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SPECIALTY SECTION  
This article was submitted to  
Arachnid Ecology and Behavior,  
a section of the journal  
Frontiers in Arachnid Science

RECEIVED 14 November 2022  
ACCEPTED 05 December 2022  
PUBLISHED 22 December 2022

CITATION  
Schausberger P (2022) Grand  
challenges and bold opportunities in  
arachnid ecology and behavior.  
*Front. Arachn. Sci.* 1:1097945.  
doi: 10.3389/frchs.2022.1097945

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# Grand challenges and bold opportunities in arachnid ecology and behavior

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## KEYWORDS

arachnid, ecology, behavior, invertebrate, spider, mite, scorpion, harvestmen

## Background

The Arachnida represent a mega-diverse lineage within the Arthropoda and are the second largest (speciose) class of invertebrates (first are the insects with around 955,000 described species), with about 91,200 (<https://www.catalogueoflife.org/>) to 114,200 (Zhang, 2013) species named and described (90% of which are spiders and mites/ticks) but an estimated 1 to 1.5 million species, especially mites, waiting to be detected and named (Krantz and Walter, 2009; Walter and Proctor, 2013; Zhang, 2013). The number of currently known arachnid species is more than all vertebrates together, although the arachnid species number is just about 1/10<sup>th</sup> to 1/15<sup>th</sup> of the estimated number of species truly present, yet is in comparison close to being complete in the vertebrates (70,300 described species) (<https://www.catalogueoflife.org/>). Arachnids are similar to insects in evolutionary success and history. The fossil history of the Chelicerata, to which the Arachnida belong to, dates back to 500 million years ago. The Arachnida comprise groups, such as the Acari (mites and ticks), that are extremely diverse and can be found about anywhere in the world, from aquatic to terrestrial, from rainforests to deserts, from mountain tops to valleys, from the icy Arctic and Antarctic to burning hot deserts (Krantz and Walter, 2009; Walter and Proctor, 2013), while others are almost exclusively terrestrial but similarly diverse in habitat use, i.e. the Araneae (spiders), with just one truly aquatic species (e.g. Foelix 2010, Dimitrov and Hormiga, 2021). While the Araneae are comparatively homogenous in foraging styles – all are true predators and most are prey generalists, yet showing an impressive array of true predation styles, from ambushing to active hunting to luring and trapping – the Acari are very diverse, from strictly parasitic throughout life, to changing between parasitic and free-living, to living on the same host throughout life and over several generations, to changing hosts to being always free-living, from fungivores, detritivores to herbivores, carnivores and omnivores, from habitat and diet generalists to extreme specialists exploiting just one type of food or individual host (e.g. Walter and Proctor, 2013). Extreme diversity and variability also apply to reproductive modes, which span from sexual direct and indirect sperm transfer to asexual cloning (thelytoky). Together, the arachnids are mega-diverse in all major aspects of ecology and behavior.

The grand challenges presented here are viewed from an arachnid perspective though some are not specific to arachnids, as are some overarching questions addressed in arachnid research. The challenges and opportunities mentioned are not meant to be exhaustive, are certainly partly subjective and growing out of own current interests and

research. To provide structure and ease readability, the challenges and opportunities are categorized into conceptual, topical and operational, though some bullets could be listed under either heading because touching on elements pertaining to all of them. Ecology and Behavior are such broad fields that many issues listed in other grand challenges articles of *Frontiers in Arachnid Science* also apply to, or overlap with, the section *Arachnid Ecology and Behavior*.

The aim of this contribution is not only to highlight grand challenges but also to point at magnificent opportunities for research in ecology and behavior of mites and spiders and other arachnids. Together, the discussed issues represent an eclectic collection of what I currently consider as important concepts and exciting topics in contemporary arachnid ecology and behavior.

