes for clutter reduction. ***Science Advances*** 7(10): eabf1367.

(31) Voigt CC, Russo D & Runkel V & **Goerlitz HR** (2021): Limitations of acoustic monitoring at wind turbines to evaluate fatality risk of bats. ***Mammal Review*** 51(4), 559-570.

(30) Lewanzik D & **Goerlitz HR** (2021): Task-dependent vocal adjustments to optimize biosonar-based information acquisition. ***Journal of Experimental Biology*** 224(1): jeb234815

**2020** (29) Gomes D & **Goerlitz HR** (2020): Individual differences show that only some bats can cope with noise-induced masking and distraction. ***PeerJ*** 8: e10551.

(28) Hügel T & **Goerlitz HR** (2020): Light might suppress both types of sound-evoked antipredator flight in moths. ***Ecology and Evolution*** 10(23): 13134-13142.

(27) **Goerlitz HR***, ter Hofstede HM* & Holderied WM (2020): Neural representation of bat predation risk and evasive flight in moths: a modelling approach. ***Journal of Theoretical Biology*** 486: 110082.

(26) Straka T*, Schultz S*, Greif S*, **Goerlitz HR**** **[**joint senior author]** & Voigt CC** (2020): The effect of cave illumination on bats. ***Global Ecology and Conservation*** 21: e00808.

**2019** (25) Beleyur T & **Goerlitz HR** (2019): Modelling active sensing reveals continued echo detection even in large groups of bats. ***PNAS*** 116(52): 26662-26668.

(24) Hügel T & **Goerlitz HR** (2019): Species-specific strategies increase unpredictability of escape flight in eared moths. ***Functional Ecology*** 33(9): 1674-1683.

(23) Batstone K, Flood G, Beleyur T, Larsson V, **Goerlitz HR**, Oskarsson M, Åström K (2019): Robust self-calibration of constant offset time-difference-of-arrival. ***ICASSP 2019 – 2019 IEEE International Conference on Acoustics, Speech, and Signal Processing***, 4410-4414.

(22) Lewanzik D, Sundaramurthy AK & **Goerlitz HR** (2019): Insectivorous bats integrate social information about species identity, conspecific activity and prey abundance to estimate the cost-benefit ratio of interactions. ***Journal of Animal Ecology*** 88(10): 1462-1473.

(21) Baier AL, Wiegrebe L* & **Goerlitz HR*** (2019): Echo-imaging exploits an environmental high-pass filter to access spatial information with a non-spatial sensor. ***iScience*** 14: 335-344.

**2018** (20) Egert-Berg K*, Hurme E*, Greif S*, Goldstein A, Harten L, Herrera-M LG, Flores-Martinez JJ, Valdés AT, Jonston DS, Eitan O, Borissov I, Shipley JR, Medellin RA, Wilkinson GS, **Goerlitz HR**, Yovel Y (2018): Resource ephemerality drives social foraging in bats. ***Current Biology*** 28(22): 3667-3673.

(19) **Goerlitz HR** (2018): Weather conditions determine attenuation and speed of sound: environmental limitations for monitoring and analysing bat echolocation. ***Ecology and Evolution*** 8(10): 5090-5100.

(18) Lattenkamp EZ, Kaučič R, Kaiser S, Großmann M, Koselj K* & **Goerlitz HR*** (2018): Environmental acoustic cues guide the biosonar attention of a highly specialised echolocator. ***Journal of Experimental Biology*** 221(8): jeb165696.

(17) Lewanzik D & **Goerlitz HR** (2018): Continued source level reduction during attack in the low-amplitude bat *Barbastella barbastellus* prevents moth evasive flight. ***Functional Ecology*** 32(5): 1251-1261.

**2017** (16) Hügel T, van Meir V, Munoz-Meneses A, Clarin B-M, Siemers BM & **Goerlitz HR** (2017): Does similarity in call structure or foraging ecology explain interspecific information transfer in wild *Myotis* bats? ***Behavioral Ecology and Sociobiology*** 71: 168.

