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Ground gleaning in horseshoe bats: comparative evidence from *Rhinolophus blasii*, *R. euryale* and *R. mehelyi*

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Abstract The 71 species of horseshoe bat (genus *Rhinolophus*) use echolocation calls with long constant-frequency (CF) components to detect and localize fluttering insects which they seize in aerial captures or glean from foliage. Here we describe ground-gleaning as an additional prey-capture strategy for horseshoe bats. This study presents the first record and experimental evidence for ground-gleaning in the little-studied Blasius' horseshoe bat (*Rhinolophus blasii*). The gleaning bouts in a flight tent included landing, quadrupedal walking and take-off from the ground. The bats emitted echolocation calls continuously during all phases of prey capture. Both spontaneously and in a choice experiment, all six individuals attacked only fluttering insects and never motionless prey. These data suggest that *R. blasii* performs ground-gleaning largely by relying on the same prey-detection strategy and echolocation behaviour that it and other horseshoe bats use for aerial hawking.

We also studied the Mediterranean horseshoe bat (*R. euryale*) in the flight tent. All four individuals never gleaned prey from the ground, though they appeared to be well able to detect fluttering moths on the ground. It is not known yet whether ground-gleaning plays a role in Mehely's horseshoe bat (*R. mehelyi*). In a performance test, we measured the ability of these three European species of "middle-sized" horseshoe bats (*R. euryale*, *R. mehelyi* and *R. blasii*) to take-off from the ground. All were able to take flight even in a confined space; i.e. the

willingness to ground-glean in *R. blasii* is not related to a superior take-off performance. In contrast to ground-gleaning bats of other phylogenetic lineages, *R. blasii* appears not to be a specialist, but rather shows a remarkable behavioural flexibility in prey-capture strategies and abilities. We suggest that the key innovation of CF echolocation paired with behavioural flexibility in foraging strategies might explain the evolutionary success of *Rhinolophus* as the second largest genus of bat.

Keywords Chiroptera · Foraging · Prey detection · Echolocation · Flutter

Introduction

Horseshoe bats (genus *Rhinolophus*) represent the second largest genus of bat, with 71 species currently recognized (Csorba et al. 2003). Horseshoe-bat species occur in all four Old World continents in habitats varying from rainforests to dry savannas and various temperate habitat types. Horseshoe bats have a specialized echolocation system: They broadcast long echolocation calls at a high duty cycle with a prominent constant-frequency (CF) part. Frequency and amplitude shifts modulated onto the echoes of these CF calls by fluttering insect wings are used for prey detection and evaluation (Schnitzler 1983). Hair cells and neurons responsible for frequencies at and around CF are very sharply tuned and over-represented, both on the basilar membrane and at higher levels of the hearing system, constituting the so-called "acoustic fovea" (reviewed in Neuweiler 1990). To keep the returning echoes within the acoustic fovea, horseshoe bats compensate for the Doppler shift induced by their flight speed by lowering the emission frequency accordingly (Schnitzler 1968; Trappe and Schnitzler 1982; Metzner et al. 2002).

With this CF echolocation system, horseshoe bats can specifically recognize fluttering insects as prey targets amongst clutter echoes reflected off vegetation and other background structures. In contrast, bats using frequency modulated calls (FM echolocation) can generally not find

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prey positioned directly on background by echolocation (e.g. Siemers and Schnitzler 2004), and so several bats with FM echolocation rely on passive acoustic prey detection (e.g. Arlettaz et al. 2001). From field studies, two ways are known in which horseshoe bats habitually retrieve their prey: (1) they capture flying insects out of the air, mostly using their wings as “nets”, and (2) they glean insects from vegetation; mostly in flight (Shortridge 1934; Griffin and Simmons 1974; Schnitzler et al. 1985; Neuweiler et al. 1987; Jones and Rayner 1989; McDonald et al. 1990; Pavey 1998). During a comparative study of the foraging ecologies of the five European *Rhinolophus* species in Bulgaria, we observed that freshly captured, experimentally naive *Blasius'* horseshoe bats (*Rhinolophus blasii*) readily retrieved insects from the ground. Here we present the first experimental evidence of ground gleaning as a third prey-capture technique for the large group of horseshoe bats; corroborating occasional field observations that indicate ground gleaning also for other *Rhinolophus* species (Blackmore 1964; Neuweiler et al. 1987; Jones and Rayner 1989; A. Beck and W. Metzner, personal communication).

