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**The role of echolocation strategies for niche differentiation
in bats**

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Manuscripts

1 The role of echolocation strategies for niche differentiation in bats*

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27 *This review is one of a series of papers arising from the Second International Symposium
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30 encouraged to submit manuscripts based on their talks, which then went through the normal
31 Canadian Journal of Zoology review process.

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Abstract

Guilds subdivide bat assemblages into basic structural units of species with similar patterns of habitat use and foraging modes but do not explain mechanisms of niche differentiation. Bats have evolved four different echolocation strategies allowing the access to four different trophic niche spaces differing in niche dimensions. Bats foraging in open and edge space use the “aerial-hawking or trawling strategy” and detect and localize prey by evaluating pulse-echo-trains in which the prey echo is unmasked. The pulse-echo-pairs deliver mainly positional information on the prey and only little information on its nature. Signals are highly variable and are adapted for detection and localization in open and/or edge space. In narrow space bats identify prey by solving a pattern recognition task. Bats using the “flutter detecting strategy” evaluate glint pattern in prey echoes, bats using the “active gleaning strategy” evaluate the spectral/temporal pattern of the prey-clutter-echo-complex and bats using the “passive gleaning strategy” evaluate the pattern of prey generated cues to find food and use echolocation only for spatial orientation. The less variable signals of narrow space bats are adapted for pattern recognition. The diverse and species-rich tropical bat assemblage at Barro Colorado Island, Panama is here used as an exemplar for assigning bats to guilds and, we discuss the role of echolocation and other adaptations for niche differentiation within guilds.

Keywords:

Barro Colorado Island, guild, echolocation strategy, bat, niche differentiation

Echolocating bats are ecologically highly diverse. The evolution of powered flight and echolocation are the key factors that allowed bats to use a wide range of foraging areas, foraging modes and diets and to radiate into a multitude of nocturnal niches (Arita and Fenton 1997; Fenton 1995; Kalko 1997; Schnitzler and Kalko 1998). Species richness is especially high in the tropics where bats often represent the largest group of mammals, e.g., on the 15 km² Barro Colorado Island in Panama (BCI), where the local bat assemblage comprises 76 species or about half of the recorded mammals. Such a high diversity is only possible if limited resources are so well partitioned that interspecific competition is avoided which guarantees a stable coexistence of species (Hutchinson 1957, 1959; Armstrong and McGehee 1980; Arlettaz et al. 1997). To understand the structure and dynamics of a local bat assemblage detailed knowledge on resource partitioning and niche differentiation between species is essential. In the following, we elucidate how the assignment of species into guilds according to echolocation tasks structures complex bat assemblages into functional groups with similar foraging niches, and illustrate the role of four different echolocation strategies for niche differentiation. We will use the bat assemblage at BCI as an exemplar for assigning bats to guilds, and discuss niche differentiation by echolocation and other adaptations within guilds.

Bat guilds defined by echolocation tasks

A first step to identify the driving forces that organize an assemblage is to arrange its members into functional guilds, which allows to subdivide complex communities or assemblages into basic structural units of species with similar niches. According to Root (1967) a guild is defined as “a group of species that exploits the same class of environmental resources in a similar way”. Members from the same guild thus are confronted with similar problems when exploiting the resources and evolved similar adaptations, whereas members from different guilds differ in the resources they use and in the way they obtain these.

83 Sympatric members of a guild play similar ecological roles within a community and
84 substantially overlap in their niche dimensions (Korňan and Adamík, 2007).

85

86 Several approaches have been used to define such functional groups in bats (for reviews see
87 Fenton 1990; Kalko 1998; Schnitzler et al. 2003), including foraging habitat, foraging mode,
88 diet, wing morphology, and/or feeding behavior (McNab 1971; Hill and Smith 1984; Norberg
89 and Rayner 1987; Aldridge and Rautenbach 1987; Crome and Richards 1988, Neuweiler
90 1989; Fenton 1990; Norberg 1994; Segura-Trujillo et al. 2016). In a modified approach
91 habitat and foraging mode were also used to define guilds but habitat types were based on the
92 echolocation scenes and thus on the echolocation tasks bats encounter when searching for
93 prey. Based on results of comparative studies indicating that the distance between prey and
94 background is the most important ecological constraint for the evolution of echolocation and
95 foraging behaviors, the habitat types open, edge and narrow space were defined and used in
96 combination with different foraging modes (aerial-hawking, trawling, flutter detecting, active
97 gleaning, passive gleaning) to attribute bat species to seven guilds (Schnitzer and Kalko 1998,
98 2001; Schnitzler et al. 2003; Denzinger and Schnitzler 2004, 2013; Denzinger et al. 2016). All
99 bats foraging with a similar foraging mode in the same habitat for the same class of
100 environmental resources were attributed to the same guild.