**2015** (15) Luo L, **Goerlitz HR**, Brumm H & Wiegrebe L (2015): Linking the sender to the receiver: vocal adjustments by bats to maintain signal detection in noise. ***Scientific Reports*** 5: 18556.

**2014** (14) Luo L, Koselj K, Zsebok S, Siemers BM & **Goerlitz HR** (2014): Global warming alters sound transmission: differential impacts on the prey detection ability of echolocating bats. ***The Journal of the Royal Society Interface*** 11: 20130961.

(13) Clarin BM, Bitzilekis E, Siemers BM & **Goerlitz HR** (2014): Personal messages reduce vandalism and theft of unattended scientific equipment. ***Methods in Ecology and Evolution*** 5(2): 125-131.

(12) Clare EL, **Goerlitz HR**, Drapeau VA, Holderied MW, Adams AM, Nagel J, Dumont ER, Hebert PDN & Fenton MB (2014): Trophic niche flexibility in *Glossophaga soricina*: how a nectar seeker sneaks an insect snack. ***Functional Ecology*** 28(3): 632-641.

**2013** (11) ter Hofstede HM*, **Goerlitz HR* [joint first author]**, Ratcliffe JM, Holderied MW** & Surlykke A** (2013): The simple ears of noctuoid moths are finely tuned to the calls of their sympatric bat community. ***Journal of Experimental Biology*** 216: 3954-3962.

(10) Dorado-Correa AM, **Goerlitz HR** & Siemers BM (2013): Interspecific acoustic recognition in two European bat communities. ***Frontiers in Physiology*** 4: 192.

**2012** (9) **Goerlitz HR***, Genzel D* & Wiegrebe L (2012): Bats' avoidance of real and virtual objects: implications for the sonar coding of object size. ***Behavioural Processes*** *89(1): 61-67.*

**2011** (8) ter Hofstede HM*, **Goerlitz HR* [joint first author]**, Montealegre-Z F., Robert D & Holderied MW (2011): Tympanal mechanics and neural responses in the ears of a noctuid moth. ***Naturwissenschaften,*** *98(12): 1057-1061.*

**2010** (7) **Goerlitz HR***, ter Hofstede HM*, Zeale MRK*, Jones G & Holderied MW (2010): An aerial-hawking bat uses stealth echolocation to counter moth hearing. ***Current Biology*** *20(17): 1568–1572.*

(6) **Goerlitz HR**, Geberl C & Wiegrebe L (2010): Sonar detection of jittering real targets in a free-flying bat. ***Journal of the Acoustical Society of America*** *128(3): 1467–1475.*

**2008** (5) **Goerlitz HR**, Greif S & Siemers BM (2008): Cues for acoustic detection of prey: insect rustling sounds and the influence of walking substrate. ***Journal of Experimental Biology*** 211(17): 2799–2806.

(4) **Goerlitz HR**, Hübner M & Wiegrebe L (2008): Comparing passive and active hearing: Spectral analysis of transient sounds in bats. ***Journal of Experimental Biology*** 211(12): 1850–1858.

**2007** (3) Siemers BM, Goerlitz HR, Robsomanitrandrasana E, Piep M, Ramanamanjato J-B, Rakotondravony D, Ramilijaona O & Ganzhorn JU (2007): Sensory basis of food detection in wild *Microcebus murinus*. ***International Journal of Primatology*** 28(2): 291–304.

(2) **Goerlitz HR** & Siemers BM (2007): Sensory ecology of prey rustling sounds: acoustical features and their classification by wild Grey Mouse Lemurs. ***Functional Ecology*** 21(1): 143–153.

**2003** (1) Schill RO, **Görlitz HR** & Köhler H-R (2003): Laboratory simulation of a mining accident: acute toxicity, hsc/hsp70 response, and recovery from stress in *Gammarus fossarum* (Crustacea, Amphipoda) exposed to a pulse of cadmium. ***Biometals*** 16(3): 391–401.