Bats from different phylogenetic lineages are known as specialized ground gleaners showing morphological and sensory adaptations, including large ears and sensitive low frequency hearing for passive acoustic prey detection (Ryan et al. 1983; Schmidt et al. 1984). In contrast, *R. blasii* showed a remarkable behavioural flexibility in all three approaches to foraging, raising the question about underlying sensory and motor abilities. We were interested to know whether *R. blasii* can extend their repertoire of capture strategies to ground gleaning by relying on the same prey-detection strategy and flight performance as other rhinolophids, or if they show other specializations. Specifically, we experimentally tested the hypothesis (I) that *R. blasii*, like other rhinolophids, use flutter cues for detection of ground-based prey. Further, we examined whether echolocation behaviour during ground gleaning was similar to that known from the approach flight pattern in other *Rhinolophus* species (hypothesis II). A bat sitting on the ground will—at least in Europe—be exposed to many more predators (snakes, small carnivores, rats etc.) than one hanging on a bush or tree. Therefore, it is conceivable that a bat species would be more likely to engage in ground gleaning if it can readily take off from the ground, even with an additional prey load. Building on this line of reasoning, we set up a performance test to explore the hypothesis (III) that the willingness to ground-glean in *R. blasii* reflects superior take-off performance compared to sympatric, roughly similar-sized *R. euryale* and *R. mehelyi*. We finally tested if take-off performance was correlated with body size within species.

Methods

Flight tent experiments on prey capture

Six adult *R. blasii* (one male, five females) and four adult *R. euryale* (one male, three females) were captured in southeastern Bulgaria (Aina Ini Cave, eastern Rhodopes) in September 2001. They were kept at the Madjaruvo Vulture Center, eastern Rhodopes, in an indoor gauze dome cage with 2.1×1.5 m ground area and 1.1 m height. Bats had ad-libitum access to water and were hand-fed with mealworms if they did not eat sufficiently during the experiments. A flight tent (3.5×3.5 m ground area, 2.5 m central height) was erected in an oak forest close to the Vulture Center. The ground was bare open soil. We equipped the tent with oak branches as artificial bushes. The bats were flown one at a time in the flight tent at night during their natural activity period. Behaviour was video-taped (Sanyo CCD video camera 1950, Computar 8.5 mm 2/3" lens, Orion Combi LCD recorder) under infra-red stroboscopic illumination (custom-made). Echolocation calls were picked up with a condenser microphone (custom made; flat frequency response (± 3 dB) between 30 and 120 kHz), digitized with 480 kHz sampling rate (additional 8x digital oversampling; all equipment custom-made) and recorded into a laptop computer. Sound and video-recordings were synchronized using a VITC controller. From the videos, we determined the time when the bats landed with a resolution of one video frame (40 ms). Sound analysis was performed with the colour sonograph software Selena [Tübingen University; FFT 512, frequency resolution 937.5 Hz, time resolution: 2.1 ms, improved by FFT overlap (78.74%) to a reading accuracy of 0.23 ms]. We took measurements where the signal clearly was above noise level. Fluttering and still (freshly killed) moths were presented free-flying, tethered on nylon thread (0.1 mm diameter) and tethered to foam pads (9×9 cm, 2 cm height) that were placed on the ground.

Measurement of take-off performance

We captured 7 *R. blasii* (7 females), 25 *R. euryale* (17 males, 8 females) and 28 *R. mehelyi* (19 males, 9 females) at Aina Ini Cave (see above) and at Zorovitzka Cave, northeastern Bulgaria in September and October 2002. The bats were sexed, weighed (Kern 462-41 CE balance, precision 0.1 g) and forearm length was measured (Measy 2000 caliper, Switzerland, precision 0.1 mm). Close to the cave entrance, we then put the bats into a small cardboard box (11×6×6 cm, length×width×height; open only at the 6×6 cm front side) which in turn was placed onto the bare ground within a cardboard “starting arena” (50×35×30 cm, length×width×height). From video-recordings taken from above (Sony DCR-TRV 50 MiniDV Camcorder), we determined “take-off time” as the time from the onset of the take-off to leaving the starting arena (resolution 1 video frame: 40 ms).

