STATEMENT OF RESEARCH ACTIVITIES
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The diversity of animal life on our planet is absolutely astounding and my research is driven by a fundamental interest in understanding how this diversity arose and how it currently functions. In particular, I am captivated by the variety of often spectacular ways in which animals communicate with each other – frequently incorporating specialized structures, colors, and patterns into intricate dynamic movement displays. Similarly, I am fascinated with the diverse means by which animals acquire and use information from their environment – often exploiting highly specialized sensory structures and associated central processing systems. Following from these central interests, **my research programs can be generally arranged according to two main themes: (i) evolution and function of complex communication and (ii) specialized sensory systems and behavior.**

All of my research projects, as well as those of all of my students, use arachnids as focal taxa. Arachnid diversity is quite spectacular (>40,000 species of spiders alone and the Order Araneae is only one of eleven extant arachnid orders), yet this major group of arthropods is extremely understudied, especially compared to their six-legged relatives - the insects. A focus on arachnids not only allows me to pursue the breadth (and depth) of conceptual topics that interest me (complex communication and specialized sensory systems and behavior), but allows me to simultaneously contribute basic natural history and fundamental knowledge to an understudied animal group, thus opening up the very real possibilities of new discovery [*e.g.,* underwater respiration in an amblypygid (Hebets & Chapman 2000b); spontaneous male death in the dark fishing spider (Schwartz *et al.* 2013; Schwartz *et al.* 2014)]. Below I will provide more detail concerning my major research areas.

PAST, CURRENT, AND FUTURE RESEARCH

I. Evolution and Function of Complex Signaling

Overview & Past Research - My research on complex signaling, or complex communication, broadly focuses on understanding the evolution, function, and ultimately diversification of elaborate animal displays. This topic encompasses fundamental queries into *why* animals communicate, *what* constitutes their communication displays, and *how* a display's constituent parts function to ultimately achieve an appropriate response in its intended receiver. Numerous sources of selection can independently and/or interactively influence the evolution of animal displays and as such, answering these questions requires a diversity of approaches and techniques. My research on this topic thus encompasses a multitude of focused studies addressing: transmission efficacies of display components (e.g., Hebets *et al.* 2008a; Elias *et al.* 2010; Elias & Mason 2011); receiver responses to isolated and combined display components (e.g., Hebets & Uetz 1999, 2000; Elias *et al.* 2006; Hebets *et al.* 2006; Rundus *et al.* 2010; Hebets *et al.* 2011; Rundus *et al.* 2011; Hebets *et al.* 2013); relationships between signaler quality and signal form (e.g., Hebets *et al.* 2008b; Shamble *et al.* 2009; Wilgers *et al.* 2009; Rundus *et al.* 2010; Rundus *et al.* 2011; Rosenthal & Hebets 2012; Wilgers & Hebets 2012a); and variability in signalers and receivers (e.g., Hebets 2003; Hebets & Maddison 2005; Hebets 2007; Hebets & Vink 2007; Hebets *et al.* 2008b; Hebets & Sullivan-Beckers 2010; Rundus *et al.* 2011; Sullivan-Beckers & Hebets 2011; Wilgers & Hebets 2012a; Sullivan-Beckers & Hebets 2014) (among others). Most of this work uses the North American wolf spider genus *Schizocosa* as my focal taxa and this work has been funded predominantly through a CAREER grant from the National Science Foundation.

