Horseshoe bats make adaptive prey-selection decisions, informed by echo cues

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Foragers base their prey-selection decisions on the information acquired by the sensory systems. In bats that use echolocation to find prey in darkness, it is not clear whether the specialized diet, as sometimes found by faecal analysis, is a result of active decision-making or rather of biased sensory information. Here, we tested whether greater horseshoe bats decide economically when to attack a particular prey item and when not. This species is known to recognize different insects based on their wing-beat pattern imprinted in the echoes. We built a simulation of the natural foraging process in the laboratory, where the bats scanned for prey from a perch and, upon reaching the decision to attack, intercepted the prey in flight. To fully control echo information available to the bats and assure its unambiguity, we implemented computer-controlled propellers that produced echoes resembling those from natural insects of differing profitability. The bats monitored prey arrivals to sample the supply of prey categories in the environment and to inform foraging decisions. The bats adjusted selectivity for the more profitable prey to its inter-arrival intervals as predicted by foraging theory (an economic strategy known to benefit fitness). Moreover, unlike in previously studied vertebrates, foraging performance of horseshoe bats was not limited by costly rejections of the profitable prey. This calls for further research into the evolutionary selection pressures that sharpened the species’s decision-making capacity.

Keywords: decision-making; Rhinolophus ferrumequinum; information; foraging; sit-and-wait forager; prey choice

1. INTRODUCTION

Bats use echolocation to gather information about the environment and in many species also about prey. Several field studies of the diet of echolocating bats have found that volume proportions of different prey categories in droppings of a bat colony differ from abundances of these categories in a foraging habitat estimated by arthropod trapping (reviewed in [1]). In two of these studies, the volumes of several prey categories were negatively correlated with the habitat abundance of the category that dominated the diet [2,3]. The authors suggested that bats might be able to actively select their prey. Other studies have found that selectivity determined this way may not necessarily be a consequence of the forager’s decision-making but rather result from biased information available to the predators [1]. Specifically, higher sensory conspicuousness [4–8] or activity (including movement [9,10]) of some prey types lead to their over-representation in the forager’s perception and diet. Some bats have a behavioural propensity to exploit localized aggregations of particular prey, which also leads to an over-representation of this prey type [11].

Thus, it is not clear at present whether echolocating bats are able to economically select diet in a sequential decision-making process. Specifically, three important questions about their foraging behaviour have not been addressed so far. First, do echolocating bats associate the information in prey echoes with prey profitability by learning? Second, are bats able to estimate prey-encounter rates by monitoring time intervals between successive prey items? Third, and most importantly, are bats able to use this information to make adaptive prey selection decisions, as predicted by foraging theory?

To address these questions, we designed a behavioural experiment in which we controlled the available sensory information about the prey items so that they were physically separated from the respective sensory cues. In a foraging context, predators should use those sensory cues about prey type that are connected to its profitability (energy gained per time unit of handling). Such information can be used to make decisions that benefit fitness (e.g. through a prey-selection strategy that maximizes net energy intake rate [12–14]). Hence, we selected as a model a bat species that is known to have good sensory access to prey-specific information: the greater horseshoe bat (Rhinolophus ferrumequinum). For this bat, the specialized sensory mechanisms of prey identification are very well understood. It can detect and accurately discriminate different taxa of insects based on information in the echoes of their fluttering wings [15–17]. In flight, horseshoe bats lower the emission frequency of the constant frequency (CF) elements to compensate for the Doppler shifts induced by their own flight speed [18]. Thereby, they ensure that the echoes will return with the frequency to which their auditory system is most sensitive—the frequency of the...
‘acoustic fovea’. The acoustic fovea is a mechanical filter in the bat’s cochlea that amplifies a narrow frequency band, which is then also highly over-represented throughout the auditory system [19–24]. The acoustic fovea is used to extract information about the prey type from the echoes of echolocation calls [25] (figure 1c). Upon reflection of echolocation calls from the moving insect wings, tiny amplitude and frequency modulations (‘acoustical glints’) are imprinted on the CF parts of the echoes, creating a prey-type-specific signature [15,16]. Prey parameters that are correlated to profitability (i.e. size of insect wings, their beat rate and velocity [26]) are encoded in the pattern of acoustical glints in the echoes [16]. Using this previous knowledge, we reconstructed the foraging process of this species in a controlled laboratory setting (figures 1 and 2). To produce convincing, well-distinguishable echoes of large, profitable prey items and small, less profitable prey items, we used two computer-controlled propellers of different size and rotation velocity (figure 1d,e). We assured that acoustical glints were produced at a similar rate to those from flapping wings of natural insects (figure 1b,c). Horseshoe bats can discriminate insect wing-beat rates that differ by only 5.6 per cent [27], much less than is the case for our propellers (figure 1d,e) and many insect taxa [26]. Also, the amplitude of the acoustical glints differed between propeller sizes, as is the case for natural insects (figure 1; see also [16,17]). Thereby, we provided the bats with unambiguous echo information on prey type. In contrast to dietary field studies, we could ensure that the bats detected small and large prey equally well (i.e. we excluded sensory bias towards large prey).