All bats were captured under licence of the Bulgarian authorities (MEW: no. 48-00-56/16.01.2001, no. 53-00-4428/23.05.2001, no. 33-00-276/30.01.2002) and released at the site of capture after completion of the experiments.

Statistical tests

Statistical tests were calculated using Systat 10 (SPSS) and Jump 4 (SAS). For all data sets deviating significantly from normal distribution (Kolmogorov-Smirnov test using Lilliefors adaptation; $P < 0.05$), nonparametric statistics were used. When reporting statistical results in parentheses, we abbreviated species as follows: Rb for *R. blasii*, Re for *R. euryale* and Rm for *R. mehelyi*.

Results

Flight tent experiments on prey capture

All *R. blasii* and *R. euryale* readily captured flying and tethered live moths of the families Noctuidae, Geometridae and Lasiocampidae (winglength from 14 to 39 mm) by aerial hawking in mid-air, as well as a few centimetres from oak foliage or the tent walls, as long as the moths were fluttering.

Two *R. blasii* approached spontaneously fluttering moths sitting on the ground. The bats landed, sometimes walked after the moth for up to 10 cm, and took flight from the ground with the prey item. If the moths had stopped fluttering, the bats did not find them. Based on this first observation, we began to present fluttering moths on the ground by pinning them to foam pads. Mostly starting from a perch, all six *R. blasii* readily gleaned these moths from the ground (example in Fig. 1); one of the bats did so even within 15 min after first release into the flight tent. They always landed, corrected their position when necessary by either walking or by a very short flight, covered the moth with their body or wing membranes, took it in the mouth and then took off. They remained on the ground for up to 1.92 s to get hold of the prey (mean±SD: 0.79±0.54 s, $n=16$). In a choice experiment conducted to test hypothesis (I), all six *R. blasii* always captured a fluttering moth and never attacked a non-fluttering similar-sized one that was presented simultaneously. Each individual aimed 8 capture attempts (median, range 3–9) at the fluttering moth and none at the non-fluttering one (Wilcoxon Signed Ranks Test: $Z=-2.2$, $P=0.0256$, $n=6$).

All four *R. euryale* we tested decreased flight speed when passing a moth fluttering on the ground, and several times hovered about 40 cm above it for a few seconds. However, the four *R. euryale* neither landed nor captured prey from the ground.

Echolocation behaviour

The *R. blasii* continuously emitted CF echolocation calls while scanning their surroundings from a perch and while approaching and capturing prey (Figs. 1, 2). Pulse duration and pulse interval were shortened progressively during approach flight and reached lowest values in the “terminal group” broadcast just prior to landing. To analyse the decrease of pulse interval and pulse duration statistically, we calculated a linear regression of both parameters on time for each sequence ($n=11$ sequences; data from the last 1.3 s before landing, i.e. left of the hatched line in Fig. 2; for pulse duration, Bonferroni corrected P values were $P<0.05$ for 10 sequences, $P>0.05$ for 1 sequence; for pulse interval, all 11 corrected P values were <0.05). Pulse duration decreased significantly as the bats approached the ground; i.e. the slope of all 11 regression lines was negative and differed significantly from 0 [mean slope -38.9 ± 24.5 (SD); one sample t -test

against a hypothetical mean of 0: $t_{10}=-5.27$, $P=0.0004$]. Likewise, pulse interval decreased with time [mean slope -63.8 ± 32.4 (SD); one sample t -test against a hypothetical mean of 0: $t_{10}=-6.52$, $P<0.0001$]. During the approach, the bats emitted calls in groups of 2–8, showing within-group pulse intervals around 20 ms and longer between-group intervals of about 30–50 ms (Figs. 1e, 2b).

