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Are blue land crabs (*Cardisoma guanhumi*) attracted to falling fruit?

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Abstract Many species rely on multiple modalities to acquire information about predation risk, potential mates, and food. We studied the sensory modalities of blue land crabs, *Cardisoma guanhumi*, used for food detection. We isolated the acoustic and seismic cues of falling fruit and measured latency to emerge from their burrows after hearing the sound of falling fruits, seismic signals associated with fruit drop, and a combination of both modalities. In contrast to a previous study, we found no support that either substrate-born vibration or sound-enhanced emergence time. In fact, the actual fruit drop caused slower emergence times at one site. This crab lives in a seismically variable environment and perhaps such species are likely to rely more on other modalities to identify food.

Keywords Multimodal stimulus assessment · Foraging cues · *Cardisoma guanhumi*

Introduction

Animals use sounds to detect predators (Caro 2005), mates (Gerhardt and Huber 2002), and food. Studies on the use of sound in food detection have typically focused on active acoustic location, or echolocation (Neuweiler 1990; Fenton and Bell 1979), rather than passive location (finding food using sounds generated by the food) (Hahn and Thomas 2009). Yet, a variety of species passively locate their food. For instance, Bechstein's bats, *Myotis bechsteinii*, use prey-generated noise (Siemers and Swift 2006), as well as killer whales, *Orcinus orca*, (Barrett-Lennard et al. 1996), barn owls, *Tyoto alba* (Payne 1971), grey mouse lemurs, *Microcebus murinus* (Siemers et al. 2007), least weasels, *Mustela rixosa*, red foxes *Vulpes fulva*, and coyotes, *Canis latrans* (Roche et al. 1999) and mice reduce detection by nocturnal avian and mammalian predators by selecting routes that avoid leaf litter and reduce noise (Roche et al. 1999).

Substrate-born vibrations are often as important as acoustics are to successful foraging. Determining food quality via substrate vibrations may allow subterranean animals reduce the risk of predation by reducing above-ground exposure while detecting and evaluating food sources. For example, termites rely on seismic cues to determine wood size because they are blind and avoid making themselves visible to predators by pacing the length of the wood. One study suggested that termites use bioacoustic cues generated from other termites eating to determine wood block size (Evans et al. 2005).

Using more than one signal modality allows animals to respond efficiently to different environmental cues (Hebets and Papaj 2005; Goyret et al. 2007). Animals using multiple stimuli may have advantages in "close-range searching," where the target (e.g., food) usually emits the stimuli (Goyret et al. 2007). Multimodal signals may elicit the same or an enhanced response compared to a single sensory signal (Partan and Marler 2005; Uetz et al. 2009). Multimodal food detection in invertebrates is not commonly studied but multimodal predator and mate detection in some crustaceans, insects, and spiders have been studied (Acquistapace et al. 2002; Gherardi and Tiedemann 2004; Hazlett and McLay 2000; Hölldobler 1999; Rybak et al. 2002; Uetz et al. 2009).

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Our objectives were to determine whether blue land crab, *Cardisoma guanhumi*, food detection relied more on substrate vibrations, acoustic cues, or a combination of both. We focused on this species because a previous study (Herreid 1963) suggested that both acoustic and substrate-born vibrations were used for food detection. We predicted that the blue land crabs would emerge sooner after sensing stimuli of falling fruit than they would otherwise.

Materials and methods

We conducted the study from 9 to 31 October 2009 at the Virgin Island Environmental Resource Station (18°19′19.45″ N, 64°43′22.58″ W) on St. John Island. The station is located within an Antillean tropical dry forest and is situated close to mangrove stands. Thirty-four individual crabs were used in the study, 16 from site 1 located near Great Lameshur Bay and 18 from site 2 located next to Little Lameshur Bay. Site 1 was located near the road directly outside the entrance to the (VIERS) camp. Site 2 was located slightly off the end of the trail entrance to Little Lameshur Bay. Each site had more than 100 crabs scattered throughout the forest floor. Experiments were conducted from 0600 to 1100 hours, and then from 1500 to 1800 hours.