My most significant contributions to the field of animal communication could be argued to be my conceptual contributions, beginning with the framework of functional hypotheses of complex signaling that I developed during my PhD and post-doctoral fellowship (Hebets & Papaj 2005). In this framework, I highlight two approaches to understanding complex signal function, each of which had previously been predominantly studied independently: a content-based approach which explores the information content of signals, and an efficacy-based approach which explores how the signaling environment as well as the receiver's sensory perception and processing influence signal transmission and/or reception (Hebets & Papaj 2005). Importantly, I highlighted the potential for components of complex displays to interact and my empirical work on wolf spiders provides some of the best examples of such inter-signal interactions (e.g., Hebets 2005; Hebets *et al.* 2011; Wilgers & Hebets 2012b; Stafstrom & Hebets 2013). My work has continued to lead the field of complex/multimodal signaling as I have both edited and contributed to two special journal volumes on complex signaling [*Current Zoology* 2011 Special Issue: Complex signaling (Hebets 2011; Wilgers & Hebets 2011) and *Behavioral Ecology and Sociobiology* 2013 Special Issue: Multimodal Signaling, co-edited (Hebets *et al.* 2013; Higham & Hebets 2013)]. Importantly, my work has also shown that there is a tremendous amount of variability among receivers in their response to signal components. For example, in multiple species we have demonstrated that females only attend to visual courtship components in the presence of vibratory components (Hebets 2005; Wilgers & Hebets 2012b; Stafstrom & Hebets 2013) or that foreleg ornamentation can ease a male's reliance on courtship vigor for mating success (Hebets *et al.* 2011). Finally, recent work from my lab highlights the interactive nature of male-female reproductive encounters and demonstrates that males can attend to female feedback cues and those that adjust their behavior accordingly receive significant payoffs in terms of increased mating success as well as decreased likelihood of being attacked (Sullivan-Beckers & Hebets 2011; Sullivan-Beckers & Hebets 2014).

Current & Future Research - Understanding the evolution and function of complex traits continues to be a major goal of scientists across disparate disciplines. Courtship displays exemplify evolutionary complexity, as many species incorporate distinct, yet interconnected components between different sensory modalities (*e.g.,* visual/ acoustic). Despite significant progress in characterizing such multimodal communication across diverse taxa, the field of complex animal signaling has become largely descriptive. My current research aims to advance multimodal signaling research by incorporating new quantitative analytical techniques into comparative analyses to test hypotheses regarding the origin and ultimate function of complex signaling. Comparative studies offer unique opportunities to (i) study correlated traits within and across closely related species, enabling specific tests of complex signal form/function; (ii) initiate novel, testable, hypotheses of sensory system integration and processing; (iii) explore the relative roles of natural vs. sexual selection in complex signal evolution; and innovatively, (iv) examine patterns of multimodal signal evolution (*e.g.*, variance/covariance between modality-specific signal components), which will facilitate discovery of the process(es) by which species come to rely on multiple signaling modalities.

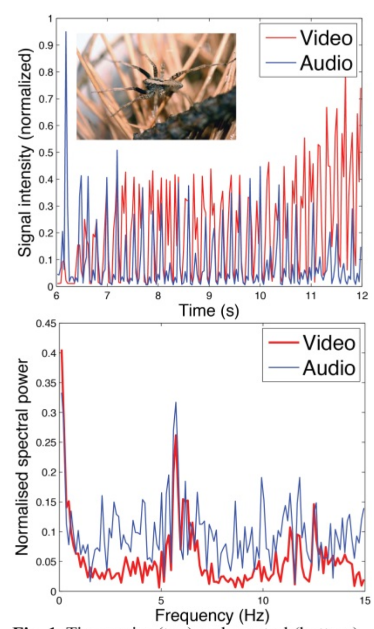

Fig. 1. Time series (top) and spectral (bottom) representation of visual and vibratory signaling in *S. retrorsa*.

Schizocosa wolf spiders are uniquely poised to advance multimodal signaling research. Among the 23 described North American species, tremendous variation exists in both visual and vibratory signal form.