## Conceptual issues

(i) Understanding the principal factors that govern the occurrence, distribution and abundance of species is a fundamental challenge in arachnid ecology and behavior. Trait-based approaches, which focus on the role and relevance of measurable organismic/individual characteristics, have recently become major conceptual viewpoints to explain species, community and ecosystem patterns and processes. Identifying, describing, collecting and linking key individual-level functional traits, i.e. phenotypic traits such as physiological, morphological, behavioral and life-history characteristics that correlate with individual, population- and community-level success is a grand challenge with the ultimate reward of allowing to compare patterns and processes across taxa and ecological contexts (Zakharova et al., 2019; De Bello et al., 2021; Green et al., 2022). Within arachnid research, trait-based approaches have already taken form in the creation of a trait-database in the Araneae (Pekar et al., 2021) and similar databases are yet to be initiated for the Acari and other arachnid groups.

(ii) Linked to fostering trait-based approaches is featuring arachnids as model animals to address overarching ecological and behavioral questions. Establish, consolidate and extend the role of arachnids as model animals in research on predator-prey interactions, mating (from thelytoky to indirect sperm transfer to direct copulation) and reproduction (from pedogenesis to sexual cannibalism as fitness-maximizing reproductive strategies) to movement and dispersal, group-living, personality formation and cognition. Arachnids are very peculiar in some aspects (e.g. silk and venom production or co-evolution with hosts) but, at the same time, some arachnid species represent formidable model organisms to test broad general concepts and hypotheses. For example, arachnids feature prominently in pioneering research on extended phenotypes (e.g. Zhou et al., 2022), multi-trophic interactions (Vet and Dicke, 1992; Van Rijn et al., 2002; Heil, 2008; Dicke, 2009; Schausberger, et al., 2021a), multimodal sensory perception (e.g.

Herberstein et al., 2014; Uetz et al., 2016), or co-evolutionary arms races (Proctor, 2003; Dicke, 2009; Noel et al., 2020; Smith et al., 2022), just to mention a few. Some mites and spiders have the potential to become similarly significant models as honeybees and bumblebees are for cognition (e.g. Jakob et al., 2011; Japyassu and Laland, 2017, Cross et al., 2020; see also bullet (vi)). Mites have served for decades as one of the prime groups in multi- and tri-trophic interaction research such as the interaction between predatory mites, herbivorous mites, plants, and below- and above-ground (micro-)organisms (e.g. Vet and Dicke, 1992; Schausberger et al., 2012). The prominent role of mites in this field started with the seminal findings by Sabelis and van de Baan (1983) and Dicke and Sabelis (1988) that plants change their volatiles upon attack by herbivorous spider mites to recruit predatory mites to help the plants defend themselves against the attackers. Spiders and mites present life styles all the way from solitary to group-living; though no eusocial arachnid species is known, some have highly evolved ways of living together (such as the group-hunting *Anelosimus* – Lubin and Bilde, 2007; Avilés and Guevara, 2017- and nest-constructing and -sharing bamboo mites - see Saito, 2010 and Schausberger et al., 2021b for an overview - or aggregating harvestmen – Escalante et al., 2022). Some mite species with fast development, high reproduction and short generation times, such as two-spotted spider mites *Tetranychus urticae*, are also amenable to experimental evolution (e.g. Belliure et al., 2010; Macke et al., 2011), which parallels some insect species, such as *Drosophila melanogaster*, and is almost impossible to achieve over reasonable timescales in any of the large long-lived animals.

(iii) Adopting multi-, inter- and cross-disciplinary research approaches. Linking diverse disciplines and approaches is a grand challenge across the biological and ecological sciences. The ascent of Behavioral Ecology in recent decades (e.g. Krebs and Davies, 1978 and later editions, and other textbooks; Stuhmann, 2022) is a prime example of a relatively young discipline being highly successful, because it is multidisciplinary, combining evolution, behavior and ecology, by its very nature. Behavioral Ecology is also one of the most integrative areas of modern biology, because of uniting the study of function and mechanisms (Monaghan, 2014). Arachnids feature prominently in Behavioral Ecology, in particular in research on animal personalities (e.g. Duran et al., 2021), group-living (e.g. Avilés and Guevara, 2017, Schausberger, et al., 2021b), sexual selection (Proctor, 1998; Herberstein et al., 2014; Oku, 2014; Andrade, 2019; Peretti et al., 2021), or phenotypic plasticity (Agrawal et al., 2002, Walzer and Schausberger, 2011; Evans et al., 2019; Yip et al., 2021; Schausberger and Rendon, 2022), just to mention some areas. One of the cornerstones of Behavioral Ecology is quantifying the adaptive value of a given behavior. Many arachnids, like other small and comparatively short-lived animals, have the enormous advantage over larger long-lived ones that it is relatively easy to measure and link behavioral, life history and fitness traits, up to lifetime reproductive success. Many of those small-sized and comparatively short-lived