## Conference Proceedings (not peer-reviewed)

**2018** (34) Kamburov A, **Goerlitz HR** & Beleyur T (2018): Geospatial modelling inside the "Orlova Chuka" cave in Bulgaria. Proceedings of the International Symposium on modern technologies, education and professional practice in Geodesy and related fields. Sofia, November 8th-9th 2018

## Selected Manuscripts in preparation

(35) Beleyur T & **Goerlitz HR**: The Ushichka dataset: multi-channel audio, video and spatial data on active sensing and collective behaviour in free-flying wild bat groups.

> *The collective behaviour and motion of animal groups has been intensely investigated, mostly in visually guided species. Here we present a novel dataset containing video, audio and environmental spatial data on the auditory sensing (echolocation) and 3D-movement behaviour of free-flying bats in their natural cave environment, to investigate active sensing and group flight in unprecedent breadth and depth.*

(36) Mysuru N*, Beleyur T*, Krishna A & **Goerlitz HR**: High duty-cycle bats in the field do not alter echolocation calls when flying in groups

> *Recent empirical and modelling evidence suggests that active sensing in dense swarms is less difficult for low-duty cycle bats than it was thought. However, this might be very different for high-duty cycle bats due to overlap of their long-duration calls. Yet, here, we show that wild bats flying in groups do not alter call structure, providing first field evidence for no jamming even in these bats.*

(37) Chang Y, Bumrungsri S, Lewanzik D, Soisook P & **Goerlitz HR**: Pronounced sexual dimorphism in echolocation call frequency in acuminate horseshoe bats and its potential for mate choice.

> *Sexual dimorphisms are often the consequence of sexual selection and used in a reproductive context. In contrast, bat echolocation calls are adapted to the sender's needs for perception, navigation and foraging. Here, we document a strong case of sexual dimorphism in echolocation call frequency and test its function and sensory mechanism for mate choice.*

(38) de Framond-Bénard L, Reininger V & **Goerlitz HR**: Effect of fluctuating weather conditions on the echolocation parameters of three European bat species.

> *Ultrasonic vocalisations are strongly attenuated in air, which limits the sensory range of bat biosonar. As attenuation depends on weather conditions, bat sensory range fluctuates daily and seasonally. Quantifying source parameters of three free-flying bat species, we show weather- and attenuation correlated changes in call parameters in one species, which partially offset weather-induced variation.*

(39) de Framond-Bénard L, Beleyur T, Lewanzik D & **Goerlitz HR**: A gleaning bat, *Plecotus auritus*, emits low-intensity calls in open environments in the wild.

> *Call intensity is crucial for echolocating bats as it determines their sensory range. While almost all bat species call as loud as possible, only a few species emit faint calls. Here, we confirm faint call amplitudes in another bat species, closing a gap within a clade of bats with diverse ecologies, and suggest two evolutionary scenarios of the evolution of low-intensity echolocation to be investigated.*

(40) Hubancheva A, Nowotny M, Senderov V, Schöneich S & **Goerlitz HR**: To live or love: bushcrickets trade-off reproduction and survival by adjusting song-cessation to predation threat and age.

> *Many predators eavesdrop on prey-generated sounds. Singing bushcrickets stop their mating calls when hearing attacking bats. Here, combining neurophysiology and behavioural experiments, we show seasonal changes in the likelihood and duration of song cessation in response to audible bat calls. With age, males reacted less and for shorter durations, to increase changes for final matings.*

(41) Hubancheva A, Hochradel K, Senderov V & **Goerlitz HR**: Acoustic jamming of bat echolocation by the courtship song of a bushcricket.

> *Sensory interference is a powerful anti-predator behaviour. Here we show that the courtship song of the bushcricket* Ruspolia nitidula*, consisting of short broadband ultrasonic clicks at fast repetition rate, also acts as anti-predator defence. Courtship song playback reduced the prey capture success of foraging bats, and thus is a powerful to interfere with bat orientation and foraging.*

(42) Hügel T & **Goerlitz HR**: Timing and threshold of moth evasive flight matches neuronal predictions.