More than 30 years of research, encompassing studies of ~13 focal species, provides a phenomenal foundation of behavioral data upon which to build. My current goals are to first test hypotheses of multimodal signal function across ~19 *Schizocosa* species using (a) newly developed techniques to quantify and analyze multimodal signal form (*e.g.* dependence/independence of modality specific signals), both at the individual- and species-level (Fig. 1); (b) field measurements of modality-specific signal range, and (c) experimental assays of receiver response range. Next, in collaboration with Dr. Jason Bond at Auburn University, we are leveraging modern phylogenomic approaches to generate a robust phylogenetic framework incorporating all North American species. Despite the prominence of *Schizocosa* as a model for studying behavioral evolution, the group lacks a robust phylogenetic hypothesis. Stratton's (2005) morphology-based hypothesis and a single gene (mtDNA COI) molecular phylogeny (Hebets & Vink 2007) failed to resolve relationships among morphologically indistinct populations that are reproductively isolated, and failed to recover well established species as reciprocally monophyletic. We have already begun to infer *Schizocosa* phylogeny using a genomics-based approach employing next generation sequencing technologies. To date we have sequenced the transcriptomes of 15 *Schizocosa* species (Fig. 2) and results indicate a number of potential unrecognized taxa, making this project event more compelling.

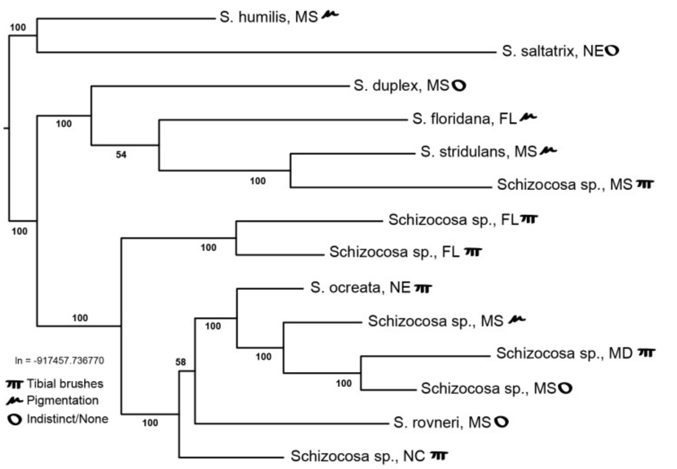

Fig. 2. RAxML maximum likelihood rapid bootstrap analysis of ~433,000 nucleotides usingGTRGAMMA. Numbers at nodes are bootstrap values; terminal labels = species, locality (state), and male ornamentation. Branch lenghts are not to scale.

Upon completion of a robust phylogenetic hypothesis, we aim to independently examine the evolutionary patterns of vibratory, visual, and multimodal (vibratory + visual) signal components. We will characterize signal complexity within and between sensory modalities and examine patterns of complex signal evolution. Combined, our data will enable us to answer such questions as: How has phylogenetic history facilitated and/or constrained multimodal signal evolution? What can the patterns of variance/covariance between signaling modalities tell us about selection for complex traits (*e.g.* do particular components always co-vary)? Does multimodal signaling facilitate/constrain species divergence?

In addition to empirical advances and approaches to studying complex signaling, I am currently collaborating with Dr. Andy Barron (Macquarie University) and Dr. Mark Hauber (Hunter College) on a new conceptual framework for complex signaling. We are proposing a systems approach to animal signaling that highlights the constraining nature, and misuse, of the concepts of signal redundancy/non-redundancy that are currently prevalent in multimodal signaling literature (Partan & Marler 1999; Partan & Marler 2005). This novel framework will help to bring animal signaling research into the 21st century along with fields exploring the evolution and function of complex cell and genomic signaling systems. A systems approach first (i) considers the functions of complex display components within a system in terms of the full range of possible response to each element in different contexts and states of the system and then (ii) considers how these elements can interact. We expect that this new systems approach to animal signaling will give new life, new directions, and new insights to the field of animal communication.