animals are also favorable regarding experimental replication and inter-individual variability. Laboratory or experimental populations of larger animals are often founded by one or few individuals, which compromises variability among tested individuals and with that the explanatory power and generalizability of traits measured. Though primarily concerned with questions 3 and 4, contemporary Behavioral Ecology embraces studies that implement Tinbergen's classic four approaches to studying behavior, considering both ultimate and proximate causation (Bateson and Laland, 2013).

(iv) Increasing the level of resolution in behavioral investigations, from group means to individual differences, and fostering individual-based approaches in population and community ecology. Arachnids have proven as superb animals for studying animal personalities (Réale et al., 2007) and cascading effects of personalities to higher organizational levels and interactions with other taxa (e.g. Loftus et al., 2022). In animal personality research, spiders feature similarly prominently as the much more numerous and speciose insects (search in Clarivate Analytics, Web of Science Core Collection October 30 2022, "spider" AND "personality" 232 hits, just in abstracts 80 hits; "insect" AND "personality" 210 hits, just in abstracts 76 hits) and there is more to come.

(v) Silk producing arachnids are marvelous model animals for evolutionary-grounded research into extended phenotypes (Dawkins, 1982). Web spiders (Araneae) and spider mites (Tetranychidae) have extended phenotypes through their silk threads and webs. They are constantly informed about more distant events as long as they are attached to their web for example *via* signal threads (Mortimer et al., 2015), and they can perceive changes happening in the web or on single threads *via* chemical, tactile and/or visual sensory modalities (e.g. Zhou et al., 2022). Science writer Robson (2020) has put it in flowery, albeit also provocative, words "*But we are now discovering that some arachnids possess hidden cognitive abilities rivalling those of mammals and birds, including foresight and planning, complex learning and even the capacity to be surprised. Stranger still, the delicate silk threads they spin out behind them, so easily swept up by a feather duster, help them to sense and remember their world. Indeed, spiders' silk is so important to their cognitive abilities that some scientists believe it should be considered part of their mind.*"

(vi) Extending bullets (ii), (iv) and (v) is highlighting the potential of arachnids to put vertebrate-biased (vertebrocentric) paradigms of how big a brain, or how many neurons, are needed to perform advanced cognitive tasks, and/or interpretation of mastering these tasks, to the test. Arachnids have the potential to keep up with the amazing capabilities of model insects that have, a.o., shown to master tool use (Alem et al., 2015 for bumblebees; Maak et al., 2020 for ants), flexibility in novel task solving (innovation; Loukola et al., 2017 for bumblebees), play behavior (Dona et al., 2022 for bumblebees), or teaching behavior (Coolen et al., 2005 for crickets). All these phenomena were initially thought to be only accomplishable by large brainers. Arachnid cases in point

are the amazing novel problem-solving capacities of jumping spiders *Portia* spp. (Cross et al., 2020), the orb-weaving *Cyclosa* spp. creating spider-like decoys to fool predators (Tseng and Tso, 2009; Drake, 2014) or social experience-based attentional shifts in phytoseiid predatory mites (Strodl and Schausberger, 2012). These and many other pertinent arachnid and other arthropod studies (e.g. Lihoreau et al., 2012) contribute to rethink how large a brain, or which central nervous system (CNS)/body ratio, is needed to master seemingly cognitively challenging tasks and/or to rethink interpretation of accomplishing these tasks. Due to their amenability to manipulative experimentation and the ease of linking life history and behavioral traits, arachnids are ideal models to assess the adaptive value and constitutive and operational benefit-cost trade-offs of cognitive functions such as learning (Mery and Kawecki, 2003; Mery and Kawecki, 2005). As a side note, a prominent experimental "intelligence" paradigm has recently been seriously challenged within the vertebrates, that is, the paradigm of the mirror test being suitable to provide evidence of self-awareness has been hijacked by 40 mg-brain mass cleaner fishes, *Labroides dimidiatus*, passing the mark test (Kohda et al., 2019; Kohda et al., 2022). These fishes are more than twice as large (~8 cm average body length) but inferior in CNS volume to large golden orb-weaver females *Nephila* spp. (Quesada et al., 2011).