> *The peripheral encoding of echolocation calls by eared moths is well studied, yet the resulting evasive behaviour (= the actual predator-selected trait) is only little known. Using a novel setup, we quantify onset, sound threshold, and temporal variability of evasive flight, allowing a first comparison to neuronal thresholds to establish the link from sensory input, over neuronal processing to action.*

(43) Rahman NAA, **Goerlitz HR**, Greif G & Zsebők S: From water bodies to open flyways: graded perceptual interpretation of angled smooth surfaces by echolocation.

> *Water bodies and open flyways generate a specific echo signature, consisting of an orthogonal side echo and a lack of frontal echoes, which echolocating bats interpret to detect these habitat features. Here we show that the perceptual interpretation of these echo features is continuous and depends on the echo's elevation angle, leading to angle-dependent behaviours (drinking vs. fly-through).*

(44) Stidsholt L, Greif S, Hubancheva T, Johnson M, **Goerlitz HR**, Yovel Y & Madsen PT: Prey size and availability drive foraging decisions of wild bats.

> *Using GPS- and sound-biologging and faeces metabarcoding, we studied the foraging strategy of free-flying mouse-eared bats in their natural habitats. The bat overall used two different foraging strategies with different success rates, and optimized their energy intake by targeting large prey yet at low success rates, and adjusted foraging strategy to habitat type, but did not consistently select profitable habitats.*

(45) Lewanzik D, Etzler E, Ratcliffe JM, **Goerlitz HR*** & Jakobsen L*: Stealth echolocation in the aerial hawking bat, *Barbastella barbastellus*, reflects co-option of ancestral gleaning traits, not a counter-measure to circumvent moth hearing.

> *Barbastelle bats use a rare, low-intensity echolocation strategy, allowing them to capture eared prey. Here, we challenge my own hypothesis that this strategy coevolved in response to prey hearing. Reconstructing the ancestral state of echolocation and morphology of barbastelle bats and its related taxa, we suggest that low-intensity is an adaptation to the habitat and gleaning, not moth hunting.*

## Other publications

2019
- **Goerlitz HR** (2019): Acoustic Invisibility cloaks and pricked-up ears. / Akustische Tarnkappen und gespitzte Ohren. Scientific Highlights of the Max Planck Yearbook 2018 / MPG Forschungsbericht 2018 (DOI: 10.17617/1.8I)

## Dissertation

2008
- **Goerlitz HR** (2008): Perceptual strategies in active and passive hearing of neotropical bats. **Dissertation**, Faculty for Biology, LMU Munich (available as download at LMU library)

## 118 Conference Presentations (52 talks & 66 posters)

- 19 single-, first- or last-author **talks**, presented by myself (2007 – 2020)
- 20 last-author **talks**, presented by my co-authors (2013 – 2021)
- 13 single-, first- or last-author **posters**, presented by myself (2004 - 2020)
- 48 last-author **posters**, presented by my co-authors (2013 – 2020)
- 18 co-authorships on **talks** (13; 2005 - 2020) and **posters** (5; 2012 – 2020)

# Acknowledgements

TODAY HABILITATION CREATES MORE PROBLEMS THAN IT SOLVES. […] HABILITATION IS NOW A QUESTIONALBE PROCEDURE FOR PROMOTING EXCELLENCE IN SCIENCE. THE PRACTICE DOES LITTLE TO BOOST THE INTERNATIONAL REPUTATION OF GERMAN UNIVERSITIES.