II. Specialized Sensory Systems and Behavior

Overview & Past Research – Arachnids offer unparalleled opportunities for studying the relationships between specialized sensory structures and behavior, as particular arachnid orders possess distinct sensory structures (*e.g.,* pectines of scorpions, malleoli of solifugids) with little known about their relationship to the animal's behavior. My research in this area has thus far focused mostly on the arachnid Order Amblypygi; an order which contains ~150 species, distributed worldwide in the tropics and subtropics. Amblypygids are strictly nocturnal and during daylight individuals hide in tree crevices, rocky outcrops or in burrows abandoned by small mammals. Their dorso-ventrally flattened bodies, raptorial pedipalps and their unique, elongated antenniform first pair of legs distinguish them from other arachnids (Fig. 3).

I have contributed to several of the recent overviews of amblypygid natural history and sensory biology (Foelix & Hebets 2001; Santer & Hebets 2011b). Amblypygids, like insects, walk on six legs. Their antenniform legs function solely in a sensory capacity. These legs are highly articulated and covered with thousands of sensory hairs that have mechanosensory, contact chemosensory and olfactory functions (reviewed in Santer and Hebets, 2011b). While common in other arthropods, olfactory sensilla are rare in arachnids and my prior work using electrophysiology confirmed an olfactory capacity of amblypygid antenniform legs (Hebets & Chapman 2000a). Amblypygid antenniform legs also possess giant interneurons of mostly unknown function and my prior work has explored the potential function of these giant interneurons. To date we have established that the giant interneurons are not associated with prey capture (Santer & Hebets 2009a), yet we have evidence suggesting that they may be involved in the probing phase of male-male interactions (Santer & Hebets, in prep). We have also demonstrated that amblypygids are capable of tactile learning and we suggest that these animals may provide ideal organisms for studies exploring neural coding (Santer & Hebets 2009b).

Fig. 3. *Phrynus neoparvulus* in the field. (*a*) points to an 18 cm long antenniform leg. (*p*) points to a spiny, raptorial pedipalp. (*t*) points to a radio transmitter, used to successfully track the movements of displaced individuals in the field.

Additional research in my laboratory, using both high speed cinematography and electrophysiology, has discovered that amblypygids use near-field sound to communicate during agonistic male-male interactions (Santer & Hebets 2008). Individuals generate this particle displacement using a leg vibration display involving their antenniform legs. The opponent receives this signal with long sensory hairs termed 'trichobothria', or filiform hairs, located on the patella of their walking legs. Trichobothria ablation studies have verified that in the absence of these sensory structures, antenniform leg vibrations no longer predict contest outcome (Santer & Hebets, 2011a). Taken together, our research was the first to confirm a communication function of filiform hairs in any arthropod (Santer & Hebets 2008, 2011a). Much of my prior amblypygid research was funded through grants from the Organization for Tropical Studies (OTS) as well as a Searle Scholars Fellowship.

The unique antenniform legs and olfactory sensilla of amblypygids are associated neuroanatomically with mushroom bodies (MB) that are (relative to their body size) putatively the *largest* of all arthropods (Fig. 4). MB are higher brain centers found in the first brain segment (protocerebrum) of all arthropods and their common ancestors. In insects, MB are known to be involved in contextual information processing, learning, and memory, particularly associated with odors - functions that are likely essential for successful navigation. A mark recapture study that I conducted in the lowland tropical forest of Costa Rica found that the amblypygid *Phrynus pseudoparvulus* can travel far distances and may possess territories that encompass multiple large rainforest trees (Hebets 2002). I hypothesized that amblypygids engage in complex navigational feats and indeed, the results of field-based displacement studies that incorporated radio telemetry verified that *P. pseudoparvulus* can successfully navigate home following displacements of more than 10m and that they often take indirect paths to return to their home trees (Hebets *et al.* 2014). Subsequent studies preliminarily explored the potential role of both olfaction and vision in nocturnal amblypygid homing. Using sensory-manipulated individuals (olfactory and visual occlusions) in field displacement experiments we found that *P. pseudoparvulus* appears to rely upon olfactory input, and to a lesser degree visual input, for successful nocturnal homing (Hebets et al., *in press*). These studies firmly establish the potential for multisensory input in natural navigation behavior.