During our study, there were no fruits on the ground in the land crabs' habitat. Thus, we collected small hog plums from *Spondias mombin* trees at the VIERS campsite. We weighed the fruit and selected five to record their airborne sounds and seismic sounds when dropped on the substrate at site 1. The chosen fruits weighed 18 g (±4 g SD). All crabs were randomly assigned to acoustic and seismic stimuli characteristic to one of the five fruits. Every treatment began by spotting the subject outside of its burrow (following Hill 2001, we assume that there was generally one adult crab to a burrow). To avoid the confounding effects of transmitting seismic or acoustic signal to neighboring burrows, we selected crab burrows that were 25 m apart. Each subject received one of four treatments, real fruit drop, acoustic stimulus, seismic stimulus, and control, every other day. To ensure that we treated the same individual crabs, crab burrows were marked with a unique number. The crabs were assumed to occupy the same burrow throughout the entire study.

We began an experiment by flushing the crab into its burrow by walking towards it. Once the crab was in its burrow, we started our stopwatch and set up the assigned treatment within approximately 2 min. We stood at a distance of 8 m from each burrow and directly faced the burrow entrances. We waited 5.5 min before playing the stimuli or dropping the fruit and then waited for the crabs to emerge. We stopped timing once we saw the crab's legs in its burrow from where we were standing. A few crabs emerged before the stimulus presentation, and if they did, we stopped the experiment and selected another crab. After the stimulus presentation, we waited a maximum of 30 min for a crab to emerge before ending our observation. We also estimated crab carapace width and measured the burrow diameter to the nearest centimeter, the burrow temperature to the nearest degree, and the time of day to the nearest minute.

Experimental stimuli

Of the four treatments, the real fruit drop treatment exposed the crabs to a combination of the seismic and acoustic components simultaneously. We modified a tripod so as to hold and release a fruit by attaching a 3-m vertical length of polyvinyl chloride (PVC) pipe and attached to this to a 1.5-m arm that extended over the burrow. A cup, with a hinged bottom attached to a long string, was attached to the end

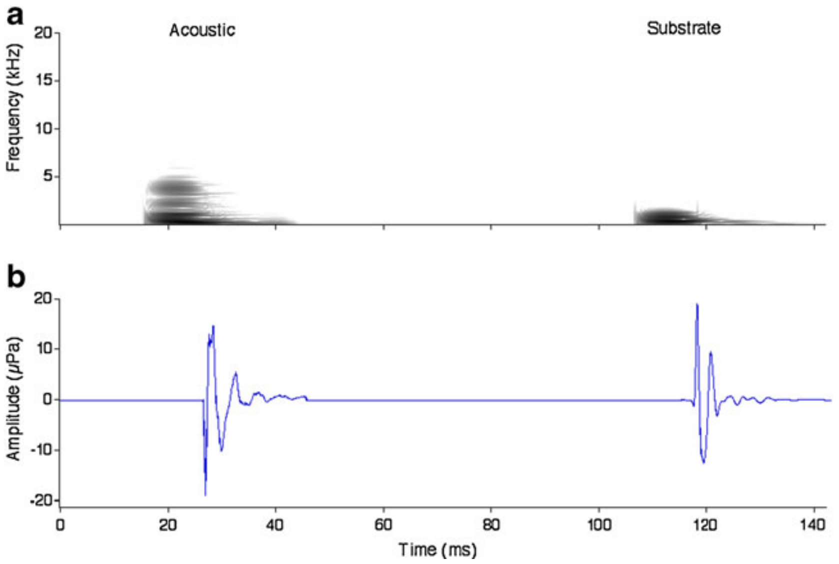

Fig. 1 **a** Spectrogram and **b** waveform of the acoustic and seismic recordings of fruit dropping