In our experiments, we simulated foraging environments of different richness to the bats. We varied the prey supply of the environment on a continuous scale by varying the time between successive prey presentations: short intervals for rich and long intervals for poor environments. We then recorded the bat’s prey-selection decisions—catch or skip—at each prey arrival as a function of environmental richness. We compared the results with the prediction of standard models of prey choice [28–30] to test whether the bats are able to choose their prey economically. A forager following such a strategy of maximizing net energy intake rate would skip small prey items in sessions with a high encounter rate of large prey, and unselectively take both prey types in sessions with low encounter rate of large prey. By ignoring small prey items in the former case, an economic forager avoids the possibility of missing a large prey item while being occupied with handling a small one. In the latter case, this possibility is too low to leave out any small prey that arrives. It is never profitable to reject a large prey item within this strategy. In sessions with an intermediate abundance of large prey, the forager is expected to reject some but not all small prey items, resulting in selectivity being a sigmoid function of the average time interval between successive profitable prey items [30].

2. MATERIAL AND METHODS

(a) Bats

Six adult male greater horseshoe bats, R. ferrumequinum (Schreber 1774), were caught for the experiments in

Figure 1. Comparison of information in echoes from fluttering insects and rotating propellers. (a) Sonogram and waveform of a representative greater horseshoe bat echolocation call. The upper part of each panel (b–e) shows a photograph of a fluttering object and in the case of propellers also of the mealworm size class that propellers were signaling to the bats in the experiments. Below each photograph are sonogram and waveform of an echo of a horseshoe bat echolocation call from a scene containing the fluttering target shown in the photograph. All panels are in the same size and time scales. Arrowheads point to the acoustic glints (i.e. frequency and amplitude modulations that are created in the constant-frequency part of the call in the instant when the moving wing is positioned orthogonally to the impinging sound). (b) A small moth, the chocolate-tip, Clostera curtula. (c) A larger moth, the dark sword-grass, Agrotis ipsilon. (d) A one-winged small propeller, which was rotated with median frequency 105.77 Hz (interquartile range 6.36 Hz). For flight towards this propeller bats were rewarded on the wing with a mealworm of 20–40 mg (right). (e) A one-winged large propeller that was rotated with median 40.84 Hz (interquartile range 1.16 Hz). Flights towards it were rewarded with mealworms of 120–155 mg (right). Signals (a,d,e) were recorded during the experiment (see the electronic supplementary methods). All sonograms were computed using a 2048 point FFT with 97.25% overlap. Photographs of mealworms and A. ipsilon: S. Greif. Photograph of C. curtula: R. Trusch.
in a custom-made flight cage (length \( \times \) width \( \times \) height: 2.4 \( \times \) 1.14 \( \times \) 2 m) at Tübingen University at 23°C and approximately 60 per cent relative humidity. Capture, transportation and keeping were done in compliance with German and Slovenian legislation and under permits from the Environmental Agency of the Republic of Slovenia (35701-13/2003, 35717-20/2004), German Federal Agency for Nature Conservation (Z3.48.05/AUS 0007/03) and Veterinary Office of Tübingen District (14/9185.89). Water was provided ad libitum whereas food was offered only during the experiments. Experiments began always at the onset of dark phase of the photoperiodic cycle (set at 13:00 CET) and were conducted 6 days a week in a flight room (length \( \times \) width \( \times \) height: 5 \( \times \) 5 \( \times \) 3 m). At the start of the experiments, bats had been in captivity for six months.