In the last 250 ms before landing, pulse duration was 14.3 ± 4.0 ms ($n=92$ calls from 9 sequences) and pulse interval 21.2 ± 9.7 ms. Accordingly, inter-pulse interval averaged 8.6 ± 9.5 ms in these last 250 ms before landing and the duty cycle (percentage of time covered with signal) ranged from 55 to 93%. Just prior to landing, the bats emitted a “terminal group” or “buzz” consisting of 5–8 calls (median 6). After the last buzz call, the bats paused echolocation for 109.7 ± 63.3 ms ($n=10$) and then echolocated continuously while sitting on the ground (Figs. 1, 2).

Interspecific comparison of take-off performance

The three *Rhinolophus* species tested could take flight from a quadrupedal stance on the ground. They either took off directly from the small cardboard box or else crawled out into the starting arena first. From the take-off to leaving the starting arena, all but four bats took less than 2 s (Fig. 3). “Take-off time” did not differ between sexes [Mann-Whitney U -test: *R. euryale*: $U=94.0$, $P=0.1277$, n (males)=17, n (females)=8; *R. mehelyi*: $U=70.5$, $P=0.4599$, n (males)=19, n (females)=9] and therefore we pooled the data from males and females for further analysis. *R. euryale* left the starting arena slightly, but significantly faster than *R. blasii*, whereas *R. blasii* and *R. mehelyi* did not differ (Fig. 3 for entire dataset and sample sizes; medians: 0.80 s (Re), 0.96 s (Rb), 1.08 s (Rm); Kruskal-Wallis test: all 3 species: $H_2=8.06$, $P=0.0177$; pair-wise post-hoc comparison under manual Bonferroni adjustment: Rb-Re: $P=0.0459$, Re-Rm: $P=0.0564$, Rb-Rm: $P=1$).

Take-off performance and body size

R. mehelyi were heavier than both *R. blasii* and *R. euryale* (Fig. 3 for entire dataset and sample sizes; mean±SD: 16.5 ± 2.1 g (Rm), 11.7 ± 0.8 g (Rb), 12.3 ± 1.5 g (Re); ANOVA: all 3 species: $F_{2,57}=44.08$, $P<0.0001$; pair-wise post-hoc comparison under Bonferroni adjustment: Rm-Rb and Rm-Re both $P<0.0001$, Rb-Re $P=1$) and had larger forearms (sample sizes as in Fig. 3; mean±SD: 47.4 ± 1.0 mm (Rb), 48.2 ± 1.0 mm (Re), 51.6 ± 1.1 mm (Rm); ANOVA: all 3 species: $F_{2,57}=87.82$, $P<0.0001$; pair-wise post-hoc comparison under Bonferroni adjustment: Rm-Rb and Rm-Re both $P<0.0001$, Rb-Re $P=0.1772$). Take-off performance was correlated significantly with body weight only in *R. mehelyi* (Fig. 3; Spearman rank correlation, Rb: $r_s=0.3243$, $P=0.4779$, $n=7$; Re: $r_s=-0.3151$, $P=0.1250$, $n=25$; Rm: $r_s=0.4903$,