Gerhard Neuweiler (1996), Nature
Chair of Zoology, LMU Munich

*A habilitation was traditionally supposed to open the door to a permanent independent academic career. In my case, it marks the likely end of my academic career, while other doors have opened.*

*I always loved scientific thinking, lively (if not heated) discussions and new ideas, and disliked various (and not always structural) aspects of (German) academia. While my Emmy Noether award gave me "early" independence, I did not obtain a permanent position in the German academic system, and I now take my journey into another direction. And what a journey the past year had been! I was shortlisted for a (in the end cancelled) professorship, published articles, applied for and won a DFG Heisenberg award, entertained and home-schooled the kids, wrote my habilitation, closed-down my lab, and interviewed for non-academic jobs. I am incredibly grateful to a lot of people that I had the pleasure and privilege to meet along the whole journey, many of which became great colleagues, good friends and role models.*

MAYBE SLEEP IS A STATION BUT LIFE IS A TRAIN
AND IF IT WILL PASS YOU BETTER JUMP ON AGAIN.

Fury in the Slaughterhouse

While often forgotten, academic research is a team-effort. This is also true for my habilitation, summarising 26 published articles, a conference article and 11 manuscripts in preparation, authored by 84 unique researchers, with 1–16 authors per article. And not only the authors, but many other colleagues contributed to and supported my work all along. It not only takes a village to raise a child, but also for great work to be accomplished – and it's more fun together.

Björn Siemers and Lutz Wiegrebe – you advised me during my first steps as a scientist, and trusted, pushed and supported me again in Seewiesen. Your scientific work and your humanity shine and are remembered – by me and all your colleagues. *Merzi Vazaha*, hoch die Tassen!

Hannah ter Hofstede – the best colleague that I can imagine. Your knowledge, respect and openness made our PostDocs and collaborations since them an outstanding experience. Keep going, you rock!

The whole Acoustic and Functional Ecology team in Seewiesen, whether tightly integrated or just loosely connected – forgive me if I don't name you all. You did most of the hard work, put up with me, trusted in me, generated a pleasant atmosphere, and brought our research to life. Thank

you tons! I hope I did give something back, and that you will follow your journeys through wide-open doors.

Many excellent colleagues and collaborators on various finished and still ongoing projects – again sorry for not naming all of you. Thank you for your trust and encouraging words, and for thinking, discussing and doing science together. Keep up the great work and fascinating research!

Everyone at the MPI for Ornithology in Seewiesen who made working enjoyable and smooth – particularly everyone at House 11, as well as animal care, workshops, IT, mensa, administration, management, and beyond.

The directors at the MPIO, Manfred Gahr and Bart Kempenaers, for hosting and supporting my work form 2014-2021, providing infrastructure and scientific freedom.

Marc Holderied, Daniel Robert and Gareth Jones for a rich, informative and valued time at the University of Bristol.

My habilitation *Fachmentorat* at the LMU Munich, Benedikt Grothe, Niels Dingemanse, Joachim Haug and Manfred Gahr; and particularly Benedikt for support and advice.

All the many, many colleagues, friends and random humans I met along the way in Tübingen, München, Bristol & Seewiesen, in Tabachka, on field sites around the world, at conferences and who knows where else. It was a pleasure, an incredible enrichment to my life and an outstanding opportunity! No matter how many details I might forget ;) , this has been incredibly important to me. I do hope to meet as many of you again and again.

Nadine, Felix and Janne – thank you. I'm excited to keep jumping on with you.

Planegg, August 2021

# Annotated list of own publications for my habilitation

The following publications, resulting from my postdoctoral research at the University of Bristol (2008–2012) and at the MPI for Ornithology in Seewiesen (since 2012), form the basis of my habilitation. I present both **published peer-reviewed journal articles** as well as **non-peer-reviewed conference articles** and **manuscripts in preparation**, listed in chronological order, and detail my contributions to each article. References to these articles in the main text are **bold-faced**.

## Peer-reviewed Journal Articles [* indicates joint authorships]

**Goerlitz HR***, ter Hofstede HM*, Zeale MRK*, Jones G & Holderied MW (2010): An aerial-hawking bat uses stealth echolocation to counter moth hearing. ***Current Biology*** *20(17): 1568–1572*.

