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Adaptation and Survival of Marine-Associated Spiders (Araneae)

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Abstract

Aquatic environments are an unusual habitat for most arthropods. Nevertheless, many arthropod species that were once terrestrial dwelling have transitioned back to marine and freshwater environments, either as semi-aquatic or, more rarely, as fully aquatic inhabitants. Transition to water from land is exceptional, and without respiratory modifications to allow for extended submergence and the associated hypoxic conditions, survival is limited. In this article, we review marine-associated species that have made this rare transition in a generally terrestrial group, spiders. We include several freshwater spider species for comparative purposes. Marine-associated spiders comprise less than 0.3% of spider species worldwide but are found in over 14% of all spider families. As we discuss, these spiders live in environments that, with tidal action, hydraulic forces, and saltwater, are more extreme than freshwater habitats, often requiring physiological and behavioral adaptations to survive. Spiders employ many methods to survive inundation from encroaching tides, such as air bubble respiration, airtight nests, hypoxic comas, and fleeing incoming tides. While airway protection is the primary survival strategy, further survival adaptations include saltwater-induced osmotic regulation, dietary composition, predator avoidance, reproduction, locomotory responses, and adaptation to extreme temperatures and hydrostatic pressures that challenge existence in marine environments.

1. INTRODUCTION

All life, including the diversity of known terrestrial forms, evolved from water. Some terrestrial species have since reverted to a fully aquatic lifestyle (2, 39, 108), while others, including several arthropod species, have adjusted to a combination of terrestrial and either freshwater or marine aquatic habitats. More than 80% of animal species are arthropods, with representatives from the Insecta, Arachnida, Crustacea, and Myriapoda groups living in a diversity of habitats (92), including deserts, mountains, forests, water (freshwater and marine), and intertidal zones (29, 51, 58, 88, 89, 92, 121). This review focuses on discussing the adaptations—both physiological and behavioral—used by arthropods, particularly spiders, that spend at least part of their life in tidal areas.

Perhaps among the most unusual of the habitats occupied by arthropods are aquatic and semiaquatic environments, where, due to the vast differences between the physical characteristics of air and water, survival has required comprehensive evolutionary adaptation to transition back to the aquatic habitat from which life evolved (64, 92). In particular, for terrestrial arthropods to transition back to the sea, physiological, behavioral, and ecological challenges must be overcome, and it has been suggested that a transitional intermediate platform, such as salt marshes, mudflats, estuaries, or intertidal areas, is required for this transition (14, 17). Marine tidal zones are divided into the supralittoral, midlittoral or intertidal, and sublittoral zones. The supralittoral zone of coastlines, sometimes known as the spray zone, is the area above the spring high tide. The supralittoral zone does not usually succumb to submergence but is regularly splashed and can be breached during storms or extreme high tides. The intertidal zone, the shore area spanning from the high tide mark to the low tide mark, is exposed and submerged alternately once or twice daily. The sublittoral zone, which generally reaches to the edge of the continental shelf, is constantly covered with seawater (47).

Evidence suggests that the transition to water from a terrestrial habitat is exceptional, and without respiratory modifications to allow for extended submergence and the associated hypoxic conditions, survival is limited (111). Nevertheless, some arthropod species inhabit supralittoral zones and intertidal zones, while others complete the whole of their lifecycle fully submerged in either freshwater or marine environments, including the open ocean (64, 92).

Arthropod lineages that live in marine habitats but that spend part of their life history on land are generally dependent on air for respiration (120). Because they face immersion and emergence, along with the ensuing fluctuations in oxygen concentration, salinity, and hydraulic forces, they are required to overcome significant physiological challenges, including gaseous exchange and osmoregulation (6, 71, 90). In addition, abiotic stressors such as heat, cold, and hypoxia can alter the balance of mitochondrial homeostasis, often leading to cell death. Despite the challenges to the organism's homeostatic mechanisms generated by these extreme fluctuations, integral mitochondrial function needs to be maintained and restored to enable survival, and many intertidal and wetland species, such as many crustaceans, have evolved the ability to cope with these external stressors, maintain homeostasis, and survive (110).

With excellent locomotive abilities; a robust, waxy cuticle; and a simple respiratory system, arthropods are very capable of adaptation to both terrestrial and aquatic habitats (29, 121). Indeed, many arthropods with presumed low adaptive tolerance to aquatic environments are found in marine and freshwater environments. Moreover, fully terrestrial arachnids share a similar morphology, such as a waxy cuticle and the placement and type of setae, with their semiaquatic and fully aquatic counterparts (113, 120). Arachnids exemplify this flexibility: Those that do not associate with water are still capable of responding to inundation through physiological and behavioral means, including maintaining an underwater air bubble, using specialized osmoregulatory mechanisms, sheltering in crevices, or inhabiting air pockets while submerged (4, 14, 44, 45, 114, 121).

While respiration and osmoregulation are key survival factors, overcoming competitive disadvantages in newly transitioned environments is also crucial (6, 120, 121). Because of competition, successful adaptations in one environment may not be transferable to a novel environment (120). Equally, if the novel environment poses little competitive risk, then the invasive species has a greater chance of establishment and survival (121). Other life history components, such as diet, predator avoidance, reproduction, and locomotion, are affected by a transition to aquatic environments (24). In addition, external stressors, such as hydraulic forces and extreme temperature variation, affect the ability to adapt and survive. While these physical factors are similar for both freshwater and saltwater, terrestrial arthropods have recolonized freshwater environments more frequently than saltwater environments and have significantly stronger impacts on freshwater ecosystems than on marine ones (120). While freshwater arthropods do not face the challenges posed by salinity, they do face similar challenges to their intertidal and marine counterparts when they encounter inundation from flooding events (2, 38, 83, 111). Some species respond to flooding by using dormancy strategies, such as quiescence, while some riparian species have the ability to survive for several months with the aid of specialized respiration mechanisms (29, 66, 67).

Spiders are found in a wide range of environments but are limited in aquatic diversity (111). There are some numerical discrepancies regarding spider diversity in aquatic habitats, in part due to amendments of synonymization and mistaken habitat descriptors (e.g., of species actually only found in terrestrial habitats). Crews et al. (22) reported that nearly 20% of all 132 spider families (74) are associated with either freshwater or saltwater habitats, including 11 families with species living in intertidal zones. In 2018, the World Register of Marine Species reported 125 marine spider species from 19 families and 74 genera (42). This list of species comprises 0.24% of spider species, which are found in 1.7% of genera and 14.4% of spider families, illustrating that, while living in marine areas is very rare, the underlying adaptations enabling it are likely to be relatively ancestral, possibly due to early convergent evolution, as evidenced by the wide array of families in which it is present (**Figure 1**). Notably, families adapted for survival in aquatic environments tend to be ground-dwelling species from the webless RTA clade of spiders, which radiated especially quickly during the Cretaceous period, when there was a large increase in nonflying insects that could act as prey (35).