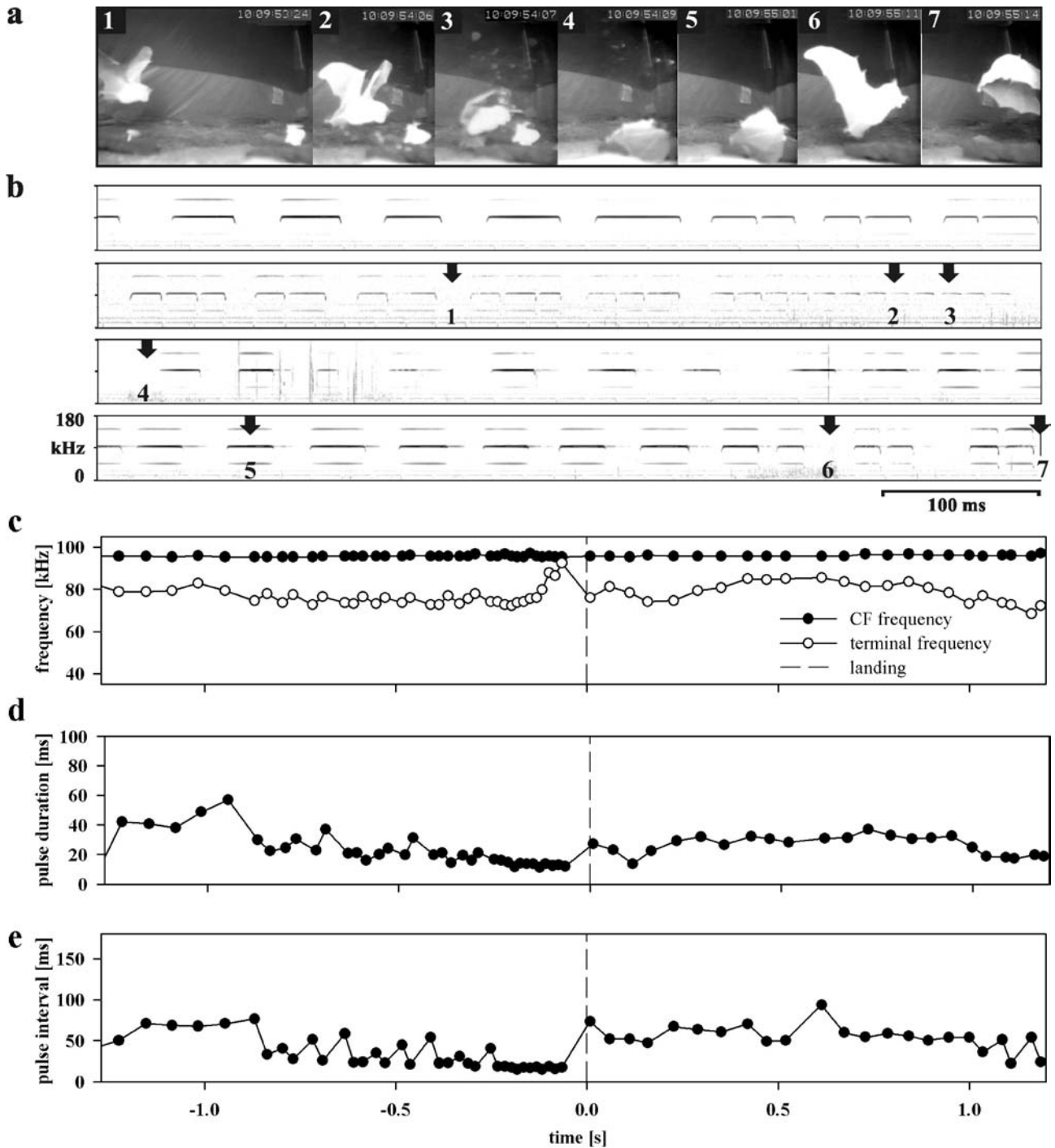


Fig. 1a–e Typical sequence of a *Rhinolophus blasii* that is gleaning a fluttering moth from the ground. Single frames taken from video sequence (a) and synchronously recorded echolocation calls in sonagram representation (b). Arrows and numbers in the call sequence indicate the position of the corresponding video frame.

Change of call parameters over time is depicted for CF and terminal frequency (c), pulse duration (d) and pulse interval (e). The *hatched vertical line* indicates the moment of landing (corresponding to video frame no. 4). The increase in terminal frequency just prior to landing (c) is probably an artefact caused by a poor S/N-ratio

$P=0.0081$, $n=28$). If the two outliers (Fig. 3; Mahalanobis distances outlier analysis) are removed from the analysis, the correlation of take-off performance and bodyweight is no longer significant in *R. mehelyi* ($r_S=0.3630$, $P=0.0684$, $n=26$). Take-off performance was not significantly correlated with forearm length in all three species (Spearman

rank correlation, Rb: $r_S=0.0180$, $P=0.9694$, $n=7$; Re: $r_S=0.3149$, $P=0.1252$, $n=25$; Rm: $r_S=0.2210$, $P=0.2585$, $n=28$).

