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Dolomedes fishing spider biology: gaps and opportunities for future research

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Dolomedes may easily be considered to be among the most charismatic spider taxa. Known colloquially as fishing or raft spiders, this clade of dolomedid cursorial hunters is speciose with about 100 valid species names. Most *Dolomedes* are large spiders that inhabit water bodies across all continents except Antarctica and, interestingly, South America. *Dolomedes* have captured the attention of researchers and the public alike for their ability to walk on and submerge under water, fish for prey (including small vertebrates), and for their often-bizarre mating behavior that includes examples of male spontaneous death and sexual cannibalism. In this review, we critically evaluate what is known of *Dolomedes* biology, focusing on their systematics and morphology, ecology, behavior, and conservation. Given their close association with water, *Dolomedes* may be particularly vulnerable to the impacts of anthropogenic change and provide an important group of indicator species for understanding the effect of pollution, habitat loss and climate change. We outline a roadmap for future studies that, in our view, will consolidate *Dolomedes* as an ideal model lineage among spiders for addressing a vast array of questions across multiple fields of biology.

KEYWORDS

raft spiders, behavioral ecology, diversity, physiology, evolution, conservation, Dolomedidae

1 Introduction

Spiders are estimated to kill a staggering 400–800 million tons of prey per year globally and serve as generalist predators in terrestrial ecosystems where they contribute significantly to ecosystem function (Nyffeler and Birkhofer, 2017; Michalko et al., 2019). Spiders also comprise important food sources for reptiles (e.g., James, 1991; Manicom and Schwarzkopf, 2011), birds (e.g., Gunnarsson, 2007; Pagani-Núñez et al., 2011), and mammals (e.g., Schulz, 2000; Alves-Costa et al., 2004). In a world increasingly impacted by anthropogenic change, spiders can act as environmental indicators due to their sensitivity to habitat changes and pollution (Pearson, 1994; Milano et al., 2021). Ultimately, the diversity, biomass, and abundance of spiders can reflect ecosystem stability and condition (Büchs, 2003; Oxbrough et al., 2005; Buchholz, 2010).

Although freshwater wetlands cover only 1% of the earth's surface, they are important biomes that harbor more than 40% of global biodiversity (Mittra et al., 2003). A group of spiders that inhabits freshwater bodies and terrestrial habitats is *Dolomedes* Latreille, 1804, commonly known as fishing or raft spiders (Figure 1), a genus comprising over a hundred species found across most continents (Figure 2). Behaviorally and morphologically, *Dolomedes* provide unique opportunities to

explore evolutionary adaptations to life on and near water (e.g., waterborne locomotion, diving and 'fishing' behavior, etc.). *Dolomedes* have also been the subject of numerous behavioral studies that place them in the center of theoretical and empirical research aimed at interrogating evolutionary puzzles such as the evolution of extreme mating behaviors including sexual cannibalism and spontaneous male death, and mating system diversification. The limited observations of reproductive behavior across the genus provide a snapshot of intriguing species-specific variability in sexual cannibalism, female and male mating rates, and more. As species-specific studies accumulate, it is important to synthesize them in a manner that facilitates the recognition of patterns and that enables the testing of general hypotheses. We aim to provide just such a synthesis.

Our authorship team encompasses a group of researchers with diverse interests in *Dolomedes* and thus with distinct knowledge and expertise. Through new and ongoing collaborations, we are surprised by just how frequently *Dolomedes* has featured in studies across a wide range of biological fields. We have each appreciated how knowledge gained in one field of study may be directly or indirectly connected to our own area of research. Additionally, we have identified areas of research for which *Dolomedes* are particularly well suited. Given the expanding