Marine spiders are especially poorly studied. Very few described spiders are found in the lower intertidal habitat, with most species located in the upper intertidal and supralittoral zones or among salt-tolerant vegetation, where a greater number of prey can be found (92). Roth & Brown (92) also noted that, while some spiders have physiological and/or behavioral adaptations to survive periods of inundation and submergence, few species have made intertidal zones their permanent habitat. Nevertheless, intertidal species are present, with the intertidal genus *Desis* (Desidae), comprising 15 species (74), being found on rocky coasts around the world. Each *Desis* species appears to have unique niche characteristics. For example, *Desis formidabilis* lives on rocky shorelines under large boulders and can be found sheltering in barnacle shells, while *Desis marina* lives in holdfasts of bull kelp and rock crevices (5, 52, 53, 60, 62, 63, 92, 122). While some intertidal spiders, such as *Pardosa lapidicina* and some *Arctosa* spp. (Lycosidae), adeptly manage to avoid submergence by retreating from incoming tides to the supralittoral zone (48, 72, 92), possibly through some form of periodic (circadian or lunar) rhythm, the majority of intertidal spiders have to face inundation and submergence and consequently have evolved physiological adaptations to survive.

This review aims to synthesize knowledge of how and why spiders, a mostly terrestrial group, survive periods of submersion underwater, such as in intertidal zones. After a brief overview of the fossil evidence, we review both semi- and fully aquatic arthropod taxa to provide background and context, with a key focus on intertidal spiders. In particular, we examine the survival mechanisms that enable spiders to remain in this habitat. These include physiological adaptations, such as

Figure 1

Examples of marine-associated spiders from different families. (*a*) *Pirata piraticus* (Lycosidae). Photo reproduced with permission from Chris Moody (2011, CC BY-NC 2.0; **https://www.flickr.com/photos/zpyder/5532889376**). (*b*) *Desis martensi* (Desidae). Photo reproduced from Marcus F.C. Ng (2015, CC BY-NC-ND 2.0; **https://www.flickr.com/photos/budak/29236730344**). (*c*) *Alopecosa* sp. (Lycosidae). Photo reproduced with permission from Marshal Hedin [2009, CC BY 2.0; **https://commons.wikimedia.org/wiki/File:ImperialBeachAraneomorphs-20_(4131846401).jpg**]. (*d*) *Oramia chathamensis* (Agalenidae). Photo reproduced from Peter de Lange (2015, CC0 1.0; **https://www.inaturalist.org/photos/2229682**). (*e*) *Marpissa marina* (Salticidae). Photo by X.J.N. (*f*) *Desis bobmarleyi* (Desidae). Photo reproduced from Robert Raven (2017, CC BY 4.0; **https://commons.wikimedia.org/wiki/File:Desis_bobmarleyi_male_holotype.jpg**). **Supplemental Table 1** provides further details.

Supplemental Material >

respiration, osmoregulation, and quiescence or hypoxic comas, and behavioral adaptations, such as diet, building airtight nests, predator avoidance, reproduction, and locomotion (**Supplemental Table 1**). We also discuss abiotic factors, including external stressors such as hydraulic forces and extreme temperature variation, affecting spiders that associate with water.

Supplemental Material >

2. EVOLUTIONARY ORIGINS

Researchers have conflicting ideas regarding land arrival times for arthropod taxa, and early fossil evidence is therefore somewhat contentious. It has been suggested that some arthropod-type organisms were able to move, albeit temporarily, across terrestrial sediments during the Cambrian-Ordovician cusp, approximately 488 Mya (29). The fossil record of the terrestrial colonization of the Chelicerata, i.e., horseshoe crabs (Xiphosurida: Limulidae), scorpions (Arachnida: Scorpiones), spiders (Arachnida: Araneae), and mites (Arachnida: Acari) (30), from their marine ancestors suggests that this occurred approximately 445 Mya, in the Ordovician period (**Figure 2**). However, some researchers have hypothesized that terrestrial colonization may stretch as far back as the Cambrian period (103). While some present-day chelicerate groups remain marine, most arachnids became terrestrial. However, some arachnids have since transitioned back to the water, either as semiaquatic species or, more rarely, as fully aquatic species (22). Other evidence points to arachnids and myriapods living on land during the Silurian period (approximately 416–443 Mya), and hexapods were found in coastal environments during the Devonian period (approximately 398–416 Mya) (25, 29, 121).

Fossil records of spiders are often of poor quality and are limited in number (25, 84, 102, 123). This may be because spider bodies are tenuous and soft, resulting in most spider fossils being found embedded in amber in the Cenozoic era, approximately 66 Mya (28, 84). The oldest reported spider-like arachnid dates from the late Carboniferous period, approximately 310 Mya, but was missing some distinctive features of true spiders (36, 43, 105), which may have originated in the late Silurian or early Devonian periods, with major radiations of the modern spiders (Araneomorphae) occurring in the late Palaeozoic or early Mesozoic eras, approximately 300–200 Mya (18, 102, 104). Despite a scarcity of fossilized spiders, a considerable number of the fossil spiders that have been

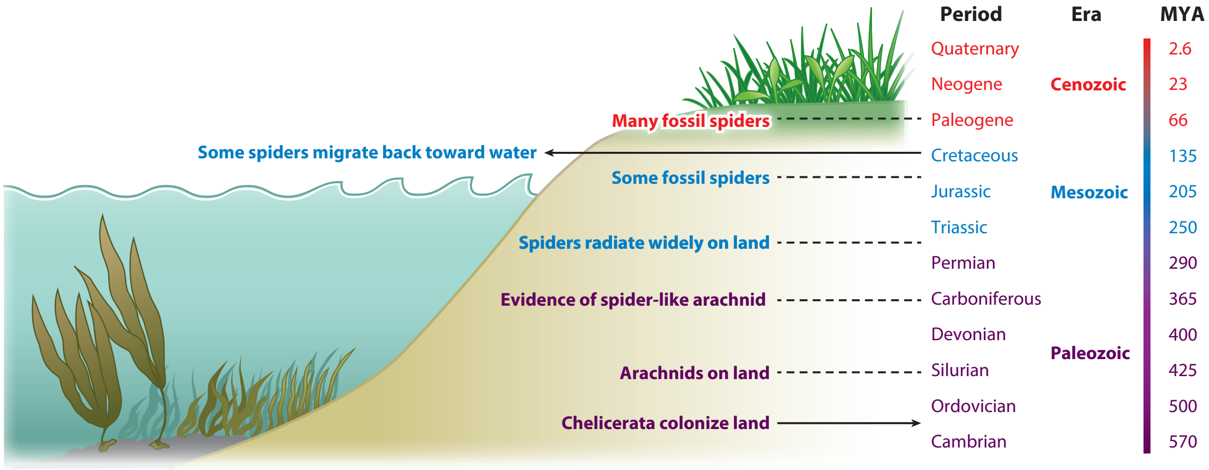

Figure 2

Timeline of spider migration from water to land and the transition back to aquatic habitats.