> I contributed to study design, collected and analysed the bat data, performed the modelling, prepared all figures, contributed to data interpretation, and lead the writing.

ter Hofstede HM*, **Goerlitz HR***, Montealegre-Z F., Robert D & Holderied MW (2011): Tympanal mechanics and neural responses in the ears of a noctuid moth. ***Naturwissenschaften****, 98(12): 1057-1061*.

> I substantially contributed to study design, I analysed parts of the data and prepared all figures; and I substantially contributed to data interpretation and paper writing.

Dorado-Correa AM, **Goerlitz HR** & Siemers BM (2013): Interspecific acoustic recognition in two European bat communities. ***Frontiers in Physiology*** 4:192.

> I supervised the final data interpretation and contributed to final writing.

ter Hofstede HM*, **Goerlitz HR* [joint first author]**, Ratcliffe JM, Holderied MW** & Surlykke A** (2013): The simple ears of noctuoid moths are finely tuned to the calls of their sympatric bat community. ***Journal of Experimental Biology*** 216: 3954-3962.

> I substantially contributed to study design, contributed to data collection and analysis, prepared all figures; and substantially contributed to data interpretation and writing.

Clare EL, **Goerlitz HR**, Drapeau VA, Holderied MW, Adams AM, Nagel J, Dumont ER, Hebert PDN & Fenton MB (2014): Trophic niche flexibility in *Glossophaga soricina*: how a nectar seeker sneaks an insect snack. ***Functional Ecology*** 28(3): 632-641.

> I performed the modelling and substantially contributed to data interpretation and writing.

Clarin BM, Bitzilekis E, Siemers BM & **Goerlitz HR** (2014): Personal messages reduce vandalism and theft of unattended scientific equipment. ***Methods in Ecology and Evolution*** 5(2): 125-131.

> BMC and I devised and designed the study. I substantially contributed to data collection, data interpretation and paper writing.

Luo L, Koselj K, Zsebok S, Siemers BM & **Goerlitz HR** (2014): Global warming alters sound transmission: differential impacts on the prey detection ability of echolocating bats. ***The Journal of the Royal Society Interface*** 11: 20130961.

> I contributed to study design, data analysis, data interpretation and writing.

Luo L, **Goerlitz HR**, Brumm H & Wiegrebe L (2015): Linking the sender to the receiver: vocal adjustments by bats to maintain signal detection in noise. ***Scientific Reports*** 5: 18556.

> I contributed to data interpretation and writing.

Hügel T, van Meir V, Munoz-Meneses A, Clarin B-M, Siemers BM & **Goerlitz HR** (2017): Does similarity in call structure or foraging ecology explain interspecific information transfer in wild *Myotis* bats? ***Behavioral Ecology and Sociobiology*** 71: 168.

> I designed the study, analysed part of the data, and substantially contributed to data interpretation and writing.

Lewanzik D & **Goerlitz HR** (2018): Continued source level reduction during attack in the low-amplitude bat *Barbastella barbastellus* prevents moth evasive flight. ***Functional Ecology*** 32(5): 1251-1261.

> I devised and designed the study, and contributed to data analysis and writing.

Lattenkamp EZ, Kaučič R, Kaiser S, Großmann M, Koselj K* & **Goerlitz HR*** (2018): Environmental acoustic cues guide the biosonar attention of a highly specialised echolocator. ***Journal of Experimental Biology*** 221(8), jeb165696.

> I devised and designed the study, developed the experimental methods, analysed parts of the data, and contributed to data analysis and writing.

**Goerlitz HR** (2018): Weather conditions determine attenuation and speed of sound: environmental limitations for monitoring and analysing bat echolocation. *Ecology and Evolution* 8(10): 5090-5100.

> I performed all parts of this research, from study idea over data analysis to writing.

Egert-Berg K*, Hurme E*, Greif S*, Goldstein A, Harten L, Herrera-M LG, Flores-Martinez JJ, Valdés AT, Jonston DS, Eitan O, Borissov I, Shipley JR, Medellin RA, Wilkinson GS, **Goerlitz HR**, Yovel Y (2018): Resource ephemerality drives social foraging in bats. ***Current Biology*** 28(22): 3667-3673.

