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Cues for acoustic detection of prey: insect rustling sounds and the influence of walking substrate

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SUMMARY

When insects walk, they generally produce sounds. These can reveal the walkers' presence and location to potential predators such as owls, bats and nocturnal primates. Additionally, predators might extract information on taxon, palatability, size or profitability from the rustling sounds. In contrast to ear morphology, hearing physiology and psychoacoustics of acoustically oriented predators, little attention has hitherto been paid to the acoustic structure and information content of prey sounds. An important element in the ecology of acoustic prey detection remained virtually unexplored: the influence of the substrate type on rustling sounds. In this study, we analysed amplitude and frequency parameters from insects walking on various natural substrates, in both Germany (*Carabus* beetles) and Madagascar (various beetles and cockroaches). The data show that rustling sound amplitude and frequency content depend on substrate type. On moist substrates arthropods produced less intense and less broadband rustling sounds than on dry substrates. Sound pressure level was reduced by about 6 dB, halving the detection range for the predator. For a given insect, rustling sound amplitude increased with walking speed. Finally, we found that the previously established correlation of arthropod size and rustling amplitude holds across multiple substrates. Based on these data, we provide for the first time estimates of realistic detection distances in the field. These distances range from below 1 m to over 13 m, depending on the substrate, insect mass, walking speed and background noise level. These estimates are crucial for an understanding of the foraging ecology, foraging efficiency and sensory ecology of acoustic predators.

Key words: auditory, detection distance, foraging, hearing, prey detection, sensory ecology.

INTRODUCTION

When animals walk, they generally produce sounds. These can reveal the walkers' presence to conspecifics, prey and predators (Wagner et al., 1997; Magrath et al., 2007). Predatory foragers of such diverse taxa as owls, bats and primates use prey-generated rustling sounds to detect and localize prey (Konishi, 1973; Fuzessery et al., 1993; Goerlitz and Siemers, 2007). A considerable body of literature describes the outer ear morphology and hearing physiology of animals, especially bats and owls, that are specialized in the acoustic detection of prey (Neuweiler et al., 1984; Guppy and Coles, 1988; Coles et al., 1989; Obrist et al., 1993; Wagner et al., 1997). Likewise, psychoacoustics, prey detection and foraging behaviour have been studied in some detail (Konishi, 1973; Marimuthu and Neuweiler, 1987; Faure and Barclay, 1992; Arlettaz et al., 2001; Swift and Racey, 2002; Ratcliffe et al., 2005; Siemers and Swift, 2006; Goerlitz and Siemers, 2007). Much less attention has hitherto been paid to the flip side of the coin, namely the acoustic structure and information content of the prey sounds. The lab-based behavioural experiments conducted to date have for the most part relied on presenting prey insects on 'noisy' substrate (e.g. Swift and Racey, 2002; Jones et al., 2003), such as several mealworms rustling on dry leaf litter. By contrast, in the wild, predators are faced with the task of finding single prey that move on a variety of backgrounds, most of which will produce much less conspicuous rustling sounds than dry leaves. Furthermore, not just one prey species, but rather a large variety of animals produce rustling sounds in the field. Hence, it might be advantageous for a foraging predator to extract information from the sounds on taxon, palatability, size or profitability of the rustling animals. Two recent studies showed that the amplitude and the frequency bandwidths of rustling sounds signify the size of a rustling arthropod (Siemers and Güttinger, 2006; Goerlitz and Siemers, 2007). The increase of rustling amplitude with body size to some degree depends on the arthropod taxon, e.g. the respective regression slope is steeper for carabid beetles than for centipedes or millipedes, which have a very different body conformation and number of legs (Siemers and Güttinger, 2006). On a given substrate, larger and hence potentially more profitable arthropods are louder, more broadband and therefore acoustically more conspicuous than smaller, potentially less profitable ones. This can have important consequences for predator–prey ecology. Indeed, as an example, acoustically conspicuous arthropods were overrepresented in bats' diet (Siemers and Güttinger, 2006). Mouse lemurs spontaneously preferred louder over fainter rustling sounds (Goerlitz and Siemers, 2007). Mechanistically, both passive (sensory bias) and active (decision-making) prey selection might interact in shaping a species' diet (Arlettaz and Perrin, 1995; Siemers and Güttinger, 2006; Whitaker et al., 2009). It stands to reason that the sensory and cognitive adaptations of animals are tightly linked to the sensory conspicuousness and cues of their potential food. In recent years, a growing field of research has started integrating sensory and behavioural approaches to better understand the role of acoustic, as well as visual, mechanical and chemical sensory cues for the performance of foraging animals and ultimately for their overall fitness (Anjum et al., 2006; Catania, 2006; Siemers and Swift, 2006; Melin et al., 2007; Vogel et al., 2007; Casas et al., 2008). Comparative studies have found sensory adaptations to closely mirror the physical challenges of species-specific foraging niches (Siemers and Schnitzler, 2004; Greiner et al., 2007).