found, encompassing numerous species, including representatives from many modern families, are from the Jurassic and Cretaceous periods (18, 123).

In insects, it is estimated that there have been 70 genus-level instances of invasion from freshwater to sea, as well as over 40 from land to sea without an intermediary freshwater platform (14, 121), and it is believed that more than half of the insects that have invaded intertidal areas have come directly from land, rather than from freshwater (14). However, insect recolonization of water from land does not appear to have taken place much before the Jurassic period (120, 121). It has been suggested that terrestrial arachnids migrated back to the sea on at least 47 independent occasions, although there is little evidence outlining the timing of these instances (92). However, this is unlikely to have occurred much before 100 Mya, in the Mesozoic, as illustrated by a recent study by Li et al. (57) on the evolutionary history of aquatic spiders. Li et al. used complete mitochondrial genome sequencing of the intertidal spider, *Desis jiaxiangi*, and performed comparative mitochondrial analyses with 45 other spider species, including the freshwater, fully aquatic spider *Argyroneta aquatica* (Dictynidae) (57). These two species share similar—and unusual—aquatic habitats and share similar morphological features to prevent asphyxiation while underwater. This work suggested that the most recent common ancestor of these spiders diverged approximately 98 Mya (57), a finding supported by Spagna et al. (111), who noted that major adaptations of aquatic spiders occurred in the late Mesozoic (mid-Cretaceous) period.

3. PHYSIOLOGICAL ADAPTATIONS TO AQUATIC ENVIRONMENTS

3.1. Respiration

In wetland and intertidal habitats, there is risk of respiratory compromise and drowning, and thus adaptations to prevent asphyxia are paramount to the survival of aquatic arthropods. This has resulted in the modification of a respiratory mechanism evolved for land to one that can endure variable periods of time underwater (38, 83, 108, 111), sometimes aided by behavioral attributes. Due to tidal action and flooding events, aquatic arthropods face alternation of air exposure and inundation (2, 38, 52, 59). For oxygen levels to meet respiratory demand while the arthropod is submerged, animals must be able to endure periods of low oxygen availability and/or have the ability to absorb oxygen via the cuticular surface, maintain specific oxygen concentrations through physiological structures that are gill like, or employ modes of trapping air while submerged (6).

Some species with flexible respiratory systems can move from land to water, maintaining similar rates of oxygen consumption in both. Crustaceans, the most represented aquatic (mainly marine) arthropods (82, 121), are among the limited number of arthropods that can survive both on land and in water, relying on similar respiratory structures in both habitats (77). Several intertidal brachyuran crabs, which are hypothesized to be in an evolutionary transition process from water to land, exemplify this based on their reduced gill area and superior ventilatory capabilities (tracheal capacity; see below) compared to aquatic crabs (96).

Supplemental Material >

Spiders have several adaptations to obtain adequate oxygen in aquatic habitats (**Supplemental Table 1**). These include trapping air bubbles, having commensal relationships with other organisms, inhabiting air-filled burrows, and behavioral quiescence, among others (6, 17, 22, 52, 55, 67, 83, 93, 108, 117, 122) (**Figure 3**).

Spider respiration is achieved through internal branching tubes and sacs. This gaseous exchange system opens via spiracles, which are external openings to the atmosphere and are positioned laterally in the pleural wall of the abdomen. Spiracles open and close by a valvular system and can remain open or partially closed for long periods, minimizing water loss (37). Without