Table 1 Tobit regression analysis table

		Coefficient	SE	*P* value
Treatment	Multimodal	10.503	3.720	0.006
	Seismic	2.993	3.268	0.362
	Sound	−2.635	2.813	0.351
	Control	0.000		
Site	Site 2	−59.073	20.763	0.005
	Site 1	0.000		
Site × treatment	Multimodal	−14.855	4.756	0.002
	Seismic	−7.516	4.953	0.132
	Sound	0.112	4.293	0.979
	Control	0.000		
Temperature	Site 2	−1.080	0.587	0.068
	Site 1	0.000		
Temp × site	Site 2	2.421	0.866	0.006
	Site 1	0.000		
Time	Site 2	0.303	9.789	0.975
	Site 1	0.000		
Time × site	Site 2	−3.408	17.565	0.846
	Site 1	0.000		
Constant		40.722	15.236	0.009

of the PVC arm. By pulling the string, we were able to drop the fruit from the cup 25 cm away from a burrow.

The acoustic stimuli were audio playbacks of the sound of dropped fruit (Fig. 1) 25 cm away from the microphone (AT835b, Audio-Technical U.S. Inc., Stow, OH, USA) connected to a direct disk digital recorder (Marantz PMD670, Marantz America, Inc. Mahwah, NJ, USA). The playbacks were edited and normalized on Sound Edit 16 version 2. The sounds were played using an iPod (iPod Classic 60 GB, Apple, Cupertino, CA, USA) connected to an iPal speaker (Tivoli Audio, LLC, Cambridge, MA, USA). Using a sound meter (840029, Sper Scientific Ltd., Scottsdale, AZ, USA) set to weighting A, fast response and held 25 cm away from the speaker, we calibrated the setup to play each of the hog plum recordings at approximately 75±1 dB SPL. The speaker was elevated 0.3 m from the ground using a Bushnell tripod insulted with foam to eliminate substrate vibration during playbacks. After the treatment was set up 25 cm away from the targeted burrow, we stood approximately 8 m away from the burrow and waited for 5.5 min before playing the stimulus.

The seismic stimuli (Fig. 1) were geophone (GS-30CT with Marsh Case, Oyo Geospace Technologies, Houston, TX, USA) recordings of dropped fruit from 25 cm away. These seismic recordings were edited and normalized on Sound Edit 16. The speaker and iPod were again calibrated to play the recording at 75±1 dB SPL. After we flushed the crab, we used a shovel to dig a small depression 25 cm from the burrow entrance to fit the speaker, enclosed in a gallon-sized Ziploc bag, facing down into the substrate. To reduce acoustic transmission during playback, we covered the speaker with a bag of sand. A bin filled with insulation was then placed over the bag of sand. Once again, we stood 8 m away from the burrow and waited 5.5 min before playing the stimulus.

The control treatment, silence, used the same initial setup as the acoustic treatment but no stimulus was played. Strictly, this control does not replicate the digging associated with the seismic stimulus, but does control for the presence of humans and flushing the crabs into their burrows.