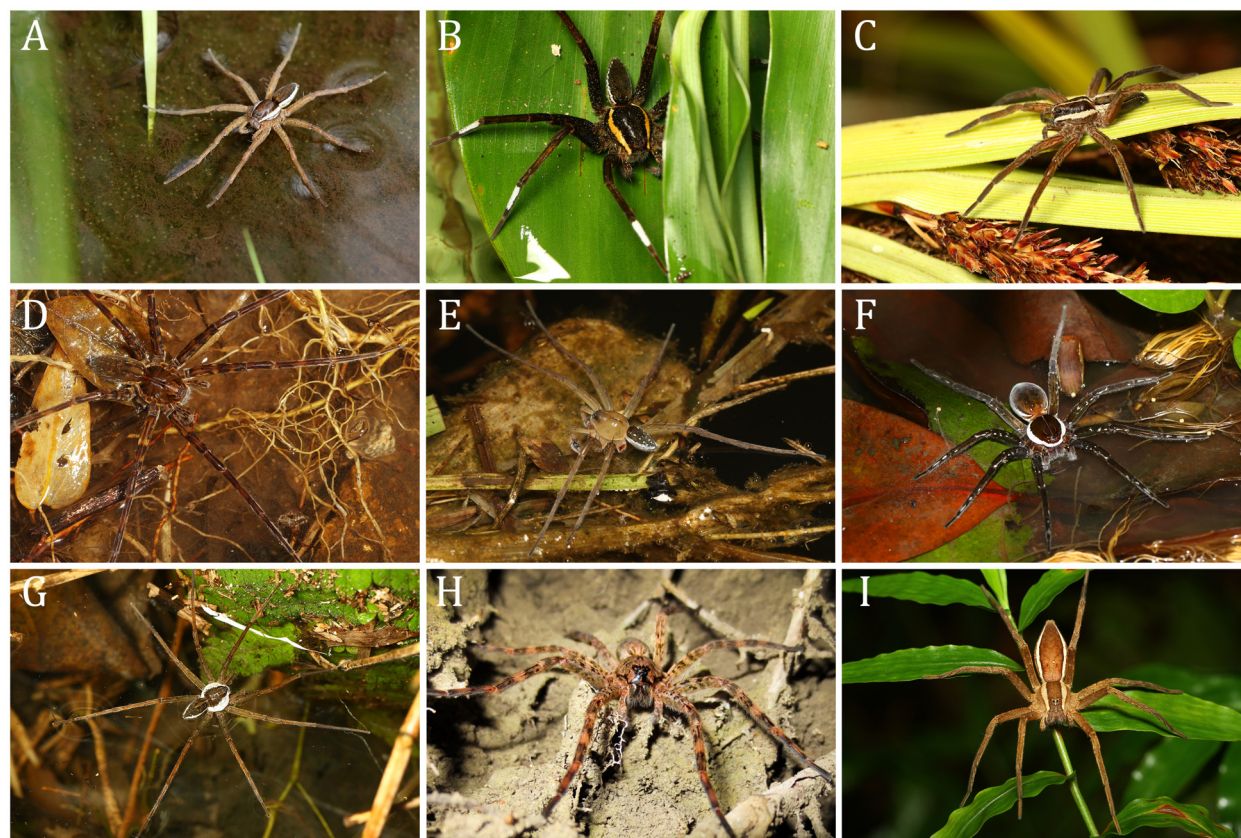


FIGURE 1

A glimpse into diversity of fishing spiders, genus *Dolomedes* Latreille, 1804 in their natural environments, except H: (A) male *D. fimbriatus* (Clerck, 1757); (B) female *D. raptor* Bösenberg and Strand, 1906; (C) female *D. minor* L. Koch, 1876; (D) female *D. bedjanic* Yu and Kuntner, 2024; (E) male of an undescribed *Dolomedes* species from Madagascar; (F) female *D. horishanus* Kishida, 1936; (G) male *D. mizhoanus* Kishida, 1936; (H) female *D. tenebrosus* Hentz, 1844; (I) female *D. sulfureus* L. Koch, 1878.