101

102 The three habitat types open, edge and narrow space reflect whether the food echo is masked
103 by clutter echoes from the background or not. In open space prey is so far away from the
104 background that clutter echoes play no role and bats do not react to these. In edge space prey
105 is closer to the background but not yet masked by clutter. However, bats react to the
106 background in their echolocation behavior. The definition of open and edge space includes
107 that bats perceive the prey echo in unmasked conditions. In narrow space the food items

(animals, fruits, flowers) are so close to the background or even part of it that the separation of masking clutter and food echo is impossible or at least difficult.

The role of different echolocation strategies for niche differentiation

Bat guilds are basic functional units that structure bat assemblages but they do not describe the fine-grained resource partitioning between species. Species from different guilds differ distinctly in the environmental resources they exploit and in their foraging behaviours (Root 1967). Thus, the niches of bats living in sympatry but belonging to different guilds are so far apart that members of different guilds usually do not compete for food even if they have a similar diet. Members of the same guild, however, have similar foraging strategies, exploit similar food sources with similar echolocation systems and therefore may compete with each other (Simberloff and Dayan 1991). According to the niche concept the species-specific utilization of resources should be clearly partitioned to avoid interspecific competition and to guarantee a stable coexistence of species (Hutchinson 1957, 1959). Therefore, species of the same guild should differ from each other in at least one niche dimension.

Community studies in many different taxa have shown, that microhabitat selection, foraging strategies, resource use and trophic diversity substantially contribute to high diversity of communities (Terborgh et al. 1990; Giannini and Kalko 2004). The most crucial niche dimensions that define species-specific niches therefore depend on where and when an animal searches for food and on what kind of food it feeds. In bats echolocation plays a crucial role in determining trophic niche dimensions. Bats rely on echolocation for spatial orientation, for recognizing biotopes that provide specific resources, and in most species also for detecting localizing, classifying and acquiring food (Schnitzler et al. 2003; Denzinger and Schnitzler 2013; Denzinger et al. 2016). This raises the question which information is provided by echolocation for fine-grained resource partitioning.

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135 The role of echolocation for niche differentiation is not the same for all species. Depending on
136 where bats forage and how they find and classify prey they have evolved different
137 echolocation strategies (Tab.1). Bats foraging in edge and open space detect and localize their
138 prey by evaluating pulse-echo-trains that contain unmasked prey echoes clearly separated
139 from clutter echoes produced by background and from their own loud emission. Bats that
140 forage in narrow space have to identify food echoes that are masked by background clutter
141 echoes (Schnitzler and Kalko 1998; Schnitzler et al. 2003). For these bats prey detection and
142 classification is basically a pattern recognition task which is solved in three different ways.
143 Either they use long signals and identify fluttering prey by evaluating the glint pattern in the
144 echoes produced by the moving wings of insect prey, or they use short broadband signals and
145 evaluate spectral/temporal patterns in prey echo clutter complexes to find insects on leaves, or
146 fruits, or flowers, or they use echolocation only for spatial orientation and find masked prey
147 by evaluating patterns of prey generated cues (Schnitzler et al. 2003; Denzinger et al. 2013).
148 The four main echolocation strategies give access to four different trophic niche spaces
149 (Denzinger et al. 2016), which differ in the combination of niche dimensions that can be
150 assessed. Within each strategy echolocation and in passive gleaning bats other sensory cues
151 deliver information for niche differentiation. The different echolocation strategies are
152 adaptations to specific echolocation tasks which have also been used to define bat guilds.
153 Therefore, each echolocation strategy is either used by a single guild or by a group of guilds.

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155 Bats using the “aerial-hawking or trawling strategy” search in edge and open space with
156 echolocation for unmasked airborne prey or prey drifting on water surfaces (Denzinger and
157 Schnitzler 2013). The main echolocation task here is to detect a prey echo in an otherwise
158 echo free time window and to determine the prey’s position. The information is decoded by
159 analysing pulse-echo-pairs. The most relevant niche dimensions are the position of prey