Fig. 2 Call duration (a) and pulse interval (b) over time for 11 ground-gleaning sequences from 4 different *Blasius* horseshoe bats (total of 461 calls). Each call sequence is depicted by a different *symbol* type. The sequences are arranged in a way that the origin (0 ms) of the time axis marks the landing of the bat in each sequence. For statistics see text

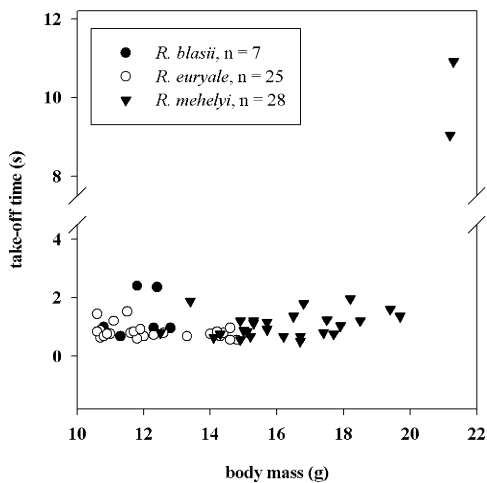
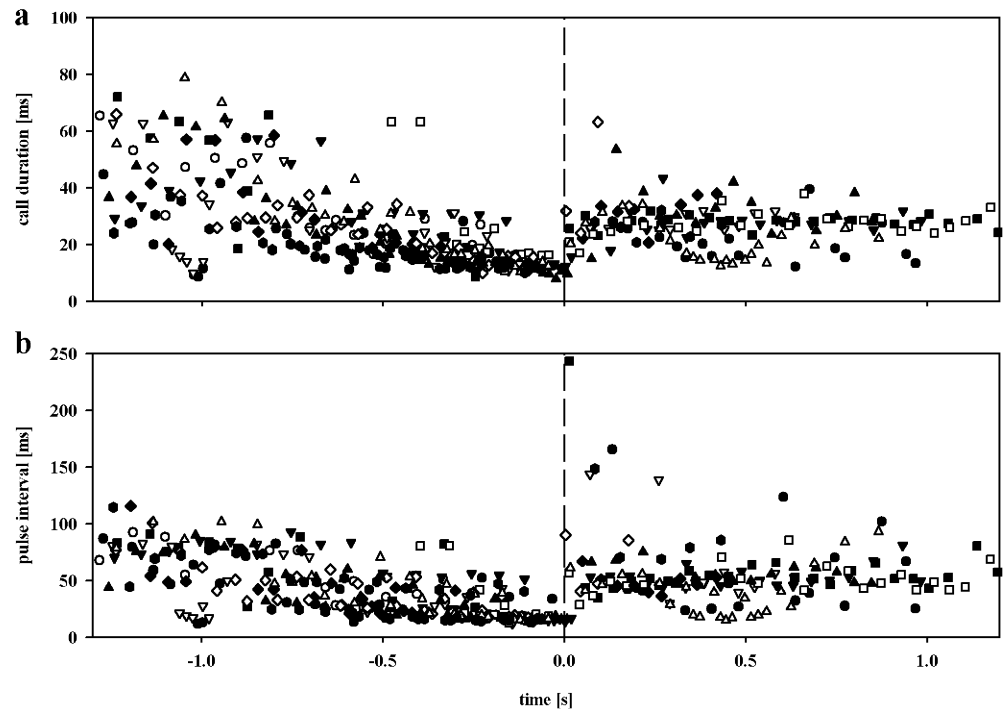


Fig. 3 Take-off performance from the ground in *Rhinolophus blasii*, *R. euryale* and *R. mehelyi*. “Take-off time” was defined as the time bats took from the onset of the take-off to leaving the “starting arena” (see Methods). For statistics see text

Discussion

The sensory basis of prey detection

Our data show that *R. blasii* are able to and readily do glean prey from the ground, including landing, quadrupedal walking and take-off from the ground. Our choice experiment showed that all six bats detected and captured only fluttering moths, corroborating our hypothesis (I) that *R. blasii* use flutter cues for prey perception, and also for the detection and localization of prey sitting on the ground. It is very likely that they used the fluttering-target

detection mechanism as described for the genus *Rhinolophus* in general (Neuweiler 1990; Schnitzler and Kalko 2001), i.e. they listened for “acoustic glints” imprinted by the insect wingbeats onto the echoes of their CF calls. The only dietary analysis available was conducted in Zambia and found that *R. blasii* preyed almost exclusively on moths in that region (Whitaker and Black 1976). There was no evidence for wingless or non-flying arthropods in the *R. blasii* diet, which fits our finding that flutter-cues are essential for prey detection.