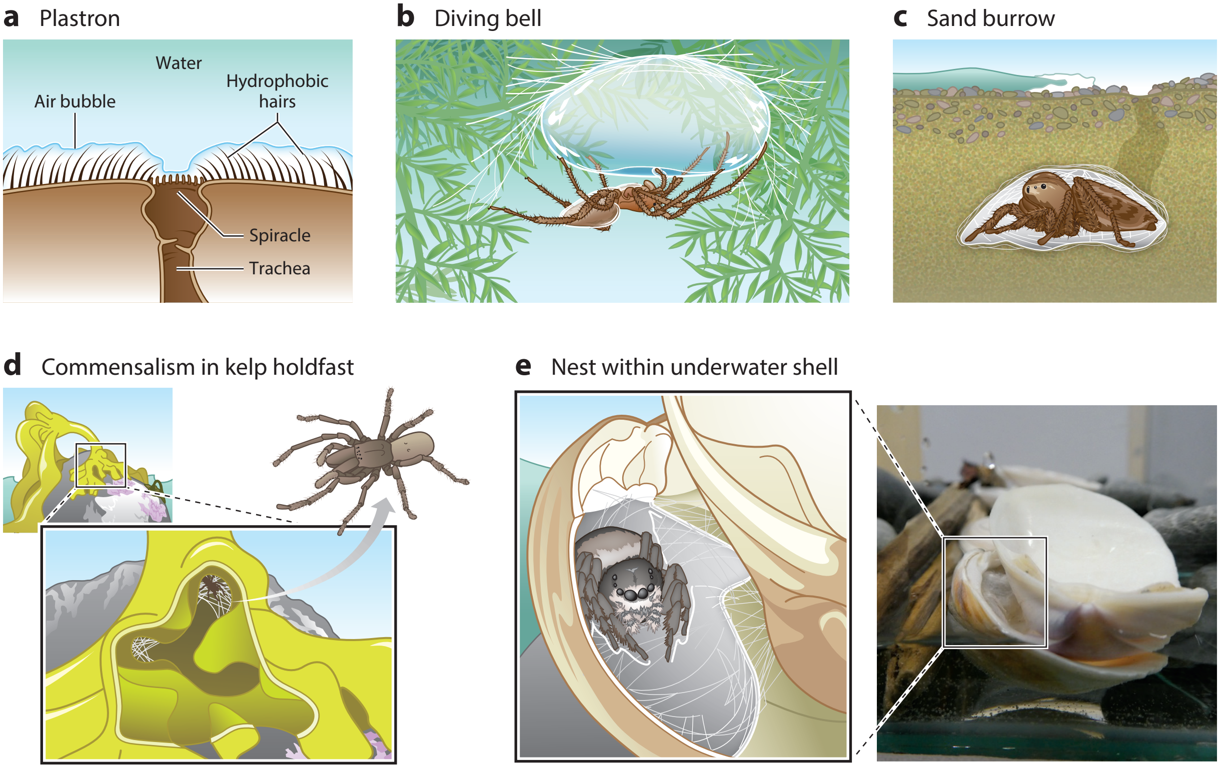

Figure 3

Some mechanisms used by arachnids to respire under water. (*a*) The plastron, a noncollapsible gas store retained by hydrophobic hairs, found among some mites and amblypygids but unknown in spiders to date. (*b*) A diving bell, used by the freshwater species *Argyroneta aquatica*. This silken diving bell acts as an oxygen collection apparatus that is replenished with air bubbles carried from the surface to the bell by the spider. (*c*) Sand burrows, whereby spiders, like *Yllenus arenarius*, build nests under sand, protecting them from inundation, with waterproof silken walls functioning as a physical gill. (*d*) Commensalism, as found in the intertidal species *Desis marina*, which has a commensal relationship with the holdfasts of bull kelp; the spider spins webs inside the holdfast, which traps sufficient air for it to survive tidal inundation. (*e*) Other spiders, like *Desis formidabilis*, *Amaurobioides africanus*, and *Marpissa marina*, build nests inside shells, which trap air for the period of tidal inundation. Photo by M.A.L.

the need for a circulatory system, gases are either diffused across the epithelial layer of the gill-like book lung and the tracheae or are actively pumped, delivering oxygen and excreting carbon dioxide (37, 83, 108).

Book lungs are exclusive to five extant arachnid orders (Scorpiones, Araneae, Amblypygi, Uropygi, and Schizomida) (26, 27). Book lungs evolved from book gills when spiders and scorpions transitioned to land (29, 100, 104). Book gills were an external mechanism evolved for aquatic respiration and were unsuitable for a terrestrial environment, as they would collapse under the weight of atmospheric pressure and/or desiccate swiftly (29). Book lungs can be either absent or present in varying numbers in different arachnid taxa. Some groups, such as scorpions, have four pairs of book lungs, while other taxa have two pairs [e.g., tarantulas (Theraphosidae), whip scorpions (Uropygi)] or one pair [e.g., whip spiders (Amblypygi)]. Spiders (Araneae), discussed in detail below, have zero to two pairs of book lungs, with tracheae present in most species (55, 79). Both the book lung and the tracheae open to the spiracles play a role in controlling the respiratory system and evaporative water loss (29, 33).

The book lung provides a large surface area for gaseous exchange and comprises multiple folds of cuticular lamellae, or pages. Hemolymph-filled lamellae alternate with air-filled lamellae and are nearly entirely closed but for a slit-like opening and a muscle-controlled spiracle opening to the environment (43, 104). Hemolymph, analogous to vertebrate blood, is composed of liquid plasma and oxygen-binding proteins, but unlike the hemoglobin found in vertebrate red blood cells, hemolymph has a low oxygen-carrying capability. Hemolymph circulates around the arthropods' body in direct contact with the tissues to which it supplies oxygen (37).

There is considerable morphological and physiological diversity in the respiratory characteristics of different spider families (49, 79, 97). Ancestral spiders (Mygalomorphae), such as trapdoor spiders (e.g., Ctenizidae, Barychelidae) and tarantulas, lack tracheae and have two pairs of book lungs (49, 55, 79). The respiratory system of modern spiders is unique in that most species use both tracheae and book lungs simultaneously to maintain respiratory function (97). For example, in jumping spiders (Salticidae), which use a sit, wait, stalk, and pounce hunting strategy, both the lungs and tracheae operate together to provide optimum respiratory function (98). In other species, such as wolf spiders (Lycosidae) and funnel web spiders (Agelenidae), the main respiratory organs are the book lungs (97), although most of these species have a bimodal form of respiration in which the second pair of lungs has been replaced by tracheae (43, 55, 79, 97, 108). During sedentary periods with low oxygen consumption, oxygen requirements are easily met by the lungs or tracheae. However, during times of high oxygen demand, the demand is met by both lungs and tracheae working in synergy (98). Additionally, in some modern species, the first lung pair may also be reduced, while other species are devoid of book lungs and only possess tracheae (43, 49). For example, the fully aquatic freshwater spider *A. aquatica* has an advanced tracheal system and greatly reduced book lung (55, 101, 111).

Tracheal respiration is simpler than book lung respiration, essentially functioning as a combination of transport tubes and tracheal lungs (33, 79, 97). Tracheal respiration allows oxygen to be delivered directly to the tissues that require it, with the advantage of allowing spiders to have flexible respiratory behaviors (67, 79). Salticids and sheetweb weavers (Linyphiidae) are examples of spiders with well-developed, flexible tracheal systems (97). Along with their role in water conservation and providing oxygen to specialized organs, such as the nervous system (79, 80, 97), tracheae provide oxygen to extremely active leg muscles, as found among salticids (97). It is thought that, when spiders have oxygenation needs that are met by a competent tracheal system, book lungs play a lesser role and are therefore less well developed; conversely, spiders with less extensively developed tracheae have more developed book lungs (78).

In the event that the tracheal system becomes flooded with water, or the spiracles become wet, spiders and insects will typically die (108); air bubbles and plastrons (or gas stores) are common adaptations for underwater survival. In air bubble respiration, animals carry bubbles beneath the water surface to maintain respiration. Air bubbles, which are held in place by hydrophobic hairs, function as a physical gill by accumulating dissolved oxygen from the surrounding water (93, 108, 117). Air bubbles only provide a short-term supply of oxygen, as they cannot resist the surrounding water compression and will slowly dissolve unless the organism surfaces to renew the bubble (52). Air bubble respiration differs from plastron respiration (discussed below) in that air bubbles are collapsible, while the plastron is not (117).