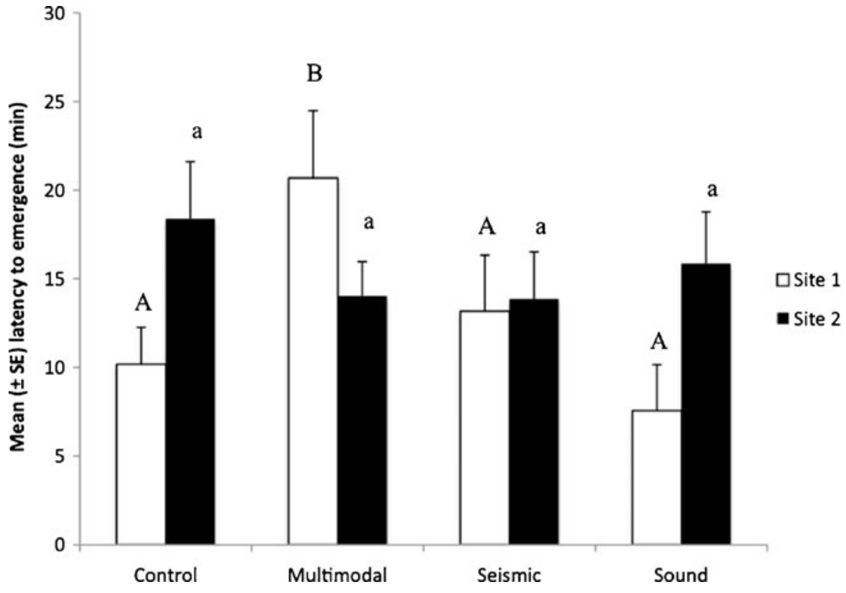

Fig. 2 Mean (±SE) latency to emergence for each of the four treatments (control, multimodal, seismic, and sound) at both sites. Significant differences between treatments are illustrated with *letters*; *capital letters* are used to compare site 1 only and *lowercase letters* are used for site 2 only

Quantifying substrate transmissions

We measured seismic attenuation at each site using the geophone and sound recorder, placing the geophone at 25 cm intervals (25 cm–1 m) away from the experimental setup used in treatment 3. This was repeated ten times per site. The recordings were edited using Sound Edit. The root mean square (RMS) pressures were measured using Canary 1.2.4 (Cornell Lab of Ornithology, Ithica, NY, USA) and compared using an ANOVA in Statview 5.01 (Abacus Concepts, Berkeley, CA, USA).

Statistical analysis

We fitted a Tobit regression analysis (McDonald and Moffitt 1980; Amemiya 1984)—a within subjects survival analysis—to analyze our data. The Tobit analysis was used because it could account for crabs that did not emerge before the cutoff by allowing us to censure the data at 30 min. The analysis was done in Stata 11 (Stata Corp LP, College Station, TX, USA) because it has a cluster option that can handle the repeated data for each crab. The Tobit used the latency from the stimulus until emergence as the dependent variable with treatment and site as independent variables and temperature and time of day as covariates. Following the Tobit regression, we tested for treatment differences using simple main effects tests and pairwise comparisons. We interpreted *P* values less than 0.05 as significant.

Results

Our prediction was not supported after studying a total of 34 different individual crabs (16 at site 1; 18 at site 2). Each crab experienced the four treatments. In 23 of 136 cases, the crabs failed to emerge from their burrows within 30 min—six for the control, five for acoustic and seismic stimuli, and seven for the fruit drop. The Tobit regression analysis showed that there were significant effects within the model ($P=0.002$, pseudo $R^2=0.019$, Table 1), but, contrary to our prediction, none of the presented stimuli from either site caused earlier emergence times than our control. Crabs took longest to emerge following the multimodal fruit drop ($P=0.006$). There was a significant site effect ($P=0.005$); the crabs emerged more quickly at site 2. There also was a significant interaction with the crabs emerging slower in response to the multimodal fruit drop at site 1 when compared to site 2 ($P=0.002$, Fig. 2). At site 2, there were no differences in emergence time as a function of stimulus presented ($P=0.465$). At site 1, multimodal took longer than all other treatments (multimodal/control $P=0.005$, multimodal/seismic $P=0.027$, and multimodal/sound $P=0.001$) and there was no significant difference between the time to emerge following the seismic and sound treatments ($P=0.069$). *P* values for all other site 1 pairwise comparisons were >0.3. Temperature had no effect on the crabs ($P=0.068$), but there was a significant interaction between temperature and site ($P=0.006$). As it got warmer at site 2, the crabs stayed in their burrows longer than the crabs at site 1 (Fig. 3). There was no effect of time of day ($P=0.975$), as well as no interaction between time of day and site ($P=0.846$).