relative to background, distance to prey, prey size, prey movement pattern and search volume. Niche partitioning is to a large extent determined by echolocation parameters, such as frequency, bandwidth, call duration, pulse interval and source level. Frequency and source level determine the maximum detection distance (Lawrence and Simmons 1982; Stilz et al. 2012), call duration the minimum detection distance (Schnitzler et al. 2003). According to the size filtering hypothesis (Schnitzler and Kalko 1998) long signals with long durations are suited to detect larger insects at longer distances and shorter signals with higher frequencies are adapted for the detection of smaller insect at closer range. The echolocation systems of bats foraging in open space are adapted for long range detection of dispersed prey. Search signals are shallowly modulated, have long duration, low frequency, long pulse intervals and are emitted with high source level (Fig. 1). Bats foraging in edge space react to background and keep the prey echo within the overlap free window to prevent masking. Search signals consist of steeply modulated components suited for localization and classification of background targets and a shallowly modulated or quasi-constant frequency component of moderate frequency suited for detection of prey (Schnitzler and Kalko 1998; Schnitzler et al. 2003). Source levels are somewhat lower than in open space foragers. Signals have an intermediate duration and are emitted at every wingbeat. Bandwidth correlates negatively with the minimal distance between prey and background at which bats just can detect prey items (Siemers and Schnitzler 2004; Schmieder et al. 2012). Echolocation delivers information on the position and movement of prey but only limited information on the nature of prey and there is little evidence that the echoes encode enough information to identify favourable prey (reviewed in Jones and Rydell 2003). The aerial-hawking or trawling strategy is used by bats of the guilds open space aerial hawking, edge space aerial-hawking and edge space trawling foragers.

Bats that use the “*flutter detecting strategy*” forage with long CF-FM signals and high duty cycle (Fig. 1) for fluttering insects mostly in narrow space. The echolocation systems have been adapted to find and classify fluttering prey according to prey specific amplitude and frequency modulation patterns in the echoes. Prey echoes often overlap with non-modulated echoes from the background. The especially long CF signals in combination with Doppler shift compensation and flutter information processing with an auditory fovea allow the assessment of relevant niche dimensions such as wingbeat rate, movement pattern, position, size, and nature of prey (Schnitzler and Denzinger 2011). The pattern evaluation system is so precise, that bats may be able to discriminate between prey species (von der Emde and Schnitzler 1991; Kober and Schnitzler 1990; Koselj et al. 2011). Frequency and SPL determine the search volume. The flutter detection strategy thus delivers the information for a detailed differentiation of the trophic niche. This group comprises the members of the guild of narrow space flutter detecting foragers.

Bats that use the “*active gleaning strategy*” forage with echolocation in narrow space for stationary food items which consists either of silent stationary animals sitting on background surfaces or of fruits and flowers that are part of the background and may be advertised by specific echolocation cues. The echolocation systems have been adapted for the recognition of spectral/temporal patterns in the echoes to distinguish between an echo train of background echoes alone and an echo train that additionally includes a specific prey echo. Animalivorous gleaners manage to bring clutter echoes and prey echoes in an optimal temporal relation to distinguish between leaves with and without prey (Geipel et al. 2013a; Clare and Holderied 2015) by generating on a micro-scale an echolocation scenario similar to that of trawling bats (Denzinger and Schnitzler 2013; Denzinger et al. 2016). Phytophagous gleaners recognize the sound reflecting properties of specific structures e.g., disc shaped petals and leaves at the inflorescences of bat pollinated plants, that produce spatially invariant echoes with a

characteristic spectral and amplitude pattern over a wide sound incidence angles (von Helversen and von Helversen 1999; von Helversen et al. 2003; Simon et al. 2011). From an echolocation perspective the most relevant niche dimensions are the position of the food item in relation to background clutter and the basic nature of food. Active gleaners use ultra-short broad signals of high frequency and of low amplitude to reduce background clutter (Fig. 1). The echolocation systems of bats using the active gleaning strategy are well suited to recognize prey-specific patterns in clutter, but also for spatial orientation and the recognition of profitable landscape elements (Denzinger and Schnitzler 2013). Echolocation may deliver sufficient information on the niche dimensions nature and position of prey (von Helversen et al. 2003; Geipel 2013a; Gonzalez-Terrazas et al. 2016a). This group includes the guilds of narrow space active gleaning foragers and narrow space passive/active gleaning foragers.

Bats that use the “*passive gleaning strategy*” forage for food items whose echoes are concealed within clutter so that they have to use other modalities than echolocation to find prey. Animalivorous species evaluate the pattern of prey generated acoustic cues like rustling noises of moving prey (Bell 1982, 1985; Arlettaz et al. 2001) or courtship signals (e.g., Tuttle and Ryan 1981; Bellwood and Morris 1987) which deliver information on the nature of prey. Rustling noises generate series of broadband clicks with variable bandwidth and frequencies ranging from 3 to 30 kHz and rarely up to 50 kHz (Goerlitz et al. 2008). The spectral information differs depending on the prey’s size (Goerlitz and Siemers 2007) and on the substrate (Goerlitz et al. 2008), and may provide information on the nature of prey. Courtship signals are species specific and offer precise information for prey selection. (Falk et al. 2015). Passive gleaning bats use echolocation only for spatial orientation and the recognition of landscape elements. Echolocation thus plays here only a minor role for resource partitioning. Passive gleaners also use faint broadband, short uni- or multi-harmonic signals (Fig. 1), which are adapted for pattern recognition, necessary to identify landmarks and landscape elements.