(vii) Explaining the relevance of fundamental research to, and translating fundamental science into, applied problem-solving. By their very nature, arachnids are great animals for translational science because many arachnid species are relevant in agriculture as either pests or beneficial natural enemies or in human and veterinary medicine as parasites and vectors of diseases. Also, arachnids are a rich source, particularly because of silk and venom production, for the development of bio-inspired products (see also Kuntner, 2022). Arachnid ecology and behavior is an excellent field for translation of fundamental knowledge to help achieve sustainability goals (alleviating global hunger, warranting food security, and natural resources preservation), *via* science-based applied ecology and behavior such as for biological control of crop and livestock pests (e.g. Knapp et al., 2018) and other ecosystem services provided by mites and spiders. Providing basic ecological and behavioral knowledge about arachnid groups transmitting human diseases such as ticks can contribute to global health. The afore-mentioned trait-based approaches are relevant in these challenges by identifying characteristics of promising biocontrol agents or invasive species or pests or human followers (Pekar et al., 2021).

## Topical issues

(i) Recurrent themes across biology and ecology, and across taxa, are interpreting the causes and effects of phenotypic plasticity and sensitivity to environmental variability. Understanding the links between genotypes and phenotypes is a prime issue in biology and ecology, particularly for the evolution and

regulation of phenotypic plasticity and reaction norms, and how behavior interacts *via* feedback loops with other types of responses (e.g. Sih et al., 2015). This applies to both within- and transgenerational plasticity and their interaction (e.g. Bonduriansky and Day, 2009; Stamps and Bell, 2021; Schausberger and Rendon, 2022). Furthering our understanding of behavioral variation and how it underlies variation in ability to cope with contemporary human-induced, rapid environmental change (HIREC), and finding out how HIRECs and climate (or global) change affect the ecology and behavior of arachnids are urgent tasks. Pertinent research must be conducted in consideration of adaptability and phenotypic plasticity; pre-experimental treatments and experimental designs must be well-thought out because artificial, abrupt exposure to extreme future conditions may lead to erroneous inferences. Behavior is typically the first response when organisms are confronted by changes in the external environment, and also, *via* choice of environment, a way whereby organisms can influence their environmental factors that affect the development and expression of all their traits. Behavior thus plays a key role in shaping the development and expression of integrated responses to the environment. Investigating adaptations to urban versus natural habitats (also linked to arachnid personality research) and trade-offs in adaptation of arachnids to “novel” human-altered or human-made habitats and ecosystems are related challenges. Spider mites and other herbivorous mites are big in applied ecology, serving as model animals for the ability to respond to agricultural intensification and environmental stressors such as pesticides and resistance development (e.g. Van Leeuwen and Dermauw, 2016). Many spiders are highly sensitive indicators to any kind of human disturbance of their habitats (e.g. Mader et al., 2016).

(ii) Conservation of arachnids is an emerging grand challenge and an especially difficult task for mites for their small size and most species as yet being undetected, undescribed and unnamed (see the arachnid groups in the IUCN species survival commission: <https://www.iucn.org/our-union/commissions/group/iucn-ssc-spider-and-scorpion-specialist-group> and <https://www.iucn.org/our-union/commissions/group/iucn-ssc-mite-specialist-group>). Many mite species will go extinct before we even knew that they existed; if lucky, future researchers will then detect some of these species embedded in amber or fossilized in some other way. At which point or when to conclude that a given minute mite species is threatened or gone extinct? Clearly, conservation efforts of arachnids, and especially mites, must be heavily concerned with knowing about and defining the habitat and microhabitat characteristics that are needed by a given species or species ensemble (Ozman-Sullivan and Sullivan, 2021). Trait-based approaches (see conceptual bullet (i)) play a role here too. Disappearance or alterations of critical habitat or microhabitat or host features may then be used to make inferences to extinction risk of the species concerned. Also, the use of exotic arachnids in biological control and their possible impact on