Rovner (93) argued that spiders were unable to maintain an air bubble or plastron in the same way that aquatic insects do due to a lack of ability to clutch the bubble. However, many aquatic and semiaquatic spiders satisfactorily use an air bubble when submerged. Some lycosids found in intertidal zones and mudflats have been witnessed surviving flooding by the use of air bubbles adhered to their hairy bodies (11, 39, 92). These observations are supported by Lamoral (52, 53) in his 1968 studies of the intertidal spider *D. formidabilis*, which maintains underwater respiration via an air bubble. Lamoral (52) noted that *D. formidabilis* can submerge for long periods of time but surfaces regularly to replenish oxygen stores. An especially good example of the success of air bubble respiration is demonstrated by the only known fully aquatic spider, *A. aquatica*. Found in slow-moving freshwater habitats in Europe and Asia (111), *A. aquatica* employs a dome-shaped diving bell to meet its respiratory and metabolic needs. Possessing reduced book lungs and a large, complex tracheal system (55, 111), *A. aquatica* weaves a silken diving bell that acts as an oxygen-collection apparatus (83, 97, 101, 107, 111). It spins its web (often connected to plants) underwater and carries the air bubbles held in place on its abdomen by hydrophobic hairs (22) down from the surface, placing them under the web and forming an air pocket. Oxygen diffuses through the bell, allowing for longer periods of submersion (107). From this site, the spider forages, mates, lays eggs, and rears its young (19, 107, 108, 111, 115).

Another method of taking air from above the surface of the water to below the surface is plastron or gas store respiration, which, in contrast to air bubbles, enables organisms to survive underwater for extended periods (38). For example, the whip spider *Phrynus marginemaculatus* (Amblypygi), which has no tracheae and two pairs of book lungs, can survive underwater for 24 hours (38), while mites (Acari) can withstand lengthy flooding periods in their habitats due to plastron respiration (87). Plastron respiration is used at egg, larval, pupal, and adult stages in aquatic and semiaquatic insects and, more rarely, among arachnids (38).

The plastron acts as an enveloping, superhydrophobic body surface, providing a thin air layer or film, a few microns thick, that acts as a gill and connects with the tracheae (117). Depending on the method of respiration, this layer is present either entirely around the body surface or only in specific areas (38, 67). The plastron gill, which is anchored on the outside of the cuticle by hydrophobic hairs or cuticular projections, provides the boundary between water and air (23, 38, 39). The denser the hairs on the spider, the more hydrophobic they are, which is well-suited to the formation of a plastron, aiding in submersion tolerance (109). Oxygen is absorbed from the surrounding water via the plastron gill and is then transported to the trachea and disseminated into the tissues (23, 34, 83, 117).

Spiders that live by lakes and rivers complement respiratory adaptations using behavioral adaptations to cope with flooding events (124). The nurseryweb spiders *Dolomedes fimbriatus* and *Dolomedes aquaticus* (Pisauridae) (**Figure 4**) live in shallow streams and can remain underwater for at least 20 minutes, aided by a plastron to achieve adequate oxygenation while submerged (83, 125), while the freshwater spider *Tylorida sataraensis* (Tetragnathidae) submerges in streams (which it can do for between 5 and 13 minutes) with air pockets along its body surface. These air pockets assist it in respiring underwater and may also assist with resurfacing (50). Among lycosids, Heckman (39) observed that *Pardosa amentata*, which is found in moist habitat near small bodies of water, survives inundation by using a hydrophobic abdominal bristle layer trapping a layer of air, while *P. lapidicina* survives flooding by maintaining a state of dormancy (46). Other spider species, lacking morphological or physiological adaptations, survive flooding events by migrating up shrubs and tree trunks (66).

Abraham (1) first described how salticids, when inundated by rising tides, can survive in their hydrophobic silken retreat nests among rocks, protected from the water by an airtight door. Rocky shores provide useful habitat for intertidal spiders, supplying retreats that can be used for shelter. These include spaces among the rocks and crevices and/or shells where air can be trapped and sandy areas where burrows can be made (6). For example, the intertidal salticid species *Diplocanthopoda marina* builds its silken nest in rock crevices that are frequently inundated by shifting tides (1, 92), an adaptation also observed in the intertidal salticid *Marpissa marina* (M.A. Leggett and X.J. Nelson, unpublished observations). Barnacle shells can also be used by spiders as air reservoirs (92), and *D. marina* builds its silken retreat within shells, as well as in rock crevices, between

Figure 4

New Zealand nurseryweb spider (*Dolomedes aquaticus*) with an 18-mm-diameter ring for scale. Photo reproduced with permission from Daniel Crosby (2009, CC BY-SA 2.0; **https://www.flickr.com/photos/judd/4218811534/?edited=1**).

stones, and within kelp holdfasts attached to rocks (122). In these instances, silk is woven across the openings of retreats with such resilience that the retreat can resist tidal encroachment, allowing the spider to remain dry and oxygenated for hours (19, 62). Spider silk in aquatic and semiaquatic spiders is composed of spidroins (the principal structural proteins of spider silks) with a particularly hydrophobic amino acid motif. To date, these hydrophobic amino acid motifs (56) have only been found in the water-associated species *A. aquatica*, *D. marina*, and *Dolomedes triton* and are hypothesized to be related to silk use in water (19).

Further retreat or nest adaptation is displayed by *D. formidabilis* and *Amaurobioides africanu*s (Anyphaenidae), both of which build nests inside mollusk shells with the open side downward, suggesting a mechanism to prevent efflux of air trapped in the shell while underwater (52). Burrowing into damp sand is demonstrated by intertidal lycosids from the *Arctosa* genus (92), and survival in sand dunes is demonstrated by the salticid *Yllenus arenarius*, which builds nests under the sand, protecting it from periodic rain inundation, with the nest's waterproof silken walls functioning as a physical gill (7).

Some intertidal spiders have commensal relationships with vegetation, such as bull kelp holdfasts, which are root-like structures that anchor the kelp to the substrate. In this case, spiders spin webs deep inside the base of the holdfasts that trap sufficient air for them to survive tidal inundation. In turbulent intertidal habitats, holdfasts, as the name suggests, firmly anchor the seaweed to rock surfaces (60, 63). Such is the reliance of *D. marina* on bull kelp holdfasts that it is proposed that its biogeography is limited by the distribution of the holdfasts themselves (62), although Vink et al. (122) note that *D. marina* is also found in areas without bull kelp holdfasts. While *D. marina* is found in intertidal areas, it has no apparent need for specialized respiratory adaptations to maintain long periods of submergence, likely due to the trapped air within the kelp holdfasts being sufficient to meet the spider's respiratory needs (62). Additionally, *D. marina* has an unusually low respiratory rate (and therefore decreased oxygen demand) and, with the trapped oxygen in its silken nest, is able to survive for up to 19 days submerged under water (60, 63).