This group includes the guild of narrow space passive gleaning foragers. The passive gleaning strategy is also used by phytophagous gleaning bats who belong to the guild of narrow space passive/active foragers. They are attracted over long distances by the species-specific odor bouquets of flowers and fruits to find the approximate location of the food item but may also use odor on close ranges (Muchala and Serrano 2015; Gonzalez-Terrazas et al. 2016b).

Is pattern recognition innate or learned?

The evaluation of patterns in narrow space bats operating with pattern recognition strategies may either be innate or learned. High duty cycle bats, which evaluate flutter information in the echoes have a highly specialized auditory system with an auditory fovea and use Doppler shift compensation to keep the echo frequency constant within the specialized frequency range of the fovea (Schnitzler and Denzinger 2011). These adaptations in the emitter and the receiver imply that the ability of flutter pattern recognition is innate. However, the pattern generated by different prey species may be learned (von der Emde and Schnitzler 1990; Koselj et al. 2011). Active gleaners, at least *Micronycteris microtis* (Miller, 1898), most likely have to learn the pattern of prey sitting on background (Geipel et al. 2013b). Passive gleaning bats that evaluate the pattern of prey generated cues may have an innate sensory bias towards specific call features of prey (Trillo et al. 2012; Falk et al. 2015) but results of behavioral experiments are not clear-cut (Jones et al. 2014, 2016).

Flexible use of echolocation strategies

Most bats use mainly the echolocation strategy of the guild to which they are attributed. However, under favorable conditions some species can switch to another strategy to get access to other niche dimensions. An extreme example is *Phyllostomus hastatus* (Pallas, 1767), an omnivorous bat (Giannini and Kalko 2005), which finds flowers with an active gleaning strategy, rustling prey with a passive gleaning strategy, and airborne prey possibly

with the aerial hawking strategy. *Myotis myotis* (Brockhausen, 1797), a passive gleaner, can be trained to take mealworms from a flat surface by using the trawling strategy where the acoustic scene is similar to that of bats catching drifting prey from the water surface (Flick 2008). Some passive gleaners can switch to the aerial hawking strategy and catch airborne prey (Faure and Barclay 1994; Ratcliffe et al. 2006). Whether they detect flying insects by echolocation or by the sounds produced by the wings is still unclear.

The proposed echolocation strategies describe how bats use echolocation when searching for food. However, during approach all bats have to perform a rather similar task, independent of the echolocation strategy. Approach signals are broadband and emitted in groups, and pulse duration and emission SPL are reduced (Fig.1). In aerial hawking or trawling bats approach signals often differ from the search signals, whereas in active and passive gleaners the short broadband search signals are also well suited for target approach. Flutter detecting bats also reduce pulse duration and emphasize the terminal frequency modulated part of the signal. When bats have to fly in cluttered environments, e.g., when leaving the roost in a forest or when avoiding obstacles, they also emit signals similar to approach signals (Schaub and Schnitzler 2007).

Niche differentiation in the Bat Assemblage of Barro Colorado Island

The niche of a species consists of multiple niche dimensions and is determined by the ecological conditions and the resources it uses (Hutchinson 1957, 1959). Each species is adapted to its specific niche not only in echolocation, but also in morphology (e.g., body size, wing morphology, bite force and dentition), physiology, sensory and cognitive abilities, and foraging behaviour (e.g, spatial and temporal strategies). Extensive studies of the bats of BCI and surrounding areas of the Barro Colorado Nature Monument in Panama, including long-term sampling at the community level and species-specific studies on a variety of topics (e.g.,

habitat use and foraging strategies), have led to the most comprehensive data base on structure, dynamics, and functionality of a bat assemblage at any single site in the Neotropics (for review see Kalko et al. 1996a, 2008). This enormous data set enables an assignment of species to guilds and allows tentative predictions on niche differentiation within guilds.