There were significant main effects of both site and distance from the geophone in the RMS amplitude (site $P=0.026$, distance $P=0.031$), but no significant interaction between the two ($P=0.665$). Site 1 attenuated the seismic vibration more than site 2 (Fig. 4).

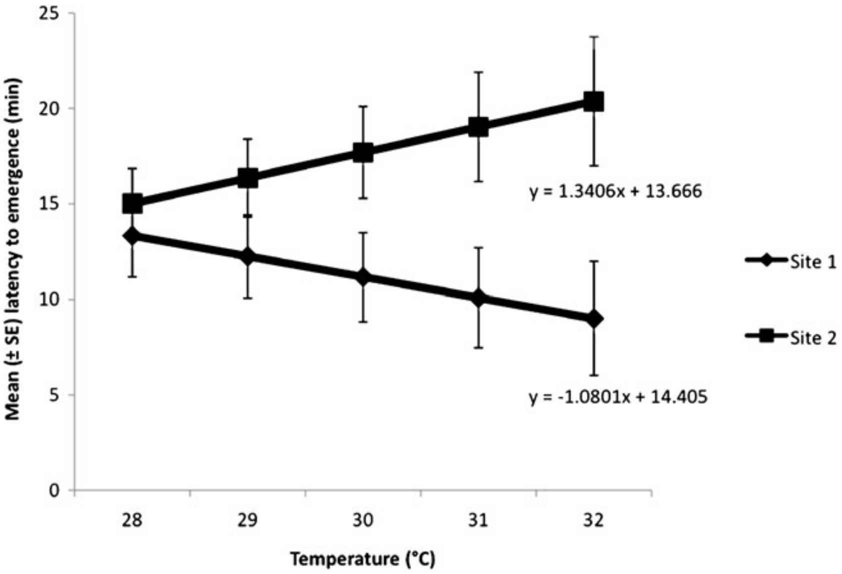

Fig. 3 The effect of mean (±SE) temperature on hiding time by site

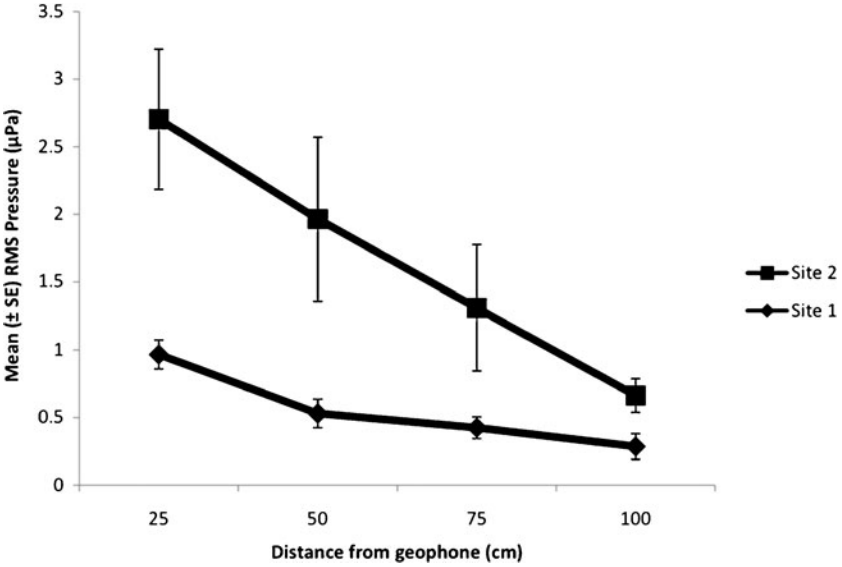

Fig. 4 Mean (±SE) substrate transmitted RMS pressure as a function of distance from speaker at the two sites