An important element in the ecology of acoustic prey detection remains virtually unexplored: the influence of the substrate type on rustling sounds. In a classic paper, Fuzessery and colleagues measured the sounds of impact of anaesthetized crickets tossed on different artificial substrates (Fuzessery et al., 1993). Predatory pallid bats (*Antrozous pallidus*) responded best to the loudest sounds with the broadest spectra. Marimuthu and colleagues showed that dead frogs dragged over a dry sandy floor produce a louder noise than when dragged over an asbestos surface or wet sand (Marimuthu et al., 2002). Accordingly, captive individuals of the carnivorous bat *Megaderma lyra* were more likely to attack the former than the latter experimental prey. Here, we present the first study analysing the influence of substrate type on the rustling sounds of live, naturally moving arthropods on different natural substrates. We recorded insects in both Germany and Madagascar to test the following specific hypotheses. (1) Rustling sound amplitude and frequency content depend on substrate type. (2) On moist substrates arthropods produce less intense and less broadband rustling sounds than on dry substrates. (3) For a given insect, rustling sound amplitude increases with walking speed. (4) The correlation of arthropod size and rustling amplitude holds across substrates. (5) There is an interaction of the effects of substrate type and arthropod size on rustling sound parameters. Based on our account of rustling sound amplitudes of potential prey arthropods on a series of natural substrates, we can for the first time provide estimates of realistic detection distances in the field. These estimates are crucial for an understanding of the foraging ecology and foraging efficiency of acoustic predators.

MATERIALS AND METHODS

Insects

In Germany, insects were recorded at the University of Tübingen in a sound-attenuated chamber; in Madagascar they were recorded at the field station of QIT Madagascar Minerals in the Mandena littoral rainforest (Tolagnaro, Fort-Dauphin). Insects were collected in the field manually and, in Madagascar, additionally by using a light-trap. They were maintained in plastic boxes on natural substrate with access to water and, for longer husbandry of the German carabid beetles, food. In Germany we used six individual ground beetles (all from the species *Carabus monilis*) of 23–26 mm body length and 0.5–0.7 g. In Madagascar we recorded 36 individuals from a variety of beetle (Coleptera) and cockroach species (Blattodea); see Table 1 for species identity, and mass and size ranges. A detailed list of all individual insects recorded in Madagascar can be found in the electronic appendix of Goerlitz and Siemers (Goerlitz and Siemers, 2007). Walking sounds of these Madagascan insects on dry leaf litter were analysed by Goerlitz and Siemers for size-related acoustic cues (Goerlitz and Siemers, 2007). This data set was amended by recordings on two other natural substrates and re-analysed in the present study with respect to a new question: substrate dependence of rustling sound parameters. For reasons of comparability, some analyses were run only on a subset of the Madagascan recordings, namely on 10 beetles (*Kheper subaeneus*) with a roughly similar mass range (0.42–1.07 g) to the European *Carabus*.

Recording set-up and procedure

In Germany, we used a measurement microphone especially designed to pick up faint sounds (1/2 inch low noise microphone system type 40HH, G.R.A.S., Holte, Denmark; frequency response ±1 dB between 0.5 and 10 kHz; ±8 dB between 10 and 50 kHz). Note that the drop in amplitude from 10 kHz upwards in the respective spectra is in part due to a drop in the microphone frequency response; this does not affect comparability within the German recordings. In Madagascar, we used a custom-built condenser microphone (Animal Physiology, University of Tübingen, frequency response ±4 dB between 7 and 20 kHz; ±3 dB between 20 and 160 kHz). Signals were digitized *via* a custom-built external A/D converter (PCTape; Animal Physiology, University of Tübingen, 16 bit depth, 8× oversampling, digital anti-aliasing) connected to a laptop computer running custom-made recording software. Sampling rate was 192 kHz for German and 480 kHz for Madagascan recordings.

For the German recordings, the beetles walked naturally on one of three substrates in 50 cm×50 cm plastic arenas (10 cm smooth cardboard wall; inclined outward at about 15 deg.). To ensure optimal recordings in these rather large arenas, the walking beetles were tracked manually with the microphone, which was held perpendicular to the substrate at about 10 cm distance. Walking speed of the beetles was categorized by the recording person into (1) slow,

Table 1. Summary list for the recorded Madagascan insects

Order	Species	Mass range (g)	Body length range (mm)	No. of individuals recorded		
				Leaves	Bark	Sand
Coleoptera	*Oryctes boas*	3.66–3.94	40–43	3	3	3
	Prosopocoilus natalensis	1.62	35	1	1	1
	Haplotrachelus lissotonus	1.90	42	1	1	1
	Kheper subaeneus	0.42–1.07	1722	10	7	7
	Oryctes sp.	0.40–0.42	16–18	2	2	2
	Gymnopleuris sp.	0.04	7	1	0	0
	Phalos sp.	0.19–0.42	12–17	10	5	5
	Inscutomonomma sp.	0.08	9	1	0	0
	Evides sp.	0.33	21	1	1	1
	Adoretus sp.	0.06–0.16	9–11	10	0	0
	Morphospecies 1	0.98–1.31	31–33	2	2	2
	Morphospecies 2	1.18	23	1	1	1
	Morphospecies 3	0.47	16	1	1	1
	Morphospecies 4	0.23	16	1	1	1
	Morphospecies 5	0.11	12	1	1	0
Blattodea	*Aptera* spp.	0.07–10.10	12–64	4	4	4