Current & Future Research - Our working knowledge of the relationship between brain structures, sensory integration, and complex behavior is surprisingly limited. Navigation, as a behavioral/experimental context, is particularly intriguing as it is arguably a tangible manifestation of higher cognitive abilities – making it especially appropriate for broad studies aimed at understanding the neural substrates of complex behavior. Traditionally, navigation research has focused on a small subset of taxa, with modality-specific approaches used to determine sensory system reliance during navigation. While such single-taxon/single-modality research has been crucial for advancing our understanding of navigation, transformational advancements now necessitate the integrated investigation of multimodality, complex navigation and neural substrates.

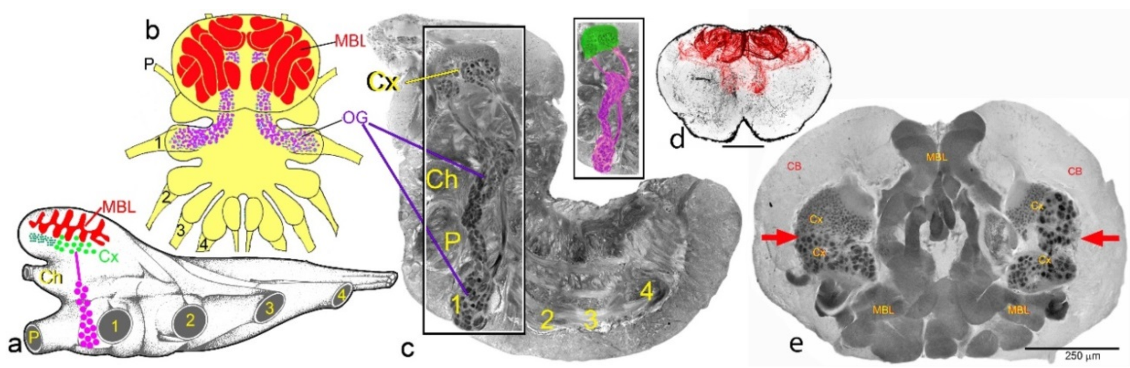

Fig. 4. Amblypygid central nervous system: (**a**) diagram lateral view; (**b**) diagram dorsal view (after Strausfeld et al. 1998); (**c**) osmium-stained section, lateral view (*inset*: olfactory glomeruli (purple) and calyx (green) color-coded); (**d**) Golgi-stained brain, Kenyon cells forming MB lobes rendered in red; (**e**) brain, osmium-stained horizontal section, arrows point et calyx (Cx). CB cell bodies; Ch cheliceral ganglion; MBL - mushroom body lobes; OG olfactory glomeruli; P pedipalpal ganglion; numbers - leg neuromeres 1-4; leg 1 (antenniform leg) gives rise to olfactory glomeruli.

In collaboration with colleagues at Bowling Greene State University (V. Bingman & D. Wiegmann) and the University of Arizona (W. Gronenberg), we are implementing a cross-disciplinary study of the role of multisensory input during nocturnal, 3-dimensional navigation in amblypygids. Prior work suggests that amblypygids rely on multisensory input for nocturnal navigation (Hebets *et al.* 2014) and we propose that these multisensory inputs converge in a central integration center – the mushroom bodies. Our current research aims to test the hypothesis that nocturnal navigation in the amblypygids *Phrynus pseudoparvulus* is enabled by multimodal sensory cues *and* their neuronal convergence in a central integration center. The most likely site of this neuronal convergence is the paired arthropod brain structure called the *mushroom body*. To test this hypothesis, we have three major aims. Using quantitative behavioral analyses, our first aim is to conduct controlled laboratory assays of navigation using a combinatorial design incorporating visual, mechanoreceptive (*i.e.* tactile), and chemosensory (*i.e.,* olfactory) stimuli. Individuals will be challenged with navigational tasks in environments providing specific combinations of sensory stimuli. Next, we will examine the projections from the peripheral sensory system to central brain regions, specifically testing the hypothesis that the subdivisions of the particularly large amblypygid mushroom body (MB) receive convergent, multisensory input. Finally, we will directly test the role of the MB in complex navigation and higher-order learning tasks by comparing the performance of MB-ablated and MB-intact amblypygids during navigational and higher-order learning challenges. Preliminary histology work has confirmed the highly elaborate amblypygid olfactory glomeruli and has uniquely identified two distinct calyces in the mushroom bodies (Fig. 4). The field portion of our amblypygid navigation research is currently funded through a National Geographic grant while the above-highlighted aims are part of an invited full NSF proposal currently under review.