Discussion

Although studies have shown that some animals can use acoustic and seismic cues to detect food (Barrett-Lennard et al. 1996; Narins and Willi 2007; Payne 1971; Roche et al. 1999; Schnitzler et al. 2003; Siemers et al. 2001), our results suggest that blue land crabs are neither attracted to the sound nor the substrate-born vibration associated with falling fruit. Interestingly, these results failed to replicate a previous study (Herreid 1963), even though blue land crabs take fallen fruit into their burrows (Wolcott and Wolcott 1987). Herreid observed that *C. guanhumi* in the U.S. Plant Introduction Station in southern Florida emerged from their burrows from the sound of falling fruit and leaves hitting the ground. Furthermore, the ground vibrations from throwing small pebbles on the ground elicited the same behavior (Herreid 1963). Large populations of land crabs burrowed under *Fiscus* trees and Florida holly trees, *Schinus terebinthifolius*, but crabs at this location ate plant material from 35 different families of plants (Herreid 1963).

This failure to replicate may have been from the equipment used and the presence of observers. Also, the hog plum trees were not immediately above the crab burrows, and while both study sites had many trees, none were fruiting at the time of our study. Thus, at this time of year, it is possible that crabs were primed or had learned that vibrations do not signal food. Indeed, the multimodal stimulus led to an enhanced hiding; a finding more consistent with fear than food.

However, there was some spatial heterogeneity in crab response. There was a significant interaction between site and multimodal fruit presentation. While emergence times at site 2 were not influenced by treatment, at site 1, crabs responded much more slowly to substrate vibrations caused by the fruit drop. There were differences in habitat and substrate between the two sites that could account for this heterogeneity. The site 1 substrate was dryer and contained many smaller rocks while site 2 was muddier. Seismic signals were more attenuated in the site 1 substrate. This difference in seismic signal attenuation could account for the differences in the crabs' response to seismic signals. The quicker attenuation at site 1 could have caused the crabs to not receive the signal and thus have no extra motivation to emerge faster. The crabs not only may have not received the signal, but been more scared by the experimental setups for both the fruit drop (longer periods of movement around the burrow as we set up) and the seismic treatment (digging above the burrow, which could have created similar stimuli to those produced during predatory attacks).

We also noted a difference in how the crabs responded to ambient temperature. At site 2, the crabs became less active as temperature increased and latency to emerge increased. At site 1, this trend was reversed. Latency was decreased as temperature increased, indicating the crabs were more active when it was hotter. Quantitatively, this is what we observed in the field but this was not our impression because very few crabs were out of their burrows as the day got hotter. Regardless, temperature was not confounding and was controlled for in our analysis.

More generally, these results suggest that more attention should be played to the role of environmental or seasonal heterogeneity in determining which of several modalities animals may use when assessing biologically meaningful stimuli. If the signal value of certain stimuli varies seasonally, animals' responses should vary seasonally as well. Since animals spend much of their time foraging for food, it is expected that learning throughout their lifetimes would significantly influence their foraging behavior (Shettleworth 2001). Future work will be required to properly test whether or not land crab food detection varies seasonally with fruiting trees.

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References

Acquistapace P, Aquiloni L, Hazlett BA, Gherard F (2002) Multimodal communication in crayfish: sex recognition during mate search by male *Austropotamobius pallipes*. Can J Zool 80:2041–2045

Amemiya T (1984) Tobit models: a survey. J Econ 24:3–61

Barrett-Lennard LG, Ford JKB, Heise KA (1996) The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. Anim Behav 51:553–565

Caro T (2005) Antipredator defenses in birds and mammals. University of Chicago Press, Chicago

Evans TA, Lai JCS, Toledano E, McDowall L, Rakotonarivo S, Lenz M (2005) Termites assess wood size by using vibration signals. Proc Natl Acad Sci U S A 102:3732–3737

Fenton MB, Bell GP (1979) Echolocation and feeding behaviour in four species of *Myotis* (Chiroptera). Can J Zool 57:1271–1277