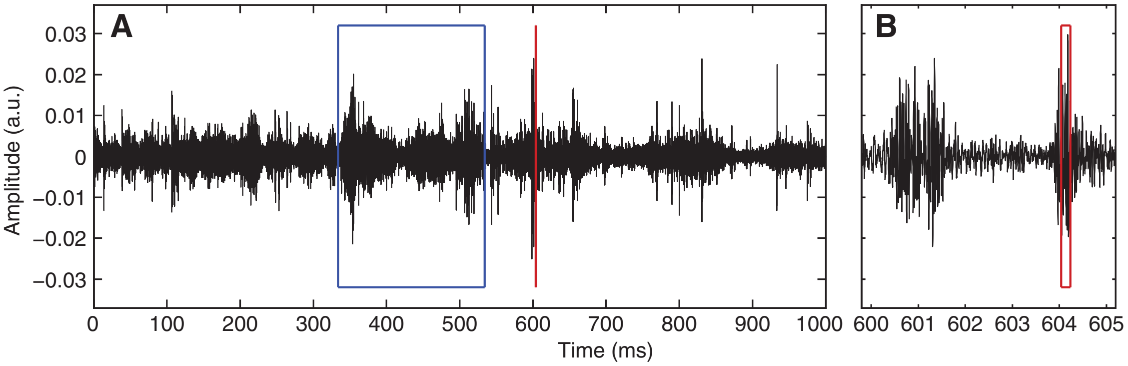

Fig. 1. Example of a rustling sound from a walking *Kheper subaeneus* on dry leaf litter in waveform representation. (A) For this example sound sequence, the blue frame indicates the highest root mean square level (MaxRMS) for a gliding 200 ms time window and the red frame the 0.2 ms time window with MaxRMS. The latter is shown on an expanded time scale in B. a.u., arbitrary units.

(2) medium and (3) fast. Roughly, 'medium' walking speed corresponded to 1.5 m min^{-1}; 'slow' was about half this speed, and 'fast' about twice this speed. Walking speed effects are only reported for dry substrate. Recordings where beetles buried themselves into the substrate were excluded from analysis (<1% of all recordings taken; *N*=498 recordings were analysed).

For the Madagascan recordings, the insects walked naturally on the floor of plastic bowls (diameter bottom, 26 cm; diameter top, 33 cm; height, 15 cm), which was covered with one of three substrates. The microphone was mounted 20 cm above the centre of the bowl, facing straight down (*N*=1448 recordings analysed).

For better comparison, all absolute sound pressure levels given in the Results have been converted to the value corresponding to 10 cm from the walking insect.

Walking substrates

For the German recordings, we dug 50 cm×50 cm patches out of natural habitats: (1) forest floor from a beech forest (*Fagus sylvatica*, Fagaceae) covered in leaf litter (leaf length about 6 cm; many leaves broken, also little twigs present); (2) meadow with grass length cut to about 4 cm (spacing between grass blades a few millimetres to about 1 cm); and (3) bare soil from a freshly ploughed field. We measured walking sounds on each substrate in two conditions: moist and dry. For the moist treatment, we sprinkled the habitat patches with 250 ml water, 5 min prior to the recordings and added moisture with a spray bottle roughly every 15 min. Every beetle was repeatedly recorded in each of the resulting six conditions.

In Madagascar, we used natural substrates collected in the Mandena littoral forest: (1) dry leaf litter (*Syzygium emirnense*, Myrtaceae; leaf length 26.6±6.3 mm, width 16.8±2.5 mm, means ± s.d., *N*=20); (2) bark with a coarse structure, collected from a logged tree; and (3) sifted sand.

In both sites, recordings were taken only while the insect was walking without physical contact with the wall of the bowl. Madagascan recordings had a duration of 1 s; German recordings ranged from 0.5 to 10 s duration. For each insect we aimed to take at least 10 recordings per substrate condition (Germany: min. 10, max. 20; Madagascar: min. 3, max. 25; the number of recorded Madagascan insects was 51, 31 and 30 on dry leaves, bark and sand, respectively; for details, see Table 1).

Analysis of rustling sounds

The rustling sounds were analysed offline in Matlab 5.3 (The Mathworks, Inc., Natick, MA, USA) with custom-written scripts. Recordings were high-pass filtered at 1 kHz (fourth-order Butterworth filter) and the first and last 5 ms deleted to remove filtering artefacts.

We calculated two MaxRMS levels directly from the time signal. The MaxRMS level is the highest root mean square level of two gliding windows with 0.2 or 200 ms duration, given in dB SPL (sound pressure level) re. 20 μPa in 10 cm distances from the insect. An example of a rustling sound with the two windows is shown in Fig. 1. We chose window sizes corresponding to the range of different temporal integration times found in the mammalian auditory system. For the gleaning bat *Megaderma lyra*, a very short integration time of 0.2 ms was found (Wiegrebe and Schmidt, 1996; Weissenbacher et al., 2002), whereas most other mammals show temporal integration times of up to 200 ms (Moore, 2004).

We calculated the spectral characteristics of the rustling sounds from averaged fast Fourier transformations (FFTs) for the signal corresponding to the 0.2 ms MaxRMS (FFT, 256 point, Hann-window, 50% overlap=128 sample points). Averaged FFTs for the signal corresponding to the 200 ms MaxRMS yielded similar results at a lower absolute amplitude (data not shown).

Statistics

Statistical test were run in SPSS 15.0.0 for Windows (SPSS Inc., Chicago, IL, USA). To avoid pseudo-replication, data were averaged per individual and substrate condition for statistical analysis. We used repeated measures ANOVAs to explore the effect of substrate type and moisture condition on the rustling amplitude of the European *Carabus* and the Madagascan *Kepher*. We employed a generalized linear model (GLM) to test for walking speed effects in *Carabus* (speed as categorical variable, see above; dry substrate condition). Finally, an ANCOVA (analysis of covariance) served to assess the relationship between arthropod body mass (covariate) and rustling amplitude across different substrates for the Madagascan data set. In the latter two tests, we specified individual as random factor to account for the repeated measures design.