(b) Experimental set-up

Before the beginning of the experiments, the bats were trained to catch mealworms hanging on a thread held in the experimenter’s hand and to land on a perch after every catching attempt. Perch-hunting is the usual foraging mode of this species [31]. The perch was a wooden cuboid hung on the weigh-below hook of an electronic precision balance (Ohaus Adventurer AR3130) connected to a laptop computer. A custom-programmed (MATLAB v. 6.5, Matworks Inc.) instrument control system enabled the experimenter to weigh a bat with a precision of approximately ±2 mg between foraging attacks. After initial training, we started using computer-controlled propellers (figure 1d,e) to signal prey arrival to the bats. Propellers were mounted on two servomotors (maxon motor EC 16, order no. 232242) which were controlled with two DEC 50/5 1-Q-EC amplifiers (maxon motor, order no. 230572) connected to a laptop computer through a data acquisition card (PC-CARD-DAS16/16-AO, Measurement Computing). Both motors were mounted 1.5 m away from the perch on a single clamp; one motor with the propeller was facing upwards, while the other propeller faced downwards. Only the upper propeller could be echolocated by the bat through a slit in a round box that enclosed the propellers. The experimenter was able to turn the clamp and thereby put either the small or large propeller in the upper part of the box, where it could be echolocated through the slit. The box, motors and a cabin, in which the experimenter was seated, were covered with sound-absorbing foam that prevented the bat from echolocating any movements by the experimenter (figure 2). We precluded the bats from using all but echo-aoustic cues on prey identity (see the electronic supplementary material for details).

(c) Experiments

Each foraging session consisted of a pseudo-random sequence of an equal number of large and small prey items. To prevent too much variation in inter-presentation intervals of each prey type, the maximum number of successive presentations of each type was set to three. The presentation consisted of a 2.5 s rotation of both propellers. The upper propeller, which could be echolocated by the bat, signalled prey type (figure 1). If the bat decided to attack the prey during the presentation (i.e. if it flew towards the propeller) the experimenter’s hand holding a tethered mealworm popped out of the cabin, enabling the bat to pull the mealworm from a thread (electronic supplementary material, movies S1 and S2). Flights towards the presentation of the large propeller were rewarded with a mealworm of 120–155 mg body mass, whereas a mealworm of 20–40 mg was rewarded to a bat flying to the presentation of the small propeller. Among the different individual bats, profitability, calculated as energy content divided by handling time, ranged from 46.5 to 57.1 Js\(^{-1}\) for large mealworms and from 17.3 to 22.2 Js\(^{-1}\) for small mealworms (see the electronic supplementary material for details of its measurement). If a bat stayed on the perch or arrived at the propeller after it had stopped rotating, no mealworm was given. After each presentation the propeller was removed from the upper position behind the slit, even if the next presentation was to be done with the same propeller. The bat’s decision was scored online as either eating the prey, rejecting the prey (e.g. skipping it by remaining on the perch) or as an unsuccessful capture attempt. The next presentation could start after the bat returned to the perch. We avoided large variation in time intervals between successive presentations to minimize the variation in encounter rate of each prey type within a foraging session. Thus, coefficients of variations in time intervals between successive large prey items ranged from 0.33 to 1.54. Each bat had one foraging session of about 40 mealworms (20 small and 20 large) per day, 6 days a week. The number of prey presented was adjusted to keep the bats’ body masses, as measured before each foraging session, constant. However, the proportions of both prey types were kept equal.
(1 : 1). The quality of the bats’ foraging environment was varied by changing the average time intervals between successive presentations among foraging sessions, thereby varying average encounter rate of the large prey type. This was shown to be a better predictor of selectivity than encounter rate of small prey type by comparing sessions with different proportions of large and small prey (1 : 1 versus 3 : 1 [32]). A prey-selection strategy is based on the predator’s estimates of prey-encounter rate in a current foraging bout, which may be partly influenced by the extent of change from the previous bout. To minimize the latter effect in our data, bats were presented with foraging sessions of about the same prey-encounter rate for four longer periods (of 22–47 sessions). Thus, only three transitions between sessions of very different encounter rates were made. Before the start of data collection, the bats had experienced foraging sessions of the entire range of average prey-presentation intervals that they were going to be subjected to during data collection sessions.