> I contributed to data interpretation and paper writing and provided infrastructure and funding.

Baier AL, Wiegrebe L* & **Goerlitz HR*** (2019): Echo-imaging exploits an environmental high-pass filter to access spatial information with a non-spatial sensor. ***iScience*** 14: 335-344.

> I contributed to study design and substantially contributed to data analysis, data interpretation and paper writing.

Lewanzik D, Sundaramurthy AK & **Goerlitz HR** (2019): Insectivorous bats integrate social information about species identity, conspecific activity and prey abundance to estimate the cost-benefit ratio of interactions. ***Journal of Animal Ecology*** 88(10), 1462-1473.

> I devised and designed the study, and contributed to experimental supervision, data analysis and interpretation and to paper writing.

Batstone K, Flood G, Beleyur T, Larsson V, **Goerlitz HR**, Oskarsson M, Åström K (2019): Robust self-calibration of constant offset time-difference-of-arrival. ***ICASSP 2019 – 2019 IEEE International Conference on Acoustics, Speech, and Signal Processing***, 4410-4414. (DOI: 10.1109/ICASSP.2019.8683221).

> I contributed to study design and paper writing, and provided infrastructure, funding and supervision for one part of the data collection.

Hügel T & **Goerlitz HR** (2019): Species-specific strategies increase unpredictability of escape flight in eared moths. ***Functional Ecology*** 33(9): 1674-1683.

> I devised and designed the study, and I substantially contributed to setup development, data analysis and interpretation, and to paper writing.

Beleyur T & **Goerlitz HR** (2019): Modelling active sensing reveals continued echo detection even in large groups of bats. ***PNAS*** 116(52), 26662-26668.

> I substantially contributed to study development and model design, and contributed to data analysis and interpretation, and to paper writing.

Straka T*, Schultz S*, Greif S*, **Goerlitz HR** [**joint senior author]** & Voigt CC** (2020): The effect of cave illumination on bats. *Global Ecology and Conservation* 21, e00808.

> I provided experimental methods and funding, and I substantially contributed to supervision, data analysis, data interpretation and paper writing.

**Goerlitz HR***, ter Hofstede HM* & Holderied WM (2020): Neural representation of bat predation risk and evasive flight in moths: a modelling approach. ***Journal of Theoretical Biology*** 486, 110082.

> I collected and analysed parts of the data, I performed the modelling, prepared all figures and lead the study design, data interpretation and paper writing.

Hügel T & **Goerlitz HR** (2020): Light might suppress both types of sound-evoked antipredator flight in moths. ***Ecology and Evolution*** 10(23), 13134–13142.

> I was involved in devising and planning the study and in experimental supervision, and I contributed to data interpretation and paper writing.

Gomes D & **Goerlitz HR** (2020): Individual differences show that only some bats can cope with noise-induced masking and distraction. ***PeerJ*** 8, e10551.

> I devised the study and provided experimental methods and supervision, I analysed the acoustic data and contributed to data analysis, data interpretation and paper writing.

Lewanzik D & **Goerlitz HR** (2021): Task-dependent vocal adjustments to optimize biosonar-based information acquisition. ***Journal of Experimental Biology*** 224, jeb234815.

> DL and I devised and designed the study. I contributed to data analysis, data interpretation and paper writing.

Voigt CC, Russo D & Runkel V & **Goerlitz HR** (2021): Limitations of acoustic monitoring at wind turbines to evaluate fatality risk of bats. ***Mammal Review*** 55(4), 559-570.

> I contributed to the ideas of the study, analysed the data, prepared two figures, and contributed to paper writing.

Stidsholt L, Greif S, **Goerlitz HR**, Beedholm K, Macaulay J, Johnson M & Madsen PT (2021): Hunting bats adjust their echolocation to receive weak prey echoes for clutter reduction. ***Science Advances*** 7(10), eabf1367.