STUDENT RESEARCH PROJECTS

Current research projects in my laboratory include: the evolution and function of sexual size dimorphism in crab spiders (PhD student – Marie-Claire Chelini), sensory system trade-offs in the net-casting spider (PhD student – Jay Stafstrom), variation in female mate choice and its associated fitness benefits in wolf spiders (PhD student – Malcolm Rosenthal; (Rosenthal & Hebets 2012)), sexual conflict in a fishing spider (PhD student – Alissa Anderson), vibratory signal form and function in a wolf spider (PhD student – Elise Knowlton), mechanisms of sperm activation in spiders (undergraduate – Rachael Schmidt), and a characterization of sexual dichromatism in *Schizocosa* wolf spiders (undergraduate – Alex Hansen).

Additionally, a past PhD student, Dr. Steven Schwartz, discovered an unusual mating system in a sexual dimorphic local fishing spider, *Dolomedes tenebrosus*. Male *D. tenebrosus* spontaneously die upon transferring sperm to a female and females always, when given the chance, eat their dying partners (Schwartz *et al.* 2013; Schwartz *et al.* 2014). In collaboration with Steve and a colleague in Germany, Dr. Peter Michalik, we have begun to explore the details of this terminal mating strategy, including a test of the permanent sperm depletion hypothesis. We plan to pursue this system further in a comparative context to test hypotheses regarding the evolutionary causes and consequences of sexual size dimorphism, terminal investment strategies, and male-bias operational sex ratios.

LITERATURE CITED

Elias, D.O., Hebets, E.A. & Hoy, R.R. (2006). Female preference for complex/novel signals in a spider. *Behav. Ecol.*, 17, 765-771.

Elias, D.O. & Mason, A.C. (2011). Signaling in variable environments: Substrate-borne signaling mecahnisms and communication behaviour in spiders. In: *The use of vibrations in communication: properties, mechanisms, and function across taxa* (ed. O'Connell-Rodwell, CE). Transworld Research Network Kerala, India.

Elias, D.O., Mason, A.C. & Hebets, E.A. (2010). A signal-substrate match in the substrate-borne component of a multimodal courtship display. *Current Zoology*, 56, 370-378.

Foelix, R. & Hebets, E.A. (2001). Sensory biology of whip spiders (Arachnida, Amblypygi. *Andrias*, 15, 129-140.

Hebets, E.-A. (2002). Relating the unique sensory system of amblypygids to the ecology and behavior of Phrynus parvulus from Costa Rica (Arachnida, Amblypygi). *Can. J. Zool.-Rev. Can. Zool.*

Hebets, E.A. (2003). Subadult experience influences adult mate choice in an arthropod: Exposed female wolf spiders prefer males of a familiar phenotype. *Proc. Natl. Acad. Sci. U. S. A.*, 100, 13390-13395.

Hebets, E.A. (2005). Attention-altering signal interactions in the multimodal courtship display of the wolf spider Schizocosa uetzi. *Behav. Ecol.*, 16, 75-82.

Hebets, E.A. (2007). Subadult female experience does not influence species recognition in the wolf spider Schizocosa uetzi Stratton 1997. *J. Arachnol.*, 35, 1-10.