Quiescence and hypoxic comas are adaptations used by some freshwater and intertidal arthropods when they are unable to rely on respiratory adaptations, such as air bubbles or plastrons (8, 17, 41). Quiescence is a state of dormancy (decreased activity, growth, and development) that is generated by adverse environmental conditions and is reversed when conditions are once again favorable (8). For example, many beetles (Coleoptera) found on stream edges or salt flats enter a quiescent state, enabling them to survive periods of anoxia, when submerged (32, 41). Among spiders, the only known example of quiescence is in the lake-dwelling lycosid *P. lapidicina*, which survives extended periods of submersion due to a quiescent state, with complete activity resumed upon exposure (46). Due to the minimal amount of research in this area on invertebrates, the Lycosidae currently represent the only known example of a hypoxic coma, or metabolic depression (66), related to submergence in water. Hypoxic comas instigated by inundation cause organisms to be unresponsive to external stimuli, resulting in decreased metabolism and enabling survival (86). The lycosid *Arctosa fulvolineata* inhabits salt marshes and survives tidal inundation, apparently by being in a comatose state. The researchers noted that these spiders are unresponsive to external stimuli but are able to resume activity approximately eight hours after removal from water (86).

3.2. Osmoregulation

Osmoregulation is one of the most important physiological processes to enable successful establishment in marine habitats (13). Adaptations to combat osmotic stress include the cuticular structure; a reduced metabolic rate (90); and, for some marine invertebrates, extracellular fluid that is comparable to the surrounding sea water (54, 71). Numerous marine arthropods are osmotic conformers, i.e., the osmotic concentration of the arthropod's extracellular fluid is similar to that of the ambient seawater (54), and marine crustaceans have a highly specialized mechanism of osmoregulation (65, 91, 104). However, intertidal arthropods are required to regulate osmotic body water loss and increases in body concentrations of sodium chloride due to periods of inundation and emergence (54, 90). In spiders, salinity-induced hypo- and hyperosmotic stress are managed using various morphological, behavioral, and physiological adaptations (85).

The external osmotic concentration of water affects the osmotic concentration of the internal hemolymph, and concomitant internal pressure, as losses or gains in salt and water losses or gains are compensated for by their active uptake or elimination to or from the aquatic environment (31). Sea water has a much higher osmotic concentration than spider hemolymph, which will result in osmotic stress when the spider is immersed in water. Intertidal spiders must overcome not only environmental ion concentrations of seawater greater than their own body fluids, but also the osmoregulation challenge of prey ingestion (60). Very little is known about intertidal spider osmoregulatory abilities (see **Supplemental Table 1**); however, it has been demonstrated that the intertidal spider *D. formidabilis* has a hemolymph osmolarity concentration twice that of its terrestrial counterparts and comparable to other marine species (including its own prey), which in turn have sodium and chloride ion concentrations similar to seawater concentrations (71).

Supplemental Material >

4. BEHAVIORAL ADAPTATIONS TO AQUATIC ENVIRONMENTS

Behavior plays a fundamental role not only in aiding physiological mechanisms that enable survival in aquatic environments, but also possibly as a driving force behind the transition of terrestrial arthropods back into water, for example, to find alternative sources of food or escape from predators. In this section, we discuss hunting strategies that fulfil dietary requirements, predator avoidance, reproductive adaptations, and locomotion, in addition to external stressors or abiotic factors that may drive behavior (summarized in **Supplemental Table 1**).

Supplemental Material >

4.1. Diet

Feeding in aquatic environments poses significant challenges to spiders, as their feeding behavior involves bathing their macerated prey in digestive enzymes before sucking up the liquefied product, making it difficult to feed in the water and requiring feeding in a drier environment (76, 125). Both marine and freshwater arthropods have a varied diet, incorporating other arthropods, fish, frogs, and algae (21, 76, 92, 99). Approximately eight spider families prey on fish, mainly in warmer climates (76). Nurseryweb spiders, *Dolomedes* spp., consume tadpoles in freshwater environments by hunting and ambushing prey on the water surface (21, 125). Although there is little information about the diet of intertidal spiders, current evidence points toward a preponderance of intertidal insects, amphipods, isopods, and other spiders as prey items (5, 62, 92, 122).

The lycosid *P. lapidicina* lives on stony beaches and uses a cursorial hunting strategy, which includes moving up and down the intertidal zone searching for prey, although its success at retrieving prey appears to be greater in the (riskier) lower intertidal zones than in the upper intertidal zones (72, 73). Other intertidal and nocturnal spiders from the *Desis* genus hide in barnacles, corals, and holdfast air pockets at high tide and are active at low tide, feeding on amphipods, dolichopods, and isopods (62, 92, 122). Using an ambush method to catch prey, *D. marina* has even been observed eating polychete worms, which are abundant in bull kelp holdfasts (60).

Intertidal spider species may have differing physiological dietary adaptations related to prey consumption due to prey species' salt concentrations. For instance, despite eating similar prey (marine crustaceans), the hemolymph tolerance of salt concentrations differs between *D. formidabilis* and *A. africanus* (71). *Desis formidabilis*, found in the mid-intertidal zones, has a hemolymph salt concentration similar to its prey and consequently exhibits no stresses with salt loading from its consumed prey. However, *A. africanus* may possibly be restricted to the upper tidal areas, where it can obtain fresh water to counteract increased prey-induced salt concentrations in its hemolymph (71).

4.2. Predator Avoidance

While the abilities to breathe, osmoregulate, and obtain prey are integral for survival in marine and freshwater environments, predators also pose a threat to survival for aquatic arthropods (22). The hemipteran seaskaters *Halobates* spp. (Gerridae) are a small genus representing the only known fully aquatic open ocean insects (3, 45, 64). While adaptations such as specialized respiration and diet have allowed *Halobates* to survive in this habitat, predator avoidance, particularly of seabirds, remains problematic (64). One species, *Halobates sobrinus*, appears, uniquely, to use an instantaneous high-velocity jump reflex that is variable in direction, speed, and distance to escape seabirds; the success of this technique is evidenced by the lack of *H. sobrinus* found in the guts of seabirds, while other, less common, *Halobates* species were present (64).