From an echo-acoustic perspective, it is very unlikely that the bats could use echolocation to find immobile prey on the ground, because prey echoes will be masked by ground echoes (Fenton 1990; Neuweiler 1990; Schnitzler et al. 2003). Indeed, we have no evidence that *R. blasii* ever attacked an immobile moth and therefore we believe that they could not distinguish them from background. Detection of surface-based prey by echolocation is facilitated by acoustically smooth backgrounds that reflect sound impinging at an acute angle away from the sender and thereby render a prey object acoustically conspicuous (Siemers et al. 2001). In nature, calm water bodies offer smooth surfaces (Boonman et al. 1998; Rydell et al. 1999). However, neither the bare soil in our flight tent nor open ground in potential *R. blasii* foraging areas are acoustically smooth. Therefore, detection of still prey by echolocation is very unlikely.

Echolocation behaviour

In support of hypothesis (II), the echolocation sequences recorded during ground-gleaning bouts matched the typical pattern of approach sequences known from other

Rhinolophus species while hunting and landing (Griffin and Simmons 1974; Trappe and Schnitzler 1982; Vogler and Neuweiler 1983; Schnitzler et al. 1985; Neuweiler et al. 1987; Jones and Rayner 1989; Tian and Schnitzler 1997). Specifically, we observed a continuous decrease in pulse duration and pulse interval, thereby causing a slight increase in the duty cycle and a pronounced increase in repetition rate, and consequently in the number of (terminal) FM sweeps per unit time. The FM echoes are thought to give accurate spatial information needed for controlled approach and landing (Neuweiler 1990; Schnitzler and Kalko 2001). The grouping of the calls that we found in *R. blasii* is presumably correlated with the wing-beat cycle, as known from *R. ferrumequinum* (Schnitzler 1971; Hebllich 1986).

Take-off performance

The similarly good take-off ability of *R. blasii*, *R. mehelyi* and *R. euryale* falsified hypothesis (III) that the willingness to ground-glean in *R. blasii* is related to a superior take-off performance. It should be noted that we ran the performance test on take-off ability in autumn, when the bats are preparing for hibernation and are, on average, heavier than (non-pregnant) animals in spring or summer. One might therefore assume that the take-off performance in summer and spring will be at least equal or better than the autumn performance we measured.

The time the bats took from take-off to leaving the starting arena is obviously a rather coarse indicator of their take-off performance, but it still delivered consistent data. A more refined estimation of take-off performance might possibly be achieved by taking into account the angle of climb and the force exerted on the ground in addition to time (M.B. Fenton, personal communication).

Interspecific differences

Our experiments suggest that *R. blasii* performs ground-gleaning largely by relying on the same flutter-detection strategy and echolocation behaviour that it and other horseshoe bats use for aerial hawking. Furthermore, the *R. blasii* take-off and flight performance is similar to that of its congeners. However, we found no obvious lack in sensory or motor abilities that would have prevented the four *R. euryale* from landing and retrieving moths from the ground in the flight tent. A motor constraint is ruled out by the good take-off performance of *R. euryale* and, additionally, by the observation that captive *R. euryale* frequently land, walk and take-off from the ground (K. Koselj and B.M. Siemers, unpublished work). In accordance with this, D. Russo (personal communication) several times observed *R. euryale* attempting to escape from a harp-trap by taking-off from the bag bottom. A sensory constraint is an equally unlikely explanation, as the *R. euryales*' hovering flight indicated convincingly that they were able to detect the fluttering prey on the ground.

Obviously, our negative evidence from four bats does not at all exclude that *R. euryale* will never engage in ground-gleaning.