Assignment to guilds

The species list of BCI comprises 76 species and is based on data from mistnetting and acoustic monitoring by Elisabeth Kalko and colleagues including data from the literature (Kalko et al. 2008). A few of these species are unlikely to reside permanently on the island and should not be considered as part of the assemblage shaped by ecological processes, such as competition, but ca. 60 species can be estimated to permanently co-occur on BCI. More than half ($n = 41$) are New World leaf-nosed bats (Phyllostomidae) that forage in narrow space in the active, passive or passive/active mode where they glean a wide variety of food from surfaces, including fruit, nectar, pollen, invertebrates, small vertebrates, and blood (Giannini and Kalko 2004, 2005; Kalko et al. 2008) (Tab.2). With the exception of one trawling forager (*Macrophyllum macrophyllum* (Schinz, 1821), Weinbeer et al. 2007), all other phyllostomids are narrow space gleaners and, through their variety in feeding habits and food types, contribute more than any other family to the high taxonomic and ecological diversity of Neotropical bats (Gardner 1977). In most phyllostomid groups the passive, active, or passive/active gleaning mode employed is so distinct that it is no problem to assign them to a specific local guild. Only in a few species (mostly in the Phyllostominae) that show both animalivorous and phytophagous feeding habits it has to be decided whether they should be assigned according to the passive gleaning mode while foraging for animals or the passive/active gleaning mode while foraging for fruits. They are assigned here to the guild of narrow space passive/active gleaning foragers since their food consists to a large extent of fruits and, in *Phyllostomus* also of nectar. A few other phyllostomine bats (*Lamproncycteris*

brachyotis (Dobson, 1879), *Trinycteris nicefori* (Sanborn, 1949)) seem to be mainly animalivorous but may occasionally also take some fruit, although the actual diet information is rather scarce (Humphrey et al. 1983; Giannini and Kalko 2004). Because they mainly forage for insects in the passive mode, they are here assigned to the guild of passive gleaners. A highly specialized phyllostomid bat is the narrow space active gleaning forager *M. microtis* which has been shown to use echolocation to find insects sitting quiet and motionless on the vegetation (Denzinger and Schnitzler 2013; Geipel et al. 2013a). Similarities in their foraging and echolocation behaviour suggest that the two species of sucker-footed bats, genus *Thyroptera* (Thyropteridae) and the funnel-eared bat *Natalus stramineus* (Grey, 1838) (Natalidae), which catch prey near vegetation in the aerial mode and glean prey from surfaces, are also candidates for the guild of narrow space active gleaning foragers (Tschapka et al. 2000). More than one third of the bats of BCI ($n = 29$) forage for flying insects in edge and open space in the aerial mode. All molossid bats hunt in the open and nearly all vespertilionid, emballonurid and mormoopid bats prefer edge space. Exceptions within these families are the narrow space flutter detecting forager *Pteronotus parnellii* (Gray, 1843) (Mormoopidae) and the open space aerial hawking forager *Diclidurus albus* (Wied-Neuwied, 1820) (Emballonuridae). The two noctilionid species, *Noctilio albiventris* (Desmarest, 1818) and *Noctilio leporinus* L., 1758, are specialized edge space trawling foragers but are also able to catch flying prey in aerial-hawking mode. *M. macrophyllum*, a highly specialized phyllostomid bat, also belongs to the guild of edge space trawling foragers (Weinbeer et al. 2007).

Niche differentiation within guilds

The guild of open space aerial foragers comprises 12 species (11 molossids and 1 emballonurid) which emit shallowly modulated search signals with moderately low frequencies and often long call durations (Jung et al. 2007, 2014). The aerial hawking strategy

delivers mainly information about the position of prey and to a lesser extend information on its nature but species differ in their search volume which is determined by frequency, pulse duration and source level. The lowest frequencies around 16 to 22 kHz and longest call durations around 16 to 20 ms are emitted by species of *Eumops*, whereas the *Molossus* species have terminal frequencies around 30 to 40 kHz and call durations between 6 and 11 ms (Jung et al. 2014). According to the size-filtering hypothesis they should forage for different prey sizes (Schnitzler and Kalko 1998). Besides echolocation, wing morphology, flight performance and temporal and spatial foraging strategies also play important roles in resource partitioning. Some open space foragers like species of the genera *Eumops*, *Nyctinomops* and *Diclidurus* most likely fly long distances every night (Kalko 1998) whereas others have smaller home ranges. Open space foragers show great differences in the ability to follow the evasive movements of insect prey. Highly agile bats such as *D. albus* are able to catch insects in spite of fast evasive movements. The terminal groups during pursuit in these bats can be extremely long, lasting for several seconds (own observations). Since prey insects are not equally distributed in altitude, spatial separation may also account for niche differentiation. While *Molossus* species fly mostly between 5 and 20 m above the ground, *D. albus* is recorded mostly at 20 – 30 m and *Eumops glaucinus* (Wagner, 1843) and *Promops centralis* (Thomas, 1915) hunt always higher than 30 m (Stauch 1997).