> I contributed to study design, data interpretation and paper writing, and provided infrastructure, funding and supervision.

Stidsholt L, Johnson M, **Goerlitz HR**, Madsen PT (2021): Wild bats briefly decouple sound production from wingbeats to increase sensory flow during prey capture. ***iScience*** 24(8), 102896.

> I contributed to study design, data interpretation and paper writing, and provided infrastructure, funding and supervision.

## Conference Proceedings (not peer-reviewed)

Kamburov A, **Goerlitz HR** & Beleyur T: Geospatial modelling inside the "Orlova Chuka" cave in Bulgaria. Proceedings of the International Symposium on modern technologies, education and professional practice in Geodesy and related fields. Sofia, November 8th-9th 2018

> I contributed to data interpretation and paper writing, and provided infrastructure, funding and supervision.

## Manuscripts in preparation

Beleyur T & **Goerlitz HR**: The Ushichka dataset: multi-channel audio, video and spatial data on active sensing and collective behaviour in free-flying wild bat groups.

> I substantially contributed to study development and experimental methods, and provided infrastructure, funding and supervision.

Mysuru N, Beleyur T, Krishna A & **Goerlitz HR**: High duty-cycle bats in the field do not alter echolocation calls when flying in groups.

> I contributed to study design, substantially contributed to data interpretation and paper writing, and provided infrastructure, funding and supervision.

Chang Y, Bumrungsri S, Lewanzik D, Soisook P & **Goerlitz HR**: Pronounced sexual dimorphism in echolocation call frequency in acuminate horseshoe bats and its potential for mate choice.

I contributed to study design, data interpretation and paper writing.

de Framond-Bénard L, Reininger V & **Goerlitz HR**: Effect of fluctuating weather conditions on the echolocation parameters of three European bat species.

I devised the study, provided experimental methods and supervision, and substantially contributed to data interpretation and paper writing.

de Framond-Bénard L, Beleyur T, Lewanzik D & **Goerlitz HR**: A gleaning bat, *Plecotus auritus*, emits low-intensity calls in open environments in the wild.

I devised the study, provided experimental methods, and lead the data interpretation and writing.

Hubancheva A, Nowotny M, Senderov V, Schöneich S & **Goerlitz HR**: To live or love: bushcrickets trade-off reproduction and survival by adjusting song-cessation to predation threat and age.

I contributed to study design, provided experimental methods and supervision, and substantially contributed to data interpretation and paper writing.

Hubancheva A, Hochradel K, Senderov V & **Goerlitz HR**: Acoustic jamming of bat echolocation by the courtship song of a bushcricket.

I contributed to study design, provided experimental methods and supervision, and substantially contributed to data interpretation and paper writing.

Hügel T & **Goerlitz HR**: Timing and threshold of moth evasive flight matches neuronal predictions.

I devised and planned the study, and I substantially contributed to setup development, data analysis and interpretation, and contributed to paper writing.

Rahman NAA, **Goerlitz HR**, Greif G & Zsebők S: From water bodies to open flyways: graded perceptual interpretation of angled smooth surfaces by echolocation.

I contributed to study design, supervision, data interpretation and paper writing, and provided infrastructure and funding,

Stidsholt L, Greif S, Hubancheva T, Johnson M, **Goerlitz HR**, Yovel Y & Madsen PT: Prey size and availability drive foraging decisions of wild bats.

I contributed to study design, data interpretation and paper writing, and provided infrastructure, funding and supervision.

Lewanzik D, Etzler E, Ratcliffe JM, **Goerlitz HR*** & Jakobsen L*: Stealth echolocation in the aerial hawking bat, *Barbastella barbastellus*, reflects co-option of ancestral gleaning traits, not a counter-measure to circumvent moth hearing.

I contributed to study ideas and design, data interpretation and paper writing, and provided infrastructure and funding.

# Appendix: original publications and manuscripts