Bats’ body masses taken during the experiment were used to compute a measure of foraging performance. In foraging theory, net energy intake rate is generally taken as the parameter that is being maximized [29]. However, it does not depend solely on the forager’s decisions, but also on environmental parameters (e.g. prey-arrival rates). To enable comparison of foraging performance among sessions with different prey-arrival rates, we therefore standardized foragers’ net mass increase rate by dividing it by mass presentation rate. We thereby obtained the net mass increase relative to the total mass of presented prey (electronic supplementary material, figure S1).

(d) Data analysis

To compare the selectivity levels between individuals and sessions, we computed a selectivity index (SI) as follows:

\[
SI = \frac{l_R}{l_E + l_R} - \frac{s_R}{s_E + s_R},
\]

where \(l_E\) denotes the number of large mealworms eaten; \(l_R\) is the number of large mealworms rejected; \(s_E\) is the number of small mealworms eaten; and \(s_R\) is the number of small mealworms rejected. Note that the number of unsuccessful catches is not included in the formula. SI can take any value from \(-1\) (complete selectivity for small prey) to 1 (complete selectivity for large prey). An SI of 0 indicates complete unsel ectivity, either owing to the predator eating all prey items encountered or rejecting an equal proportion of large and small ones. However, since the bats virtually never rejected large prey items (i.e. \(l_R\) was 0), SI can largely be understood as a proportion of rejected small items:

\[
SI = \frac{s_R}{s_E + s_R}.
\]

The value of \(s_R\) for sessions with the same prey-encounter rates had a binomial distribution with parameters \(s_E + s_R\) and \(E[SI] = \Phi(\beta_1(\ln t) + \beta_0)\).

\[
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\]

The left side of the equation denotes the expectation of the vector of SI for different foraging sessions (SI); ln is a natural logarithm; \(t\) is the vector of average time intervals between successive large prey types per respective foraging sessions; \(\Phi\) is the cumulative standard multivariate normal distribution function (inverse function of the probit link); \(1\) is a vector of ones; and \(\beta_1\) and \(\beta_0\) denote the estimated model parameters. Their maximum-likelihood estimates were computed with the glmfit function of MATLAB 6.5 Statistics Toolbox 4.0, which we adapted to fit models with design matrices of more complex structure [33]. To test the effect of individual, which was taken as a fixed factor, the model parameters \(\beta_1\) and \(\beta_0\) were separately fitted for each individual, and, additionally, we fitted a \(\beta_1\) and a \(\beta_0\) to the entire dataset. The difference in log likelihood or deviance, respectively, of both models was used to compute the log-likelihood ratio test statistics, \(-2 \ln A\). Similarly, we also tested the eligibility of including each of the parameters \(\beta_0\) or \(\beta_1\) in the model by testing the increase in log likelihood resulting from parameter inclusion [33,34]. We used the entire response curves fitted by the model to describe the bats’ selectivity strategies (i.e. how SI varied across the whole range of average time intervals between successive large prey). It is important to note that statistics were computed using the entire dataset of 720 foraging sessions (the 720 SI values were computed from a total of 29 579 foraging decisions). To test for a correlation with bat body size and inter-individual profitability differences, we computed individual selectivity thresholds from the fitted response curves as the average intervals between successive large prey types where the fitted selectivity was \(SI = 0.5\) (§3c).