The local guild of edge space aerial foragers of BCI contains 17 species from three different families (Emballonuridae, Mormoopidae, Vespertilionidae) and use the aerial hawking strategy to find their prey. The species differ in where they hunt. *Pteronotus gymnonotus* (Natterer, 1843), *Pteronotus personatus* (Wagner, 1843), *Eptesicus furinalis* (d'Orbigny, 1847) and *Lasiurus blossevillei* (Lesson and Garnot, 1826) forage in large gaps or along forest edges, *Saccopteryx leptura* (Schreber, 1774) and *Cormura brevirostris* (Wagner, 1843) between subcanopy and canopy, *Centronycteris centralis* (Thomas, 1912) at low levels in

small gaps within dense forest and *Saccopteryx bilineata* (Temminck, 1838) above the shrub layer, in small gaps but also in the canopy (Kalko et al. 1996a, Jung et al. 2007; own observations). *Rhynchonycteris naso* (Wied-Neuwied, 1820) forages near and over slow moving water bodies (Plumpton and Jones 1992). The signals of edge space foragers differ in frequency and bandwidth, which surely has an impact on maximal detection distance of prey and on the ability to detect prey close to background targets (Siemers and Schnitzler 2004; Jung et al. 2007, 2014).

Some edge space and open space aerial foragers of the BCI bat assemblage emit search signals in pairs or triplets that differ in frequency of consecutive calls, for instance species of the genera *Saccopteryx*, *Cormura* and *Molossus* (Jung et al. 2014). The ecological function of these frequency alternations is not yet fully understood. One hypothesis is that bats avoid ambiguity generated by the assignment of echoes from a previous call to the consecutive signal (Heller and Volleth 1995; Fenton et al. 1998; Jung et al. 2007). By marking each signal with its own frequency, the returning echoes could be assigned to the correct call. However, under normal circumstances, even at maximum detection distances, echoes from prey are always back before the next call is emitted, so that ambiguity should not play a role for prey detection (Jung et al. 2007). Call alterations in pairs or triplets of consecutive signals most likely serve as a species-specific acoustic signature, which is helpful in species recognition, especially in the tropics where many species occupy the frequency range between 30 – 60 kHz.

The local guild of edge space trawling foragers of BCI contains only 3 species and use the aerial hawking strategy. They most likely differentiate by the food they forage for. *N. leporinus* preferably feeds on fish whereas *N. albiventris* hunts for insects on the water surface but also for insects in the air and over land (Schnitzler et al. 1994; Kalko et al. 1998).

Echoes from jumping fish disappear after short time (Uebernickel et al. 2016) whereas the sensory contact to flying and drifting insects is longer. This may help to classify prey type. *M. macrophyllum* takes small insects from the water surface (Weinbeer and Kalko 2007). Specific adaptations for trawling, especially in the morphology of the feet and tail membrane also reflect niche differentiation.

On BCI the guild of flutter detecting foragers comprises - as everywhere in the Neotropics - only *P. parnellii* (Mormoopidae), which forage on the wing for fluttering insects in narrow space. This contrasts with the great number of the flutter detecting hipposiderids and rhinolophids in the Old World that have radiated into many species and occupy many different niches.

The guild of passive gleaning bats comprises exclusively bats of the family Phyllostomidae. The 14 species are either animalivorous or sanguivorous. Echolocation plays only a very minor role for niche partitioning. However, differences in body size, in sensory adaptations to evaluate prey-generated acoustic patterns (Falk et al. 2015), and in morphological adaptations for prey handling are indicators for niche partitioning within this group. While small animalivorous species eat small prey organisms, i.e. almost exclusively arthropods, there is with increasing size a gradual transition to feeding on small vertebrates, such as frogs, birds and rodents. Giannini and Kalko (2005) concluded that taxonomy of food organisms does not hold for a subdividing animalivorous bats but that carnivory is merely a size-dependent extreme of animalivory so carnivorous bats are essentially just larger versions of insectivorous bats. Species range in size from the 8 g *Lophostoma brasiliense* (Peters, 1867) which feeds on insects, to the more than 150 g *Vampyrus spectrum* L., 1758, that feeds mainly on vertebrates. Niche partitioning through spatial separation is seen in *Lophostoma silvicolium* (d'Orbigny, 1836) and *Trachops cirrhosus* (Spix, 1823). While *L. silvicolium* prefer

the understory on ridges, *T. cirrhosus* are often found close to creeks (Kalko et al. 1999). On the other hand, *L. brachyotis* - most likely also a narrow space passive gleaning forager - forages exclusively in the canopy (Weinbeer and Kalko, 2004).