RESULTS

Substrate type and moisture (hypotheses 1 and 2)

For both the carabid beetles recorded in Germany (Fig. 2A,B) and 10 roughly similar-sized Madagascan beetles (*Kheper subaeneus*, Fig. 2C,D), rustling amplitude strongly depended on substrate type (for statistics, see Table 2). For the German recordings, rustling

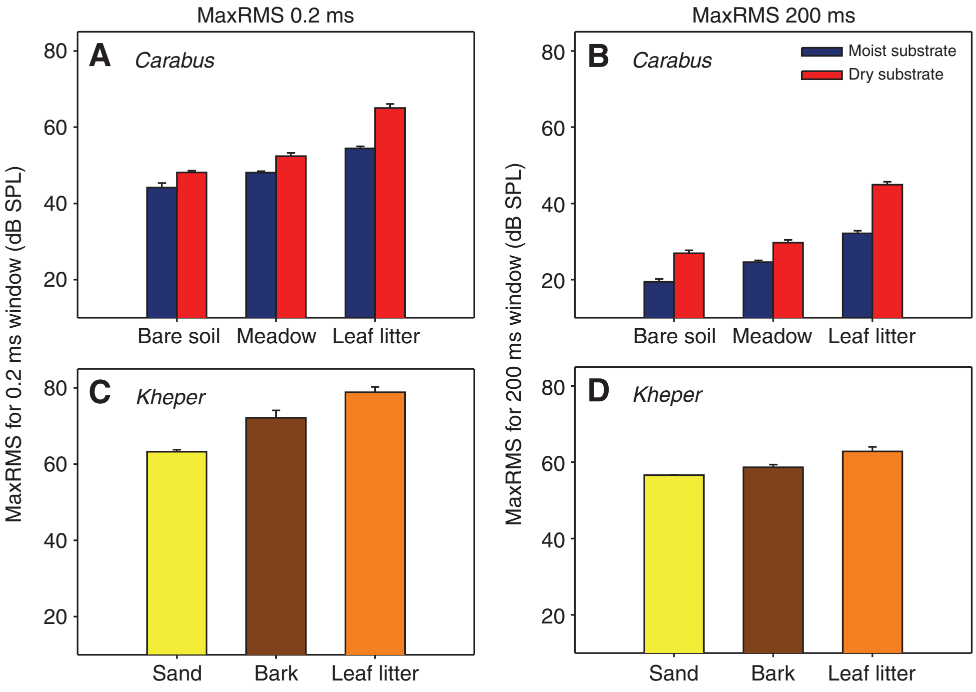

Fig. 2. Amplitude parameters for six European *Carabus* and 10 Madagascan *Kheper* beetles (second-order means ± s.e.m.) walking on different substrates. (A) *Carabus*, MaxRMS for gliding 0.2 ms window; (B) *Carabus*, MaxRMS for 200 ms window; (C) *Kheper*, MaxRMS for 0.2 ms window; and (D) *Kheper*, MaxRMS for 200 ms window. SPL, sound pressure level. For statistical analyses of substrate and moisture effects, see Table 2.

amplitude increased from bare soil *via* meadow to leaf litter. On a given substrate, rustling amplitude was louder for the dry than for the moist condition. This moisture-related difference amounted to 6.3±3.8 dB for MaxRMS for the 0.2 ms window and to 8.4±3.9 dB for the 200 ms window (means ± s.d.). As indicated by the significant interaction of substrate type and moisture condition (Table 2), the dampening effect of moisture differed slightly among substrates. It was largest for leaf litter (Fig. 2A,B).

Of the Madagascan substrates, dry leaf litter produced the highest amplitudes, bark intermediate and sand the faintest.

Rustling sounds are series of clicks (Fig. 1) caused by body contact of the arthropod with the substrate and by substrate movements induced thereby. The frequency content of the rustling sounds recorded from beetles in Germany (Fig. 3A,B) and in Madagascar (Fig. 3C) was roughly similar. They were broadband with the main energy content between 3 and 30 kHz; some energy went up to 50 kHz and for single, loud transients to 100 kHz or more. The influence of substrate type and moisture, as shown above for the amplitude parameters, was also clearly visible in the spectra (Fig. 3). While the spectral shape (amplitude distribution over frequencies) looked very similar for all substrates, the spectral bandwidth at any given amplitude threshold differed strongly, e.g. at an assumed perception threshold of 45 dB SPL, an average Madagascan rustling sound on dry leaves will have a bandwidth of 44 kHz (3–47 kHz), while a rustling sound on bark will have a bandwidth of only 28 kHz (4–32 kHz; Fig. 3C)

Effect of walking speed (hypothesis 3)

Walking speed influenced the rustling amplitude of the ground beetles both for the MaxRMS for the 0.2 ms window (dry substrate condition; GLM, individual specified as random factor; factor speed, $F_{2,31}=6.3$, $P=0.0051$; factor substrate, $F_{2,31}=110.3$, $P<0.0001$, interaction speed×substrate, $F_{4,31}=1.1$, $P=0.3951$; Fig. 4A) and for the MaxRMS for the 200 ms window (speed, $F_{2,31}=21.6$, $P<0.0001$; substrate, $F_{2,31}=357.7$, $P<0.0001$, speed×substrate, $F_{4,31}=1.6$, $P=0.1982$; Fig. 4B). Faster walking produced higher amplitudes; the difference between the slow and the medium speed class was more pronounced than that between the medium and the fast one.