Hebets, E.A. (2011). Current status and future directions of research in complex signaling. *Current Zoology*, 57, i-v.

Hebets, E.A. & Chapman, R.F. (2000a). Electrophysiological studies of olfaction in the whip spider Phrynus parvulus (Arachnida, Amblypygi). *Journal of Insect Physiology*, 46, 1441-1448.

Hebets, E.A. & Chapman, R.F. (2000b). Surviving the flood: plastron respiration in the non-tracheate arthropod Phrynus marginemaculatus (Amblypygi : Arachnida). *Journal of Insect Physiology*, 46, 13-19.

Hebets, E.A., Cuasay, K. & Rivlin, P.K. (2006). The role of visual ornamentation in female choice of a multimodal male courtship display. *Ethology*, 112, 1062-1070.

Hebets, E.A., Elias, D.O., Mason, A.C., Miller, G.L. & Stratton, G.E. (2008a). Substrate-dependent signalling success in the wolf spider, Schizocosa retrorsa. *Anim. Behav.*, 75, 605-615.

Hebets, E.A., Gering, E.J., Bingman, V.P. & Wiegmann, D.D. (2014). Nocturnal homing in the tropical amblypygid *Phyrnus pseudoparvulus* (Class Arachnida, Order Amblypygi). *Animal Cognition*, 17, 1013 - 1018.

Hebets, E.A. & Maddison, W.P. (2005). Xenophilic mating preferences among populations of the jumping spider *Habronattus pugillis* Griswold. *Behav. Ecol.*, 16, 981-988.

Hebets, E.A. & Papaj, D.R. (2005). Complex signal function: developing a framework of testable hypotheses. *Behav. Ecol. Sociobiol.*, 57, 197-214.

Hebets, E.A., Stafstrom, J.A., Rodriguez, R.L. & Wilgers, D.J. (2011). Enigmatic ornamentation eases male reliance on courtship performance for mating success. *Anim. Behav.*, 81, 963 - 972.

Hebets, E.A. & Sullivan-Beckers, L. (2010). Mate choice and learning. In: *Enclycopedia of Animal Behavior* (eds. Breed, MD & Moore, JA). Oxford: Academic Press, pp. 398-393.

Hebets, E.A. & Uetz, G.W. (1999). Female responses to isolated signals from multimodal male courtship displays in the wolf spider genus Schizocosa (Araneae : Lycosidae). *Anim. Behav.*, 57, 865-872.

Hebets, E.A. & Uetz, G.W. (2000). Leg ornamentation and the efficacy of courtship display in four species of wolf spider (Araneae : Lycosidae). *Behav. Ecol. Sociobiol.*, 47, 280-286.

Hebets, E.A. & Vink, C.J. (2007). Experience leads to preference: experienced females prefer brush-legged males in a population of syntopic wolf spiders. *Behav. Ecol.*, 18, 1010-1020.

Hebets, E.A., Vink, C.J., Sullivan-Beckers, L. & Rosenthal, M. (2013). The dominance of seismic signaling and selection for signal complexity in *Schizocosa* multimodal courtship displays. *Behav. Ecol. Sociobiol.*, 67, 1483 - 1498.

Hebets, E.A., Wesson, J. & Shamble, P.S. (2008b). Diet influences mate choice selectivity in adult female wolf spiders. *Anim. Behav.*, 76, 355-363.

Higham, J.P. & Hebets, E.A. (2013). An introduction to multimodal communication. *Behav. Ecol. Sociobiol.*, 67, 1381-1388.

Partan, S. & Marler, P. (1999). Behavior - Communication goes multimodal. *Science*, 283, 1272-1273.

Partan, S.R. & Marler, P. (2005). Issues in the classification of multimodal communication signals. *Am. Nat.*, 166, 231-245.