The guild of active gleaning forager is so far only represented by *M. microtis* which picks dragon flies (Odonata), stick insects (Phasmida), and other motionless prey from leaves (Denzinger and Schnitzler 2004, 2013; Geipel et al., 2013a) but the two *Thyroptera* species and *N. stramineus* and possibly some other small phyllostomine species may also belong to this guild. Differences in the places where they search for food, e.g., either gleaning from leaves or from vertical surfaces such as tree stems or even house walls (own observations), or whether they search for moving or stationary prey may account for niche differentiation.

The local guild of narrow space passive/active gleaning foragers contains 25 predominantly phytophagous species using a wide variety of resources from fruits to floral nectar. Bats detect and classify food items by scent and the precise localization is carried out mainly by echolocation with the active gleaning strategy, although scent information is also used at close distances (Gonzalez et al. 2016b) especially in high clutter situations (Muchala and Serrano 2015). According to differences in food items and in the places where these are found, many different niches are available which may be the basis for the high species richness in this guild (Bernard 2001; Kalko and Handley 2001; Rex et al. 2008). In frugivorous bats specific food preferences for understory fruits such as *Piper spp.* (*Carollia perspicillata* L., 1758, and *Carollia castanea* (H. Allen, 1890)) and *Solanum* (*Sturnira spp.*) and for canopy fruits such as figs (*Artibeus jamaicensis* (Leach, 1821) and *Artibeus lituratus* (Olfers, 1818)) provide the base for a high degree of niche differentiation. An additional niche dimension is fruit size. In fruit-eating bats fruit size strongly correlates with body size as the maximum fruit size a species can handle depends on its morphology (Kalko et al. 1996a,b; Kalko 1998; Wendeln et

al. 2000). Some species show additional adaptations, such as *Centurio senex* (Gray, 1842) which is adapted to feed on extremely hard fruits (Dumont et al. 2009) and *Chiroderma villosum* (Peters, 1860) who also consumes the seeds of fruits (Nogueira et al. 2003; Wagner et al. 2015). In contrast to the richness of frugivores there are only 3 specialized nectarivores which are only rarely encountered on the island. This may reflect a rather low year-round diversity of specialized chiropterophilous flowers on BCI.

Conclusion

Assigning bats to guilds identifies species that live under similar ecological constraints, that share similar sensory and motor adaptations, and that forage with the same echolocation strategy for prey. Sympatric living species belonging to the same guild often exploit the same class of resources but differ at least in one niche dimension. Niches are characterized by food-specific, environmental, temporal and spatial niche dimensions, and each species is adapted to its niche in echolocation and foraging behavior, physiology and morphology. In bats echolocation strategies play a crucial role in determining trophic niche dimensions. Bats foraging with the aerial hawking and trawling strategy evaluate pulse echo pairs and have mainly positional information of prey but only limited information on its nature. Bats foraging with the flutter detecting or the active gleaning strategy perceive echoes with spectral temporal patterns that deliver detailed information on nature of prey and bats foraging with the passive gleaning strategy use echolocation only to find profitable landscape elements. Information on the nature of prey is delivered by prey-generated cues that are often species specific.

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Tab.1: Echolocation strategies used by bats

Strategy	Aerial-hawking and trawling	Flutter detecting	Active gleaning	Passive gleaning
Acoustic scene*	<p>open space aerial</p> <p>edge space aerial</p> <p>edge space trawling</p> <p>0 20 40 60 80 100 (ms)</p>	<p>narrow space</p> <p>0 20 40 60 80 100 (ms)</p>	<p>narrow space</p> <p>0 2 4 6 8 10 (ms)</p>	<p>narrow space</p> <p>0 20 40 (ms)</p> <p>Acoustic scene with rustling noises</p>
Main task	Detection and localization	pattern recognition	pattern recognition	pattern recognition
Trophic niche space	Prey found by evaluation of pulse-echo-trains with unmasked prey echoes	Prey found by evaluation of flutter pattern in echoes	Prey found by evaluation of spectral/temporal patterns in prey-clutter echo complexes (e.g., insects on leaves or fruits or flowers)	Prey found by evaluation of patterns in prey generated cues (e.g., rustling noises, courtship calls, odor)
Signal type	Signal parameters highly variable, adapted to detection and localization tasks	Long CF signals with high duty cycle	Short, broadband, high frequency signals	Short, broadband signals used only for spatial orientation and biotope recognition
Information on nature of prey	limited information on nature of prey in pulse echo pairs, single glints in the echoes may allow a poor prey classification	detailed information on nature of prey, glint pattern delivers prey specific flutter information	Spectral/temporal patterns in the prey-clutter complex allow to find leaves with prey or flowers or fruits. Patterns, possibly learned, may deliver detailed information on nature of prey	Rustling noises, odor and courtship calls deliver specific information on nature of prey

*Echolocation signals and the echoes returning from prey are depicted in black, echo trains from background echoes are shown in white.