Correlation of arthropod size and rustling amplitude across substrates (hypotheses 4 and 5)

The amplitude of rustling sounds increased with insect mass on all substrate types (ANCOVA, individual specified as random factor, factor mass: for MaxRMS for 0.2 ms window, $F_{1,89}=14.0$, $P=0.0003$, Fig. 5A; for MaxRMS for 200 ms window, $F_{1,89}=7.8$, $P=0.0065$, Fig. 5B). The slope was substrate dependent (ANCOVA, factor substrate; for MaxRMS 0.2 ms, $F_{2,89}=119.0$, $P<0.0001$, Fig. 5A; for MaxRMS 200 ms, $F_{2,89}=29.6$, $P<0.0001$, Fig. 5B). It was steepest for Madagascan insects walking on dry leaf litter, followed by bark and then sand. There was an interaction of the effects of substrate type and arthropod mass on rustling amplitude; just above the threshold to significance for the MaxRMS for 0.2 ms and clearly significant for MaxRMS for 200 ms (ANCOVA, interaction

Table 2. Statistical results from repeated measures ANOVAs

Figure	Beetle genus	Parameter	Substrate effect	Moisture effect	Interaction substrate×moisture
2A	*Carabus*	MaxRMS for 0.2 ms	$F_{2,10}=248.6$ $P<0.0001$	$F_{1,5}=50.5$ $P=0.0009$	$F_{2,10}=10.2$ $P=0.0037$
2B	*Carabus*	MaxRMS for 200 ms	$F_{2,10}=430.5$ $P<0.0001$	$F_{1,5}=189.1$ $P<0.0001$	$F_{2,10}=9.4$ $P=0.0051$
2C	*Kheper*	MaxRMS for 0.2 ms	$F_{2,12}=47.7$ $P<0.0001$		
2D	*Kheper*	MaxRMS for 200 ms	$F_{2,12}=13.7$ $P=0.0008$		

Data taken from Fig. 2. MaxRMS, the highest root mean square level of two gliding windows with 0.2 or 200 ms duration.

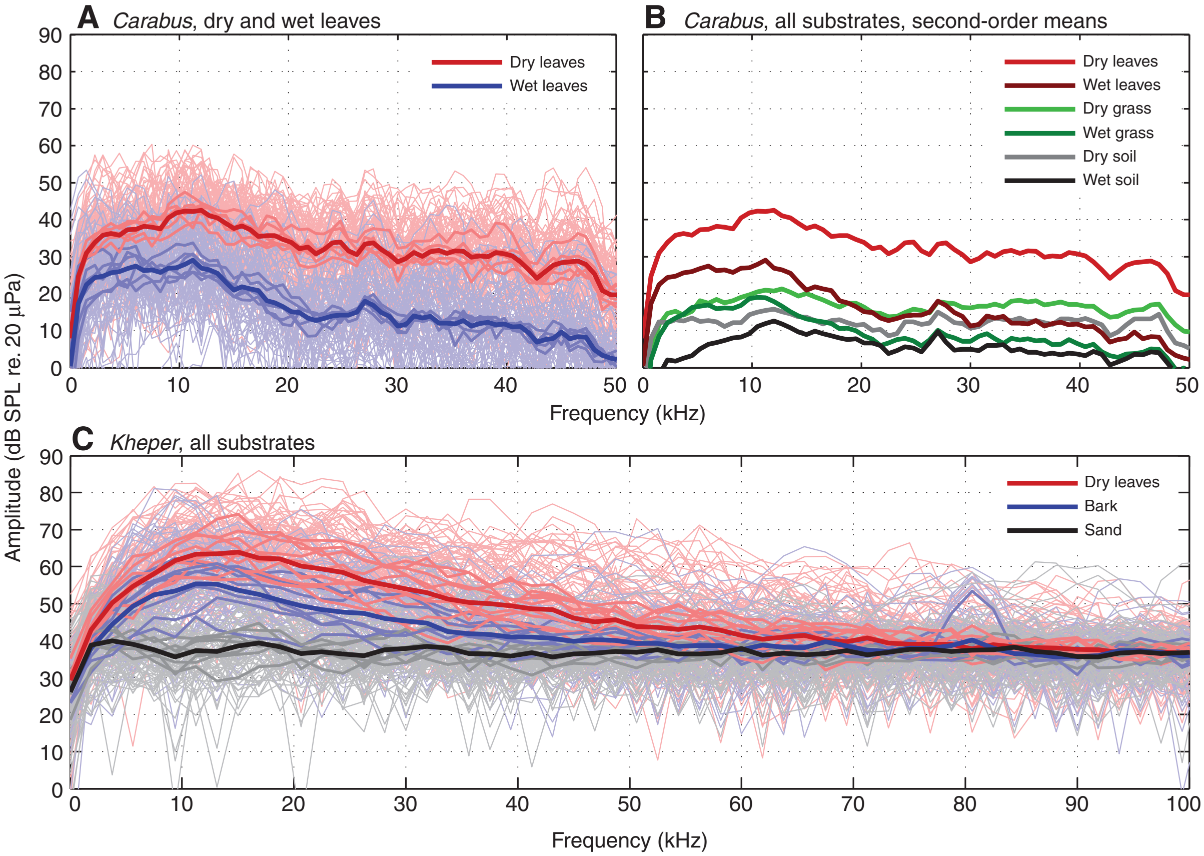

Fig. 3. Spectra of walking sounds. Spectra differ mainly in amplitude, not shape, between substrates. (A) German *Carabus*, dry leaves *versus* wet leaves. Thin, bright lines: spectrum of single recordings; medium, bright lines: mean of all recordings per beetle; thick lines: second-order mean across all beetles on a given substrate. (B) German *Carabus*, all three substrates with both moisture conditions. Only the second-order means are shown. (C) Madagascan *Kheper*, all three substrates. Thin, bright lines: spectrum of single recordings; medium, bright lines: mean of all recordings per beetle; thick lines: second-order mean across all beetles on a given substrate.

substrate×mass: for MaxRMS 0.2 ms, $F_{2,89}$=2.9, P=0.0590; for MaxRMS 200 ms, $F_{2,89}$=15.4, P<0.0001).