native fauna is an issue in conservation though one should keep in mind that many agricultural and horticultural plants are of exotic origin and so are many of their pests and natural enemies. The nowadays occurrence of many of these initially exotic plant and animal species is thus in part an inevitable phenomenon of humankind since adopting agricultural habits more than 12,000 years ago. Another issue to consider in conservation are cryptic species (applies especially to the Acari), which remains a somewhat slippery concept because of confusion which species concept is applied in the determination of crypticity (Heethoff, 2018; see also Kuntner, 2022). In most cases, entities that are considered cryptic species based on molecular data have not been tested whether they also represent different species according to the biological species concept (Mayr, 1942).

(iii) Considering arachnids as holobionts with all the micro- and macro-organisms that live on and in them permanently or at least over extended periods of time (Medina et al., 2022). Mites and spiders are rich in harboring reproductive and other-function endosymbionts and other microorganisms (Goodacre, 2011; Zhu et al., 2018; Schausberger, 2018; Pelmutter and Bordenstein, 2020; Konecka, 2022). Some of these microorganisms change between individual animals within and between species and animals and plants (Staudacher et al., 2017). Microorganisms in the belowground sphere of plants may influence the plant-inhabiting arachnids aboveground (Schausberger et al., 2012); belowground microorganisms such as mycorrhizal fungi connect individual plants with each other, with their mycelia functioning as communication railroads (e.g. Song et al., 2010) and thereby creating fascinating cross-kingdom networks. Micro- and macro-symbionts and -parasites may strongly affect the phenotypes (e.g. Goodacre and Martin, 2012; Zhang et al., 2018; Durkin et al., 2021) and take some or complete control of their host behavior such as for example observed in zombie spiders that are heavily manipulated in web-spinning behavior by their ectoparasitoids, acting as master manipulators (Takasuka et al., 2015). For many arthropods, including some spiders and mites, researchers started to unveil the composition of their microbiomes (e.g. Pekas et al., 2017; Busck et al., 2020) yet only a few of those microorganisms and their interactions are known for their functions and effects on the phenotype of their hosts. Exploring the functions of the microbiome members and scrutinizing their role in shaping the phenotypes of their hosts are grand future challenges.

## Operational issues

(i) Most arachnids are small (body length commonly between 0.5 and 15 mm when adult), with some eriophyid mites being as tiny as 0.1 mm (Krantz and Walter, 2009). Small size can be challenging in field studies and biochemical and molecular analyses but can be a huge asset in manipulative experiments. Detectability of specificities and differences in

chemical signatures used in social recognition or other contexts or in metabolism and endocrinology or in individual genetic makeup can be challenging because of little biomass. Marking, tracing and tracking multiple tiny individuals can be a challenge for videotaping and automated behavioral analyses, and is especially difficult in the field. Regarding the latter, novel marking techniques such as SmartWater open great opportunities for individual trackability even for such tiny animals as plant-inhabiting mites, which have body lengths of 0.5 mm and less (e.g. Rosser et al., 2022). On the very positive side, small size renders some mite and spider species perfectly accessible for manipulative experimentation in the laboratory; their small size allows keeping and observing single individuals and even populations and communities in small microcosms of few cm<sup>2</sup> or cm<sup>3</sup>.

(ii) Refining choice of measurable parameters that best reflect the behavioral tendencies in animal personality research and identifying critical traits for trait-based ecological approaches. These challenges are not specific to arachnids but arachnids play prominent roles in these areas, as laid out in the conceptual issues. In their review, Carter et al. (2013) provide for a nice treatise of the critical relevance of what and how and under which circumstances to measure, and determining the parameters that reliably reflect behavioral tendencies in any of the five trait categories of animal personalities, i.e. activity, aggressiveness, sociability, exploration and boldness (Réale et al., 2007). Originally developed for plants, but also applicable to animals, Lavorel et al. (2007) set out the requirements for individual traits to be useful in trait-based ecology: connected with a function; easy to observe and quantify; measurable in a standardized way across species and environmental settings; range of values that is comparable among individuals, species and habitats.