Rosenthal, M. & Hebets, E. (2012). Resource heterogeneity interacts with courtship rate to influence mating success in the wolf spier *S. floridana*. *Anim. Behav.*, 84, 1341 - 1346.

Rundus, A.S., Santer, R.D. & Hebets, E.A. (2010). Multimodal courtship efficacy of Schizocosa retrorsa wolf spiders: implications of an additional signal modality. *Behav. Ecol.*, 21, 701-707.

Rundus, A.S., Sullivan-Beckers, L., Wilgers, D.J. & Hebets, E.A. (2011). Females are choosier in the dark: environment-dependent reliance on courtship components and its impact on fitness. *Evolution*, 65, 268-282.

Santer, R.D. & Hebets, E.A. (2008). Agonistic signals received by an arthropod filiform hair allude to the prevalence of near-field sound communication. *Proceedings of the Royal Society B-Biological Sciences*, 275, 363-368.

Santer, R.D. & Hebets, E.A. (2009a). Prey capture by the whip spider Phrynus marginemaculatus CL Koch. *J. Arachnol.*, 37, 109-112.

Santer, R.D. & Hebets, E.A. (2009b). Tactile learning by a whip spider, Phrynus marginemaculatus CL Koch (Arachnida, Amblypygi). *Journal of Comparative Physiology a-Neuroethology Sensory Neural and Behavioral Physiology*, 195, 393-399.

Santer, R.D. & Hebets, E.A. (2011a). Evidence for Air Movement Signals in the Agonistic Behaviour of a Nocturnal Arachnid (Order Amblypygi). *Plos One*, 6.

Santer, R.D. & Hebets, E.A. (2011b). The Sensory and Behavioural Biology of Whip Spiders (Arachnida, Amblypygi). In: *Advances in Insect Physiology, Vol 41: Spider Physiology and Behaviour - Behaviour* (ed. Casas, J), pp. 1-64.

Schwartz, S.K., Wagner, W.E. & Hebets, E.A. (2013). Spontaneous male death and monogyny in the dark fishing spider. *Biology Letters*, 9.

Schwartz, S.K., Wagner, W.E. & Hebets, E.A. (2014). Obligate male death and sexual cannibalism in dark fishing spiders. *Anim. Behav.*, 93, 151 - 156.

Shamble, P.S., Wilgers, D.J., Swoboda, K.A. & Hebets, E.A. (2009). Courtship effort is a better predictor of mating success than ornamentation for male wolf spiders. *Behav. Ecol.*, 20, 1242-1251.

Stafstrom, J.A. & Hebets, E.A. (2013). Female mate choice for multimodal courtship and the importance of the signaling background for selection on male ornamentation. *Current Zoology*, 59, 200-209.

Sullivan-Beckers, L. & Hebets, E.A. (2011). Modality-specific experience with female feedback increases the efficacy of courtship signalling in male wolf spiders. *Anim. Behav.*, 82, 1051-1057.

Sullivan-Beckers, L. & Hebets, E.A. (2014). Tactical adjustment of signaling leads to increased mating success and survival. *Anim. Behav.*, 93, 111 - 117.

Wilgers, D.J. & Hebets, E.A. (2011). Complex courtship displays facilitate male reproductive success and plasticity in signaling across variable environments. *Current Zoology*.

Wilgers, D.J. & Hebets, E.A. (2012a). Age-related female mating decisions are condition dependent in wolf spiders. *Behav. Ecol. Sociobiol.*, 66, 29-38.

Wilgers, D.J. & Hebets, E.A. (2012b). Seismic Signaling is Crucial for Female Mate Choice in a Multimodal Signaling Wolf Spider. *Ethology*, 118, 387-397.

Wilgers, D.J., Nicholas, A.C., Reed, D.H., Stratton, G.E. & Hebets, E.A. (2009). Condition-dependent alternative mating tactics in a sexually cannibalistic wolf spider. *Behav. Ecol.*, 20, 891-900.