3. RESULTS

When a propeller was presented for the first time in a training session (this was the large one), three bats immediately tried to attack the propeller. This spontaneous reaction of the naive bats showed that our simulation of a fluttering insect was convincing. The bats quickly learned during this first session that the rewards were not the propellers themselves but the mealworms offered close by upon approach of a bat.

As detailed below, our data show that during the following sessions the bats associated (by learning) the information contained in the echoes from the rotating propeller with the profitability of the respective reward.

(a) Rapid decision-making and lack of discrimination errors

During the experiments, all the bats reached their decisions rapidly. When they did not attack the prey immediately after the beginning of propeller rotation, they stayed on their perch, clearly showing that they decided to skip the current item and wait for the arrival of next one (electronic supplementary material, movie S1). All individuals were flawlessly detecting and recognizing both prey types using differences in echoes from the large and small rotating propeller, as shown by the following two findings. First, as predicted by foraging theory, five of the six bats did not reject large prey items. The sixth individual, depicted in figure 3c, rejected 10 of 2614 large prey items presented to it (i.e. below 0.5 per cent). These exceptional cases occurred exclusively in sessions with very high presentation rate, where the individual was apparently on the limit of its feeding speed. Second, when the small propeller started rotating, sometimes a bat on the perch jerked with its wings, showing that it detected the prey, but then decided to wait for the next large item. An example of such prompt
Figure 3. Selectivity of all six individual horseshoe bats (a–f) increased with a decrease in time intervals between successive large prey items. Large intervals indicate poor foraging environments and short intervals rich environments. Each point represents one foraging session of about 40 prey items (20 large and 20 small). These were interspersed in a pseudo-random order. The variation in time intervals between successive prey arrivals was kept as low as possible during a foraging session. x-values do not range below 16 s, because the prey could not be presented faster on average than every 8 s. Since the bats virtually never rejected large prey items, SI can be interpreted as a proportion of rejected small prey items (see §2). Red lines represent the fitted GLM with equation in the form \( y = \Phi(\beta_0 + L_1x) \), where \( \Phi \) denotes the cumulative standard normal distribution function (inverse function of the probit link), \( \beta_0 \) and \( \beta_1 \) denote maximum-likelihood estimates of model parameters, and \( L_1 \) stands for natural logarithm. The inclusion of each parameter improved the model highly significantly (\( p < 10^{-3} \)), since all log-likelihood ratio test statistics \((-2 \ln L)\) are higher than the critical value of \( \chi^2_{1,0.0001} = 37.3 \).

(b) Economic prey-selection response to arrival rate of the profitable prey type
In accordance with theoretical expectations, the bats in our experiments unselectively fed on both prey items in sessions where large prey types were presented at long average inter-arrival intervals. In experimental sessions in which these intervals were short, all bats rejected small prey items (figure 3). All six bats adjusted their selectivity to the average time intervals between successive presentations of large prey in a foraging session. One bat—again the individual depicted in figure 3c—even showed full selectivity. In 14 of 46 sessions with short inter-arrival intervals of large prey, the selectivity index SI attained the value 1 (i.e. the bat rejected all small prey and took all large prey presented to it). For all bats, SI was not below zero in any of the sessions (i.e. bats never showed higher preference for small prey items than for large ones). All bats were partially selective (i.e. they rejected only some of the small items presented) in sessions with intermediate average encounter intervals between large prey types. The relationship between average encounter interval of large prey type and SI was best described by an asymmetrical sigmoid (probit model over log time intervals), levelling out at zero for long intervals (figure 3). The model fitted to the pooled data of all individuals was \( y = \Phi(4.42 - 1.55\ln x) \).