DISCUSSION

Walking arthropods produce a series of broadband, click-like sounds when their feet and body touch the substrate. They also induce movement of the substrate particles (e.g. leaves or grains of soil) against each other, which give rise to additional click-like signals. Click-like signals from foot–substrate, body–substrate and substrate–substrate contact can overlap and yield composite rustling sounds consisting of click trains and noise-like elements (Goerlitz and Siemers, 2007).

In the following we discuss the influence of substrate type and moisture, walking speed and arthropod size on the frequency and especially on the amplitude parameters of the rustling sounds and their potential use by acoustically orienting predators. Qualitatively, our amplitude results were the same for the two temporal integration windows for which we computed the loudest root mean square per

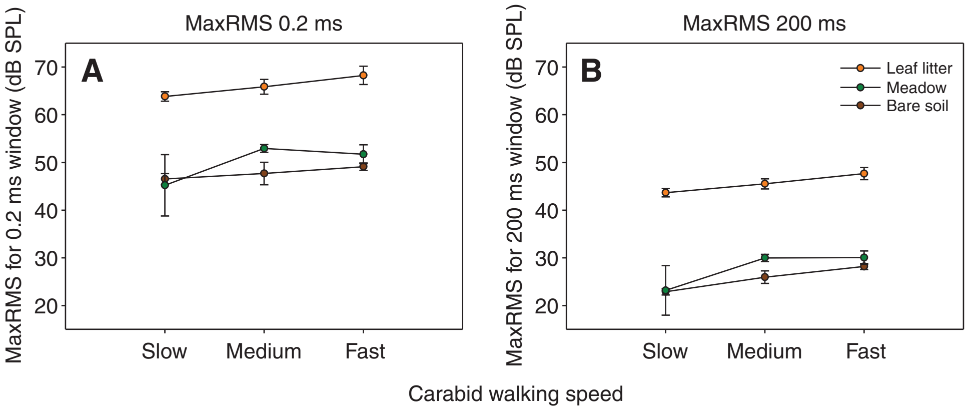

Fig. 4. Rustling sound amplitude increased with walking speed. Data for *Carabus*, walking on dry substrates only. For statistics, see text. (A) MaxRMS for 0.2 ms window; (B) MaxRMS for 200 ms window.

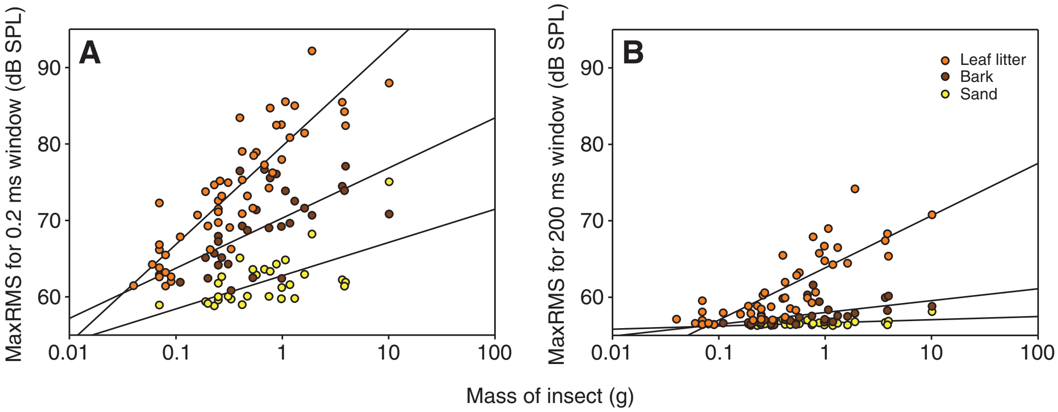

Fig. 5. Amplitude parameters for walking sounds of Madagascan insects (individual means) plotted *versus* body mass. Walking sound amplitude increased with mass and differed between the walking substrates sand, bark and leaf litter (for statistics see text). (A) MaxRMS for 0.2 ms window; (B) MaxRMS for 200 ms window.

recording (0.2 and 200 ms). This likewise holds true for three more temporal integration windows that we analysed (1 sample, 2 ms, 20 ms; data not shown). Quantitatively, a tenfold increase in the duration of the temporal integration window resulted in a decrease in the resulting amplitudes by about 7–8 dB (except for the substrate sand in Madagascar, where the amplitudes were often close to the background noise floor).