In most instances, arthropods will be found near water, rather than in open water. In this environment, behavioral strategies to avoid predators include migration to safer habitats (121), as seen in several intertidal Lycosidae that flee down plant stems with an air bubble to escape predators

(11), and hiding (anachoresis). While pebble-laden shores and the crevices and cracks of rocks may provide the platform for the respiratory needs of intertidal species, they also provide shelter from predators (6). Hiding has also been observed in *D. formidabilis* taking refuge in shells (52) and in *Di. marina* inhabiting empty barnacle tests (16).

Several species of wasps parasitize aquatic arthropods. A member of the Pompilidae spider wasp family (*Anoplius* spp.) preys on freshwater semiaquatic spiders by diving underwater to attack its prey (20), while another wasp, *Echthrodesis lamorali* (Platygastridae), lives in the nests of marine spiders, including *Desis* spp. (52, 82, 119, 120). Lamoral (52) suggested that the intertidal habitat of some spiders (e.g., *D. formidabilis*) is an antipredator avoidance strategy to escape attack from spider-hunting wasps, but it could equally be suggested that the nocturnal hunting behavior of spiders, such as *Desis* spp., could be an antipredator adaptation.

Physiological adaptations enabling respiration underwater may have been further selected to reduce predation, permitting animals to remain underwater for extended periods and avoid resurfacing to elude the waiting predator (39, 55). An especially good example is the structure of the diving bell of the fully aquatic freshwater spider *A. aquatica*; not only does the diving bell provide integral respiratory support, but its robust silk structure provides protection from predation (123).

4.3. Reproduction

Several semiaquatic arthropods need to return to freshwater or marine environments to spawn (10). Some riparian semiaquatic arthropods (e.g., Chilopoda: Myriapoda) use parthenogenic reproduction, with eggs able to survive despite very cold temperatures associated with regular and lengthy flooding and with young rapidly reaching maturity. These factors suggest adaptation to extreme climate challenges, allowing for permanent recolonization in frequent and long-lasting flooding habitat (66).

Spiders are heavily dependent on silk for reproduction, but limited research has been conducted into the reproductive behavior of intertidal spiders. Based on current knowledge, for the few species that occupy aquatic or semiaquatic habitats, silk-based adaptations also appear essential for reproduction and survival (19). The silk-lined nests of *D. marina*, found in crevices, shells, or kelp holdfasts, have sufficient space for one spider or, more snugly, for a female spider with its mate and the ensuing offspring (61). However, when *D. marina* is joined in its nest by a mate, the nest often has to be expanded or even reconstructed to accommodate the crowd (62). McLay & Hayward (60) found that *D. marina* were patchily distributed among holdfasts and proposed that mating took place between spiders living in adjacent holdfasts. This species also has a lower clutch rate than terrestrial spiders, and females reproduce once per year, producing several sequential egg sacs in the spring. Its habitat is often at the mercy of stormy weather; consequently, it reproduces successively, which counteracts recruitment losses based on inclement weather (61). Egg development in *D. marina* is slow, lasting approximately two months; spiderlings coexist with their mother in the silken nest for another two months, finally emerging in early winter (61).

4.4. Locomotion in Water

Most organisms' weight in water is negligible, and consequently, the mechanisms required for the organism to move are vastly different to those used on land (31). However, the requirements to stay afloat and protect the respiratory system while moving are fundamental. The surface of water—the interface between air and water—remains under tension. Arthropods with hydrophobic integument structures are supported by the upward force of this surface tension (116), providing them with the ability to walk on water without sinking and drowning (24, 39, 116).

Spiders from a vast number of families are capable of efficient locomotion on water (113, 114, 116). Using the same mechanisms as they do on land (i.e., walking or running) to move over water, they rely on their waterproof integument for the ability to safely travel across the water's surface. However, some families of spiders have adapted specialized aquatic gaits, including rowing, galloping, and crawling (114, 116). These traits have been described among the Pisauridae, Trechaleidae, Ctenidae, and Tetragnathidae families; are less common in the Lycosidae and Salticidae families; and are rarely observed in the Araneidae (orb-weaver) family (66, 116).

Rowing, which involves synchronizing leg movement such that the gait propels the organism across the surface of the water without sinking, is one of primary locomotory strategies used by freshwater and marine arachnids to protect the trachea and/or book lungs from getting too wet (22, 114, 116). Notably, despite having the prerequisite hydrophobic attributes to row, some semiaquatic spiders do not use rowing for aquatic locomotion. Stratton et al. (114) reasoned that the propensity for rowing among semiaquatic or aquatic spiders is explained by phylogeny, rather than recent selection pressures related to habitat. However, although phylogeny may be the driving force in determining the capability of only some species to row (22, 114), it fails to adequately explain why this behavior is found, at least to a certain extent, in families that are only distantly related.

4.5. External Stressors

Two key abiotic factors that affect the ability of intertidal arthropods to survive in the intertidal zone are dynamic, changeable hydraulic forces and thermal stress, each of which requires a suite of mostly behavioral adaptations to protect the respiratory system and avoid desiccation or hypothermia.

Some small and light arthropods can float on bodies of water, using its surface tension to support themselves, but as turbulence and wind ripples can break surface tension, larger species rely on buoyancy rather than surface tension alone to remain above water (14, 39). Hydraulic forces include the strength of wave action and/or tidal flow; wave action, which varies from lower to upper intertidal zones, has differing effects on arthropods depending on wave strength. Attempts to combat hydraulic forces are demonstrated by the hemipteran *Asclepios shiranui* (Gerridae), which adheres to the shore during low tide, fighting against the ebb current and staying in protected coves (44). In addition to providing other key survival and fitness functions, the silk-lined retreat in the kelp holdfast employed by *D. marina* provides the spider with a refuge from tidal water pressure (61), while *D. formidabilis* and *A. africanus* avoid wave action by building their silk-lined retreats in empty mollusk shells (71). Very few small arthropods inhabit intertidal areas where pounding waves are present (40, 95); however, there is some advantage to pounding waves, as there is lower predation in areas with increased wave force (68, 69). Indeed, for *D. formidabilis* and *A. africanus*, wave action is the driver of nest placement, with areas that are exposed to intense wave action being favored. Shells that provide nests in these areas are secured in sheltered crevices or under large rocks, while in areas of lower wave action, shell nests are found resting on rocks (51). Additionally, *D. formidabilis* and *A. africanus* render their shells completely watertight by lining them with silk before the tide encroaches, thus trapping air, and then shearing their way out at the thinnest part when the tide recedes (52).