(c) Individual differences in prey-selection strategy
Inclusion of individual as a fixed effect in the model led to a strong increase in log likelihood (GLM, \(-2 \ln L = 4342.1\), d.f. = 12, \( p < 0.00001 \); i.e. strategies differed among individuals). Individuals also differed in each of the two model parameters (\( \beta_0 : -2 \ln L = 110.2\), d.f. = 6, \( p < 0.00001 \); \( \beta_1 : -2 \ln L = 72.4\), d.f. = 6, \( p < 0.00001 \)). Individual selectivity thresholds were computed as average intervals between successive large prey types where the fitted selectivity equals SI = 0.5. The selectivity thresholds were not significantly correlated with either forearm lengths (a standard measure of body size in bats) or with inter-individual differences in profitability between large and small prey (Spearman’s rank correlation: \( r_S = 0.657, p > 0.05 \) and \( r_S = 0.428, p > 0.05 \); \( n = 6 \)). A possible correlation could be obscured by our limited sample size, or by the differing ability and tendency of individuals to store partly chewed prey in the cheeks, while catching another prey item.

(d) Higher selectivity led to decrease in flight costs
In sessions with large intervals between successive large prey items, the bats were less selective and took a larger proportion of all presented prey than in sessions with...
short presentation intervals, where they were highly selective. Thus, the bats’ net mass gain per total prey mass presented was larger when they were less selective than when they were very selective (electronic supplementary material, figure S1). However, when less selective, the bats flew more and hence incurred increased flight costs. As evidenced by our precision balance weight data, these flight costs significantly reduced net mass gain in sessions when the bats were less selective (electronic supplementary material, figure S2). It is interesting to note that flight costs clearly impacted foraging energetics even in our laboratory environment.

4. DISCUSSION

We were able to successfully simulate the foraging process of the greater horseshoe bat in the lab. This gave us full control over every prey arrival and the sensory information of prey type available to the bats, a prerequisite to test their active prey-selection ability. Their initial spontaneous attacks on the rotating propellers showed that the propeller echoes convincingly simulated those from fluttering insects. Despite the fact that each prey item was present for a very limited amount of time, bats decided whether to attack or not very promptly, which is necessary for successful perch-hunting. Although it was previously suggested that most echolocating bat species may not have enough time to make prey discriminations before the attack [9], the horseshoe bats’ high discrimination speed did enable them to make prey-selection decisions in time. Based on our results and previous study on the ability of these bats to discriminate echoes of natural prey [17], we predict that horseshoe bats are also able to make such rapid decisions in nature. Future field research will need to address how similar prey types can be for these bats to still discriminate among them as a basis for economic foraging decisions.

Only one of the six bats showed complete selectivity (SI = 1) in the present experiments. However, this does not mean that the strategy space of other individuals did not include full selectivity. When the animals were in another physiological state (e.g. in winter when they were quite heavy), or in sessions with larger profitability difference between prey types, three more bats rejected all small prey items presented, while the remaining two achieved relatively high selectivity values [32].