The influence of substrate type and moisture on rustling sounds

As predicted, rustling sound amplitude and frequency content depended on substrate type. While walking sounds on sand, soil and bark were faint, insects walking through meadow produced intermediate amplitudes and insects on leaf litter the highest amplitudes. On dry leaves, walking sound amplitudes were on average 12–15 dB higher than on meadow in *Carabus* and 4–6 dB higher than on bark in the Madagascan *Kepher*. The differences between meadow and bare soil were 3–4 dB and between bark and sand 2–9 dB. We assume that the grain or particle size of the substrate, the degree to which they can be moved and their material properties play a role here, e.g. dry leaves are relatively large, but are light weight and can be moved about over a millimetre or two by an arthropod touching them. They will touch other leaves, producing additional clicks. They might even experience minute twists, bends and breaks when stepped on by an insect; again, sources of click-like signals. Furthermore, dry leaves are thin and extended, somewhat membrane like, thereby functioning as resonators with good sound transmission to the air. Bark on the other hand is a solid, more or less planar surface. No particles move against each other to produce additional clicks. The insect will typically touch the surface only with its feet and largely produce foot–substrate clicks only. By contrast, it will sink into leaf litter, and touch leaves with its thorax or abdomen and thus produce additional body–substrate clicks. Sand and soil do consist of many grains, but both have a higher specific weight than leaves and are much more compacted. Therefore, an insect will induce relatively little substrate movement. Future studies will have to systematically vary substrate mechanical properties to understand their relative contribution to the characteristics of the rustling sounds generated.

For each tested substrate, moisture reduced the rustling amplitude and thereby also the over-noise bandwidths in comparison to the dry condition. This presumably is because moisture softens the material, coats the surface and buffers the insect–substrate and the substrate–substrate impact. Wet leaves stick to each other and are not stiff. Therefore, a walking insect induces much less substrate movement in wet than in dry leaf litter. While behavioural experiments conducted on acoustic prey detection typically present insects on dry, noisy substrate (e.g. Swift and Racey, 2002; Jones et al., 2003), by contrast in the wild, and especially at night, prey will often move on moist substrate and thus produce considerably less intense sounds.

Walking speed

As expected, rustling sound amplitude increased with the walking speed of an insect. A fast-walking insect will produce more footsteps per unit time than a slowly walking one (Wendler, 1964; Graham, 1972; Gabriel and Bueschges, 2007). Therefore, more foot–substrate and also more body–substrate contacts and hence more clicks per unit time will result. When measuring amplitude over a prolonged period of time, such as our 200 ms window, more clicks will increase the root mean square amplitude within that given time window. However, the MaxRMS for the very short 0.2 ms time window also increased with walking speed. This window will be too short to integrate sound amplitude over several footsteps. Therefore it is likely that the amplitude of individual clicks also increased with walking speed.

Arthropod size and the use of rustling cues for prey size selection

Previous studies have shown that rustling sound amplitude increases with arthropod size (Siemers and Güttinger, 2006; Goerlitz and Siemers, 2007). The data presented here establish that this correlation holds across substrates. On each given substrate, large insects produced louder rustling than small ones. The interaction of the effects of substrate type and arthropod size on rustling sound parameters (clearly significant only for MaxRMS 200 ms) indicates that the pattern for the increase of amplitude with mass differs between substrates. For insects on bark and especially on sand the slope of the regression line of amplitude on insect mass was less steep than for insets walking on a ‘noisy’ substrate such as leaf litter. The steeper the regression line, the smaller the prey size differences that will translate into a distinguishable amplitude difference for an acoustic predator. While noisy substrates can afford predators both more informative and more conspicuous signals on average, they may be more variable than those made by an insect walking on a ‘silent’ substrate. A predator will thus need to listen and evaluate the rustling over some time to avoid a wrong decision. The 1 s duration of our Madagascan recordings appears to be a useful listening period to overcome substrate-induced signal variability. The individual mean standard deviations for the 0.2 ms MaxRMS over 10 repetitive 1 s recordings did not differ between ‘noisy’ leaf litter and ‘silent’ bark (Student’s paired *t*-test, $P>0.3$, $N=20$). It clearly will be interesting to systematically investigate signal variability and also signal roughness (e.g. Grunwald et al., 2004) with respect to substrate and with respect to the number of walking legs (e.g. beetle *versus* centipede) in future work.

Based on handling time measurements for mouse lemurs, Goerlitz and Siemers suggested that the energetic profitability of insects can be assumed to increase with insect mass (Goerlitz and Siemers, 2007). As rustling sound amplitude is correlated with mass, acoustic predators may depend on rustling amplitude to assess prey profitability from a distance. Such an assessment is expected to optimize the effort and time associated with approaching sources of rustling sounds and markedly increase foraging efficiency (Stephens and Krebs, 1986). Walking substrate will be a confounding factor for such an acoustic prey size classification. The predator will need to recognize and account for the substrate on which an insect is walking. This could be accomplished either by a very detailed mental representation of its foraging area or by substrate-specific cues of the rustling sounds. Potential substrate-specific cues may be extracted mainly from the temporal pattern of a rustling sound and not from its spectral pattern, as the spectral patterns did not differ between substrates. Furthermore, the predator needs to account for the insect's walking speed when evaluating the amplitude cues. This is easily conceivable, as speed is coded in steps per unit time (Gabriel and Bueschges, 2007) and these will translate into click rate. Finally, the predator must also know the prey's distance to estimate the source amplitude from the received amplitude. Here again, detailed spatial knowledge might come into play. More importantly, reverberation and distance-specific loss of higher frequencies due to atmospheric attenuation are robust cues to the distance from a sound source (Bronkhorst and Houtgast, 1999; Naguib and Wiley, 2001; Naguib et al., 2002).

Detection distances for acoustically oriented predators

Based on our account of rustling sound amplitudes of potential prey arthropods on a series of natural substrates, we can for the first time provide estimations of realistic detection distances in the field. These estimates are crucial for an understanding of the foraging ecology and foraging efficiency of acoustic predators.