Gerhardt HC, Huber F (2002) Acoustic communication in insects and anurans: common problems and diverse solutions. University of Chicago Press, Chicago

Gherardi F, Tiedemann J (2004) Chemical cues and binary individual recognition in the hermit crab *Pagurus longicarpus*. J Zool 263:23–29

Goyret J, Markwell PM, Raguso RA (2007) The effect of decoupling olfactory and visual stimuli on the foraging behavior of *Manduca sexta*. J Exp Biol 210:1398–1405

Hahn TR, Thomas G (2009) Passive acoustic detection of schools of herring. J Acoust Soc Am 125:2896–2908

Hazlett BA, McLay C (2000) Contingencies in the behaviour of the crab *Heterozius rotundifrons*. Anim Behav 59:965–974

Hebets EA, Papaj DR (2005) Complex signal function: developing a framework of testable hypotheses. Behav Ecol Sociobiol 57:197–214

Herreid CF (1963) Observations on the feeding behavior of *Cardisoma guanhumi* (Latreille) in Southern Florida. Crustaceana 5:176–180

Hill K (2001) Species account: *Cardisoma guanhumi*. www.sms.si.edu/irlspec/cardis_guanhu.htm

Hölldobler B (1999) Multimodal signals in ant communication. J Comp Physiol [A] 184:129–141

McDonald JF, Moffitt RA (1980) The uses of tobit analysis. Rev Econ Stat 62:318–321

Narins PM, Willi UB (2007) Mostly malleus: ground sound detection by the remarkable ear of the golden mole. Abstract: 19th International Congress on Acoustics, Madrid, 2–7 September 2007

Neuweiler G (1990) Auditory adaptations for prey capture in echolocating bats. Physiol Rev 70:615–641

Partan SR, Marler P (2005) Issues in the classification of multimodal communication signals. Am Nat 166:231–245

Payne RS (1971) Acoustic location of prey by barn owl (*Tyto alba*). J Exp Biol 54:535

Roche BE, Schulte-Hostedde AI, Brooks RJ (1999) Route choice by deer mice (*Peromyscus maniculatus*): reducing the risk of auditory detection by predators. Am Midl Nat 142:194

Rybak F, Sureau G, Aubin T (2002) Functional coupling of acoustic and chemical signals in the courtship behavior of the male *Drosophila melanogaster*. Proc R Soc Lond B Biol Sci 269:695–701

Schnitzler H, Moss CF, Denzinger A (2003) From spatial orientation to food acquisition in echolocating bats. Trends Ecol Evol 18:386–394

Shettleworth SJ (2001) Animal cognition and animal behaviour. Anim Behav 61:277–286

Siemers BM, Swift SM (2006) Differences in sensory ecology contribute to resource partitioning in the bats *Myotis bechsteinii* and *Myotis nattereri* (Chiroptera: Vespertilionidae). Behav Ecol Sociobiol 59:373–380

Siemers BM, Stilz P, Schnitzler H (2001) The acoustic advantage of hunting at low heights above water: behavioural experiments on the European trawling' bats *Myotis capaccinii.*, *M. dasycneme* and *M. daubentonii*. J Exp Biol 204:3843–3854

Siemers BM, Goerlitz HR, Robsomanitrandrasana E, Piep M, Ramanamanjato J, Rokotondravony D, Ramilijaona O, Ganzhorn JU (2007) Sensory basis of food detection in wild *Microcebus murinus*. Int J Primatol 28:291–304

Uetz GW, Roberts JA, Taylor PW (2009) Multimodal communication and mate choice in wolf spiders: female response to multimodal versus unimodal signs. Anim Behav 78:299–305

Wolcott DL, Wolcott TG (1987) Nitrogen limitation in the herbivorous land crab *Cardisoma guanhumi*. Physiol Zool 60:262–268