Thermal tolerance among species inhabiting intertidal areas can vary considerably (45). As poikilotherms, intertidal arthropods require a wide range of strategies to cope with extreme temperature variation, as they may face lengthy periods of submergence at high tide and then be exposed at low tide, resulting in the need to avoid desiccation. Thermal stress plays a role in spatiotemporal species distribution throughout the intertidal zones (9, 95, 112). Supralittoral and upper intertidal species are more exposed to ambient air temperature, including extreme heat, than species that are found in the lower intertidal areas, resulting in a greater desiccation risk for species in higher tidal zones. Equally, those that are in more wave-affected zones are less influenced by thermal stressors than those in areas with little wave action (9, 95, 112). It has been suggested that species in the higher intertidal zones may have a greater physiological resistance to abiotic factors (i.e., extreme temperatures) than those living in the lower intertidal zones (112), but evidence for this hypothesis is lacking.

In spiders, silk-lined retreats in and under rocks, crevices, and shells provide survivable microclimates to combat temperature extremes (71). Nests built under sand provide protection from seasonal temperatures, as well as strong winds and flooding events (7). Additional strategies, such as nocturnal hunting behavior, as seen in *Desis* spp., not only allow spiders to avoid possible predation, but also protect them from extreme heat (71). Other spiders migrate: The intertidal lycosid *P. lapidicina* lives on tidal, cobbled beaches but responds to extreme cold by seasonal migration (in autumn) to the litter layer of nearby forests, where it overwinters to avoid the freezing temperatures (48, 72). Although the distance between the beach and the adjacent litter layer of the forest is only 5–15 m, leaf litter has less variable temperature extremes, providing refuge from potentially lethal frost and snow events. In their study, Kraus & Morse (48) noted that peak migration timing differed yearly (with delayed migration during milder winters, possibly to remain foraging on the beach), and thus, these spiders were likely to be responding to environmental cues that trigger migratory behavior.

5. CONCLUSIONS AND FUTURE DIRECTIONS

With a diverse array of respiratory mechanisms across families, some spiders have managed to survive the oxygen deficits of aquatic and semiaquatic environments through a series of physiological and behavioral adaptations that contribute to successful underwater respiration and survival. These include air bubble and plastron respiration, lowered respiration rates, commensal relationships with vegetation, building airtight retreats, and quiescence. The assembly of a mitochondrial genome of an intertidal spider will lead to a clearer understanding of spiders' metabolic adaptations in relation to differing environments (58), especially in regard to the question of why some spiders have evolved respiratory adaptations to cope with submersion in water, while others have not. This genome assembly is timely to understand the bases of adaptations to marine environments: Spiders associated with marine habitats comprise almost 15% of all spider families but fewer than 0.3% of species, illustrating that, while the behavior of living in these areas is very rare, the underlying adaptations enabling it are likely to be ancestral, as evidenced by the array of families in which it is present (**Supplemental Table 1**). In particular, the families that exhibit behavior and physiology adapted for survival in aquatic environments tend to be ground-dwelling species from the RTA clade of spiders, which radiated dramatically during the Cretaceous period (35).

Supplemental Material >

Coupled with the recent molecular findings indicating that adaptations enabling survival in aquatic habitats are likely to have evolved at least 98 Mya (58), this suggests that a major factor that influenced the risky transition back to aquatic and semiaquatic habitats was the opportunity to prey on ground-dwelling arthropods living in marine or riparian zones, perhaps exploiting a relatively untapped foraging niche with less competition for prey from other terrestrial arthropods.

Intertidal areas, in particular, are subject to extremes in which most animals are unable to thrive. Even among arthropods that inhabit this zone, adaptations such as moving up and down the marine zones with the tide or building and retreating into a nest or crevice with an air bubble require that the animal keep track of the timing of the tides. How do intertidal spiders sense the incoming tide? A logical hypothesis is that they use circadian, and especially lunar, rhythms, as tides are intricately connected to the lunar cycle. Circadian rhythms synchronize physiology and behavior with diurnal changes in the environment, resulting in organisms being able to predict changes, such as the day–night cycle, and circadian clocks have been found in several spider families (81, 106, 118). In intertidal areas, the influence of tidal cycles predominates, and many organisms display well-defined rhythms (94). Three biological rhythms are demonstrated by intertidal organisms: tidal, semilunar, and lunar rhythms (75). For example, an intertidal isopod, *Eurydice pulchra*, possesses both circadian and circatidal rhythms (12), while the intertidal spiders *D. formidabilis* and *A. africanus* may have an endogenous mechanism regulating their activity to tidal rhythms (52). However, nothing is known about lunar clocks in spiders, and this seems like a fruitful area for further work, particularly adopting a comparative phylogenetic approach.

Most intertidal spiders require dry land to perform some of their life history functions. Rising sea levels will affect the dynamics of this habitat, possibly inundating previously tidal rocky or sandy areas, which may present a threat to intertidal species survival (112). Nevertheless, given the diversity of both behavioral and physiological adaptations (for example, respiratory organs), spiders in these areas may be better able to cope than many other species. Further study of the natural history of intertidal spiders could provide insight into their ability to adapt to extreme environments and the potential for them to survive the effects of climate change. This research could simultaneously elucidate why fewer intertidal spiders are found in the lower mid-intertidal zones compared to the upper mid-intertidal zones, despite the existence of a myriad of mechanisms to deal with periods of submergence. Specifically, it is interesting that some intertidal spiders are limited to certain intertidal zones, while others freely move up and down the intertidal zones (72, 73); understanding this variation could enable mitigation of the effects of climate change. For example, the decrease of wetland and floodplain areas of braided rivers in Europe, which is expected to continue with climate change, has negative effects on the aquatic species *A. aquatica* and *Dolomedes plantarius* and on the riparian wolf spiders *Pardosa wagleri* and *Arctosa cinerea* (70, 124). Each of these species has its own unique adaptations to these habitats and different dispersal abilities, which likely impacts their ability to migrate to suitable habitats and is already resulting in significant losses of these spiders. It may be that the spatial distribution of intertidal spiders is driven by competitive exclusion (112), by their ability to tolerate differing hemolymph salt concentrations of prey (71), or by their ability to resist abiotic factors (e.g., wave exposure, thermal extremes, desiccation). Additionally, dietary preferences, prey availability, abundance of potential mates, and lack of predators may be key factors (60, 61, 92, 122, 124) driving spatiotemporal dynamics, but the dispersal ability of intertidal spiders should their habitat become compromised remains largely unknown. Many of these basic natural history questions could be answered with an increased awareness that riparian and tidal areas are home to many spiders. Next time you are by a rocky river bed, or on a pebbly beach, pick up some rocks—you are bound to find a spider, and it may well be the first of its kind observed in this habitat.

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