Moisture, substrate type and walking speed all influenced the amplitude of walking sounds. Generally, walking sounds were 6–8 dB louder on dry than on moist substrates. At any given auditory detection threshold, insects walking on dry substrates will thus be detectable at a distance twice as far as on moist substrates. For tree-dwelling predators or flying bats, this will increase the three-dimensional space in which a rustling prey can be detected by a factor of eight. The differences between different dry substrate types ranged from 2 dB (sand–bark, 200 ms) and 9 dB (sand–bark, 0.2 ms) to 17 dB (soil–leaves, 0.2 ms) and 18 dB (soil–leaves, 200 ms; Fig. 2). Thus, depending on its walking substrate and the auditory temporal integration of the predator, a walking insect will be detectable over an eight times larger distance, in a 64 times larger area and in a 512 times larger volume (if only attenuation by spherical spreading is considered). Likewise, the increase in amplitude with walking speed amounted to 3–8 dB, yielding a proportionally higher detection risk for the individual insect when moving faster.

To get rough quantitative estimates of absolute detection distances, atmospheric attenuation, attenuation by vegetation and predators' detection thresholds for signals in background noise have to be considered in addition to attenuation by spherical spreading. We gathered our rustling sound data in both a temperate (Germany) and a tropical (Madagascar) environment. They differ in average temperature, humidity, vegetation cover and background noise; all factors affecting sound propagation or perception. Obviously, these parameters can come in hundreds of combinations. For simplicity, we started our detection distance estimates with one rustling sound of 60 dB SPL and assumed two exemplary temperate situations (cool night: 10°C, 90% relative humidity; warm night: 20°C, 70% relative humidity) and two exemplary tropical habitats (humid habitat: 25°C, 100% humidity; arid habitat: 30°C, 30% humidity). For 12 kHz, which is approximately the peak frequency of our recordings, the atmospheric attenuation in these habitats is 0.20, 0.17, 0.11 and 0.24 $\mathrm{dB\,m^{-1}}$, respectively (Crocker, 1998). We further assumed a detection threshold for rustling sounds of –10 dB below the environmental noise floor (Huebner and Wiegrebe, 2003). A typical noise floor in tropical habitats has a level of about 50 dB SPL [data from Madagascar (measurements by H.R.G. and B.M.S.) and Uganda (Waser and Waser, 1977)] and we assumed a noise level of 30 dB SPL for a quiet night in temperate zones. Consequently, at a detection threshold of 20 dB SPL (temperate threshold), rustling of 60 dB SPL and 12 kHz would be detected at 8.2 and 8.4 m distance for the temperate situations and at 8.9 and 8.0 m distance in the tropical habitats. At a detection threshold of 40 dB SPL (tropical threshold), the rustling would be detectable at only 0.9 m distance in all four examples. The influence of atmospheric attenuation, and thus of temperature and humidity, is almost negligible at such close range. By contrast, the source level of the walking sounds and the background noise level of the habitat are a much bigger influence. The latter differs between – but only a little within – given habitats. As a result, the type of substrate on which an insect is walking will heavily influence how detectable it is and hence its specific predation risk.

Across the dry substrates, the rustling sound levels of the German *Carabus* beetles ranged from 48 to 65 dB SPL (MaxRMS 0.2 ms, Fig. 2A). Thus, depending on the substrate, the detection distances in an open habitat and with an average atmospheric attenuation of 0.18 $\mathrm{dB\,m^{-1}}$ will vary from about 2.3 (soil) to 13.4 m (leaf litter; 20 dB temperate threshold). In a closed habitat with vegetation cover between prey and predator, the detection distances would be reduced to 2.2–9.8 m (attenuation by vegetation conservatively assumed to be 0.34 $\mathrm{dB\,m^{-1}}$ based on measurements for 10 kHz signals (Marten and Marler, 1977; Marten et al., 1977; see also Hoffmann et al., 2007). Substrate type will interact with insect size in determining detection distance. As an example, we have estimated detection distances across the different substrates for the small Madagascan *Phalos* beetles and large *Oryctes boas* beetles in Table 1. The walking sound levels of the small beetles ranged from 60 to 72 dB SPL across the substrates sand, bark and leaf litter, whereas those of the large beetles ranged from 62 to 84 dB SPL across substrates (MaxRMS 0.2 ms). This relates to open-habitat detection distances for small beetles from 0.9 (sand) to 3.7 m (leaf litter) and for large beetles from 1.2 to 12.2 m, respectively (40 dB tropical threshold). Accounting for vegetation cover, the maximum detection distances (leaf litter) would be reduced to 3.2 and 9.1 m, respectively. Depending on rustling sound level, detection distances thus may easily differ by a factor of ten, thereby increasing detection volumes by three orders of magnitude. Insects producing louder walking sounds should thus be subject to a considerably higher predation pressure (Siemers and Güttinger, 2006). Our estimates substantiate the notion that predators can use acoustic cues for the detection and evaluation of insect prey over distances far greater than those accessible by vision at night (Dominy et al., 2001; Siemers et al., 2007; Piep et al., 2008).

In nature, there is considerable variability in sensory performance among closely related species that exploit different foraging niches (Siemers and Schnitzler, 2004; Greiner et al., 2007). Such variation is also found within some species (Caine and Mundy, 2000). Recent work has explored the consequences of this variability in the sensory performance of foraging animals for their fitness in the wild (Dominy and Lucas, 2001; Melin et al., 2007; Vogel et al., 2007). In the future, the integration of sensory biology, behavioural approaches, genetics and field ecology will hopefully allow a better understanding of the fine-scale evolution, diversification and adaptation of sensory systems. We anticipate that a detailed knowledge of food-specific cues, such as the insect rustling sounds we explored in the present study, will play an important part in disentangling this evolutionary puzzle.

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