776 Tab.2: Assignment of the bat assemblage of Barro Colorado Island to guilds

Species		open space	edge space...		narrow space ...			
		aerial forager	aerial forager	trawling forager	flutter detecting forager	active gleaning forager	passive gleaning forager	passive/ active gleaning forager
Emballonuridae	<i>Rhynchonycteris naso</i>		x					
	<i>Saccopteryx bilineata</i>		x					
	<i>Saccopteryx leptura</i>		x					
	<i>Cormura brevirostris</i>		x					
	<i>Centronycteris centralis</i>		x					
	<i>Pteropteryx kappleri</i>		x					
	<i>Pteropteryx macrotis</i>		x					
	<i>Diclidurus albus</i>	x						
Noctilionidae	<i>Noctilio albiventris</i>			x				
	<i>Noctilio leporinus</i>			x				
Mormoopidae	<i>Pteronotus parnellii</i>				x			
	<i>Pteronotus gymnonotus</i>		x					
	<i>Pteronotus personatus</i>		x					
Phyllostomidae	<i>Micronycteris hirsuta</i>					?	x	
	<i>Micronycteris microtis</i>					x		
	<i>Micronycteris schmidtorum</i>					?	x	
	<i>Lampronnycteris brachyotis</i>					?	x	?
	<i>Trinycteris nicefori</i>					?	x	
	<i>Macrophyllum macrophyllum</i>			x				
	<i>Tonatia saurophila</i>						x	
	<i>Lophostoma brasiliense</i>						x	
	<i>Lophostoma silvicolium</i>							x
	<i>Gardnerycteris crenulatum</i>						x	?
	<i>Phyllostomus discolor</i>							x
	<i>Phyllostomus hastatus</i>							x
	<i>Phylloderma stenops</i>							x
	<i>Trachops cirrhosus</i>						x	
	<i>Chrotopterus auritus</i>						x	
	<i>Vampyrus spectrum</i>						x	
	<i>Glossophaga soricina</i>							x
	<i>Glossophaga commissarisi</i>							x
	<i>Lonchophylla robusta</i>							x
	<i>Carollia brevicauda</i>							x
	<i>Carollia perspicillata</i>							x
	<i>Carollia castanea</i>							x
	<i>Sturnira luisi</i>							x

	<i>Uroderma bilobatum</i>				x
	<i>Uroderma magnirostrum</i>				x
	<i>Platyrrhinus helleri</i>				x
	<i>Chiroderma villosum</i>				x
	<i>Vampyroides caraccioli</i>				x
	<i>Vampyressa nymphaea</i>				x
	<i>Vampyressa thyone</i>				x
	<i>Mesophylla macconnelli</i>				x
	<i>Artibeus hartii</i>				x
	<i>Artibeus jamaicensis</i>				x
	<i>Artibeus lituratus</i>				x
	<i>Artibeus phaeotis</i>				x
	<i>Artibeus watsoni</i>				x
	<i>Artibeus intermedius</i>				
	<i>Ametrida centurio</i>				x
	<i>Centurio senex</i>				x
	<i>Desmodus rotundus</i>			x	
	<i>Diaemus youngi</i>			x	
Natalidae	<i>Natalus stramineus</i>			?	
Thyropteridae	<i>Thyroptera tricolor</i>			?	
	<i>Thyroptera discifera</i>			?	
Vespertilionidae	<i>Myotis nigricans</i>		x		
	<i>Myotis albescens</i>		x		
	<i>Myotis riparius</i>		x		
	<i>Rhogeessa tumida</i>		x		
	<i>Eptesicus furinalis</i>		x		
	<i>Eptesicus brasiliensis</i>		x		
	<i>Lasiurus ega</i>		x		
	<i>Lasiurus blossevillii</i>		x		
Molossidae	<i>Molossus molossus</i>	x			
	<i>Molossus coibensis</i>	x			
	<i>Molossus bondae</i>	x			
	<i>Molossus sinaloae</i>	x			
	<i>Eumops hansae</i>	x			
	<i>Eumops auripendulus</i>	x			
	<i>Eumops glaucinus</i>	x			
	<i>Promops centralis</i>	x			
	<i>Nyctinomops laticaudatus</i>	x			
	<i>Cynomops greenhalli</i>	x			
	<i>Eumops underwoodi</i>	x			

777

778 34

779 Figure caption:

780

781 Fig. 1:

782 Search and approach signals of representative species for each guild and echolocation strategy

783 from the bat assemblage of Barro Colorado Island.

Draft

Aerial hawking and trawling strategy

Flutter detecting strategy

Active gleaning strategy

Passive gleaning strategy

182x203mm (300 x 300 DPI)