Yet, it is conceivable that the difference in behaviour we observed between *R. blasii* and *R. euryale* reflects microhabitat selection of these sympatric species. *R. euryale* hunts in broadleaved woodland and, in anthropogenically strongly altered landscapes, olive groves with some undergrowth (Russo et al. 2002; Goiti et al. 2003). *R. blasii* occurs from southern Africa through Arabia up to southern Europe in forests and in open habitats like woodland savannas (Kock and Howell 1988; Krystufek and Dulic 2001) and dry, partially eroded landscapes like our Bulgarian study area (Popov and Ivanova 2002). In such habitats, the bare ground is easily accessible for a bat. Whether *R. blasii* indeed prefer more open habitat with accessible ground awaits further investigation, however.

The case of the (typically steppe-dwelling, Gaisler 2001) *R. mehelyi* is still less clear. In accordance with our experimental data, Schober and Grimmberger (1998) stated that *R. mehelyi* easily start from the ground. Based on this observation, they speculated whether *R. mehelyi* might also glean prey from the ground. However, we are still lacking any direct evidence for ground-gleaning in *R. mehelyi*. Our data for *R. euryale* show that one should be careful not to automatically infer ground-gleaning from a good take-off ability. We will therefore need further field studies, dietary data and behavioural experiments to assess the presence of ground-gleaning behaviour in *R. mehelyi*.

Behavioural flexibility

Specialized ground-gleaners are known, e.g. in vespertilionid bats: *Myotis myotis* (Arlettaz et al. 2001), *Antrozous pallidus* (Fuzessery et al. 1993), in megadermatids: *Cariacodermis cor* (Vaughan 1976), *Megaderma lyra* (Marimuthu and Neuweiler 1987), *Megaderma gigas* (Kulzer et al. 1984), in nycterids *Nycteris grandis* (Fenton et al. 1983, 1990) and in the Neotropical phyllostomids *Trachops cirrhosus* (Ryan et al. 1983) and *Tonatia silvicola* (Kalko et al. 1999). These species are medium-sized to large bats (approximately 20–130 g; data taken from Nowak 1994) that generally rely on prey-generated sounds for prey detection, and retrieve the majority of their prey from the ground. In comparison, *R. blasii* is certainly not a specialized ground-gleaner. This species presumably retrieves the majority of its food in aerial captures and by gleaning it from vegetation in flight. We frequently observed both of these prey-capture techniques in the flight tent. However, our data show clearly that ground-gleaning does constitute a third prey-capture technique in this horseshoe bat. I.e. in contrast to specialists, *R. blasii* shows a high behavioural flexibility in prey-capture techniques.

Behavioural flexibility supports invasion success in new environments (e.g. Mayr 1965; Sol et al. 2002), in-

creases population size in ecologically unstable, changing landscapes (Fryxell 1997; Henein et al. 1998) and predicts species richness of taxonomic groups (e.g. Miller 1956; Mayr 1965; Nicolakakis et al. 2003). In accordance with these predictions, behavioural flexibility in prey-capture strategies occurs in *Myotis*, the largest genus of bat (Faure and Barclay 1994; Siemers and Schnitzler 2000 in combination with Swift and Racey 2002; Ratcliffe and Dawson 2003). *Rhinolophus* is the second-largest bat genus. By providing the first experimental evidence for ground-gleaning in *Rhinolophus*, we show that these bats also have remarkable flexibility in the ways they capture prey. While field data are still lacking for *R. blasii*, there are field observations from other species indicating that ground-gleaning in addition to aerial hawking and vegetation-gleaning, and hence behavioural flexibility, might not be so uncommon in horseshoe bats. There is evidence for ground-gleaning in *R. ferrumequinum* (Blackmore 1964; and A. Beck, personal communication). Jones and Rayner (1989) observed one *R. hipposideros* that “pounced” at a prey on the ground. Finally, *R. rouxii* land and sometimes crawl on the ground and start again, although it is not clear if they actually caught prey (Neuweiler et al. 1987, and W. Metzner, personal communication).

The key innovation in rhinolophids and hipposiderids surely was high duty cycle CF echolocation, which facilitated flutter-detection (references as above and Bell and Fenton 1984). This powerful prey-detection system paired with manoeuvrable flight abilities apparently allows horseshoe bats a considerable behavioural flexibility in foraging and prey capture (aerial, foliage-gleaning in flight, ground-gleaning including landing) and hence in habitat use, possibly explaining the evolutionary success of the genus *Rhinolophus*.

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