(iii) Further integrating “omics” into behavior and ecology (see also Kuntner, 2022). Despite molecular biology having started to rise already six to seven decades ago, with gaining momentum three to four decades ago with the advent of techniques such as PCR, it is still a grand challenge to integrate “omics” (genomics, proteomics), epigenetics and behavioral and ecological investigations. Such efforts hold promising potential for big leaps in research concerning the link between phenotypes and gene regulation and expression, or pinpointing genes that are involved in given behaviors. Molecular tools have already allowed tremendous advances in arachnid research on tri-trophic interactions (e.g. Van Leeuwen and Dermauw, 2016; Staudacher et al., 2017), paternity determination (Schausberger et al., 2016), prey digestion (e.g. Gomez-Martinez et al., 2020; Parimuchova et al., 2021), interaction with micro-organisms (e.g. Pekas et al., 2017; Zhu et al., 2018), or taxonomy (e.g. Skoracka et al., 2015; Dimitrov et al., 2017; Starrett et al., 2017; Dos Santos and Tixier, 2017). The work by Smith et al. (2022) on hair follicle mites is an illustrative example of how the clever integration of diverse methodological approaches can result in comprehensive, multi-

faceted knowledge gains of the ecology and behavior of an arachnid.

(iv) Pre-experimental history/pipeline is often kind of a Pandora’s box in behavioral and individual-centered ecological studies. The STRANGE framework developed by Webster and Rutz (2020) is a commendable critical initiative to mitigate the risk of sampling bias, to help avoiding biased inferences and to improve representativeness and generalizability of findings in animal behavior research. STRANGE is the acronym for several inter-related pre-experimental factors being critical to interpretation and generalizability of animal behavior studies, i.e. *social background, trappability and self-selection, rearing history, acclimation and habituation, natural changes in responsiveness, genetic makeup and experience*. This framework is concerned with raising awareness of the potential of inadvertent influences before experimentation that bias the experimental outcome, strives to improve representativeness of animal behavior studies, and suggests reporting guidelines to allow viewing published studies within this context. Reporting should already start with information about where, when, how and how many specimens were sampled in the wild or obtained from other sources to found laboratory populations, how representative are they, did inbreeding occur, or the time elapsed between founding and experimentation. Individual pre-experimental history and treatments with respect to housing conditions, feeding, mating, social interactions, multiple use in experiments, or miscellaneous abiotic and biotic stressors, may all exert inadvertent influences on experimental outcomes and interpretations. The STRANGE framework and guidelines (Webster and Rutz, 2020) apply to any type of, and any taxon used in, animal behavior studies, and is encouraged by arachnid ecology and behavior.

## Conclusions

The journal *Frontiers in Arachnid Science* is the first to unite research on spiders, mites and other arachnids under one roof and thereby serves for a fresh, inspiring and stimulating outlet for arachnid research. Arachnid research is also a proud part of the entomological sciences, with many parallels and similarities between the eight-legged and the six-legged. Can arachnid researchers contribute to meet the grand challenges set out by the world’s largest entomological organization, the Entomological Society of America, i.e. global health, feed the world and invasive species (<https://entomologychallenges.org/>)? Yes, we can! Arachnid research is highly relevant to each of these global grand challenges and ready to take on many other, more specific basic and applied challenges, as illustrated by the *Arachnid Ecology and Behavior*-related issues discussed here, as well as by the field grand challenge in *Frontiers in Arachnid Science* by Matjaz Kuntner (Kuntner, 2022) and the specialty grand challenges in *Arachnid Morphology, Systematics and Evolution* by Jason Bond, in *Arachnid Diversity*,

*Conservation and Biogeography* by Ingi Agnarsson and in *Arachnid Microbiota and Diseases* by Alejandro Cabezas-Cruz, all published in this very journal.

## Author contributions

The author confirms being the sole contributor of this work and has approved it for publication.

## Funding

The author acknowledges financial support by the Austrian Science Fund (FWF; P 33787-B).

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## Conflict of interest

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