The horseshoe bats adopted prey-selection strategies that match the central predictions of foraging theory. First, the probability of less profitable prey rejection decreased with the increase in average time interval between successive presentations of profitable prey. And second, our experimental animals did not reject (or very seldom rejected) large prey items. Thus, the bats were choosing their prey economically, dependent on the supply in the environment. They reached their decisions from a distance, on the perch, solely based on the echo information available from the rotating propellers. Our experimental data show that bats can associate prey-specific echo information with prey profitability, as experienced in previous encounters, and use it to inform economic decisions. The precision balance data showed that horseshoe bats incur higher metabolic costs for prey pursuit (flight) than for prey search from the perch (electronic supplementary material, figure S2). Echolocation enabled the horseshoe bats to reach the decision at the perch as to whether to attack a potential prey and to pay the respective flight costs. In the field, horseshoe bats sometimes also search for prey during continuous flight. Based on the difference in metabolic costs evidenced by the precision balance data, we predict that a horseshoe bat will be more selective when perch-hunting than when searching in flight. More generally, we predict that sit-and-wait foragers that can categorize prey from the perch over a distance will be more selective than actively searching foragers, which have about the same costs of prey search and pursuit. This provides an interesting example how the sensory ability to detect and classify prey from a distance bears consequences for economic decisions.

Previously, field dietary data inferred from faecal analysis suggested that greater horseshoe bats followed the predictions of foraging theory. The relative volume of less profitable dipters and ichneumonids in the droppings was negatively correlated with the abundance of large moths measured by light-trapping in the foraging habitat [2]. However, apparent selectivity in field studies may not necessarily be a consequence of a predator’s decision-making [4,6,8–10]. Rather, it might, for example, reflect differential sensory conspicuousness of prey. In our experiments, we were able to exclude sensory bias and make sure that the bats could detect all potential prey equally well. Our data now clearly show that these bats indeed actively decide to either attack or skip a detected prey item as a function of prey supply in the environment. They are very likely to have estimated the supply of large prey by judging time intervals between recent encounters with them.

The general correspondence of prey choice with the predictions of foraging theory has previously been experimentally shown in fish, amphibians and birds [35–38]. Astonishingly, the animals in all these previous studies partially rejected the more profitable prey. Such a rejection is the most uneconomical of all possible decisions. Two possible explanations—forager’s satiety and distraction of attention [37,39]—have generally been excluded by experimental design. It has thus been unclear whether foragers can perform at all without uneconomical rejections of more profitable prey. In this context, it is important to stress that the horseshoe bats in our study never or very seldom rejected the more profitable prey that they could easily discriminate. Thus, our data now demonstrate that it is possible for a forager with unambiguous prey cues to avoid these costly rejections. This raises the question for the other taxa as to whether sensory prey discrimination, or rather cognitive decision-making abilities, were limiting [30,37,40,41]. Within bats, it would be interesting to test whether species groups that use short frequency-modulated (FM) calls are able to show the same high level of economical decision-making as the horseshoe bats and other bats using CF echolocation. Potential constraints need to be addressed separately for the level of prey discrimination and for the level of decision-making. It is not yet clear whether and how well FM bats can discriminate insect prey. During discrimination of prey from non-prey objects of similar size and shape, these bats perform poorly [9,42–45]. On the other hand, FM bats show evidence of hyperacute resolution of phantom targets composed of a small number of reflections [46] and
spectral discrimination of such targets [47,48]. FM bats are also able to discriminate different wing-beat rates, although not as accurately as horseshoe bats [49,50]. In the long term, the detailed comparison of CF and FM bats may elucidate whether sensory prey-discrimination ability fosters the evolution of cognitive decision-making. We thank I. Kaipf, A. Schaub, A. Boonman, M. Zagnajstjer, S. Greif, L. Baier and members of Animal Physiology Department in Tübingen for their help and discussion. R. Page, S. von Merten and Peter Korsten made valuable comments on an early version of the manuscript. S. Greif and R. Trusch photographed the insects. Moth pictures were taken at Zoological Collection of University of Tübingen and State Museum for Natural History Karlsruhe. Financial support was provided by Volkswagen Foundation (K.K.), Graduiertenkolleg Kognitive Neurobiologie (K.K.), University of Tübingen (K.K., H.-U.S. and B.M.S.), Max Planck Society (B.M.S. and K.K.) and German Research Foundation, SFB 550 (H.-U.S.).

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