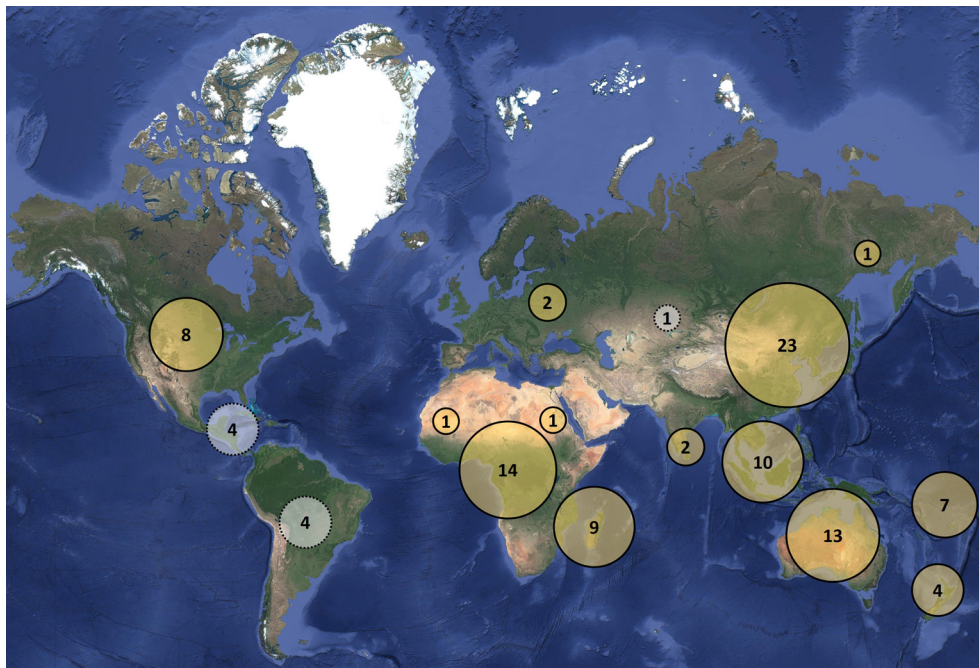


FIGURE 2

Contemporary distribution pattern of the known *Dolomedes* species. Each number represents the number of valid species in the region; yellow circles with black borders represent regions with confirmed *Dolomedes* species; gray circles with dotted line borders denote regions with historic, but doubtful, *Dolomedes* species records.

literature around various aspects of *Dolomedes* biology and the exciting opportunities for future conceptual contributions, a review of *Dolomedes* biology is not only timely, but also necessary.

Over the last 30 years, much of the research on *Dolomedes* has focused on their behavior and ecology, with a resurgence in systematics and morphology work in the early 2000s (Figure 3A). The number of publications on *Dolomedes* has steadily increased over time, although largely dominated by studies coming out of Europe and North America (Figure 3B). The few studies from Oceania are all from New Zealand, with a clear gap in research from Australia, and a similar lack of research in Africa.

Ray and Lyn Forster, the acclaimed New Zealand arachnologists, capture the beauty of *Dolomedes* with their quote “She is a magnificent creature whose body seems clothed with the finest velvet” (Forster and Forster, 1973, page 95). While we agree with the Forsters, wider society tends to lack appreciation of spiders, where arachnophobia (Gerdes et al., 2009) and misinformation (Mammola et al., 2022) abound. Mainstream media stories on *Dolomedes* tend to use hyperbole, focusing on their ability to walk on water and capture fish as prey – not necessarily in a positive light (“horrifying” and “creepiest” are among the sensationalist headings). However, given these large spiders have an ability to engage public audiences they have significant storytelling potential if we can craft narratives of their natural history and ecological importance that move beyond negative clickbait.

The aim of this review is to synthesize the current state of knowledge on the biology of *Dolomedes*. The manuscript composes four key sections. We begin by first asking the question – what is a *Dolomedes*? – and answer this by reviewing the systematics and morphology of the genus, which has recently been reclassified in the

family Dolomedidae Simon, 1876. Second, we explore the ecology of *Dolomedes*, including their habitat use, phenology, predators and parasitoids, and conservation. Thirdly, we delve into *Dolomedes* behavior, ranging from sensory adaptations to their predatory, reproductive and parental behavior. Lastly, we shine a spotlight on the many mysteries still surrounding this spider genus and offer a plethora of future avenues to explore. Our aspiration is for the review to become the go-to guide for researchers interested in this captivating group of arachnids.

2 Systematics and morphology

2.1 Taxonomic history and diversity

Dolomedes is a diverse genus containing 105 species worldwide (World Spider Catalog, 2024). With Clerck’s (1757) descriptions of “*Araneus fimbriatus* Clerck, 1757” and “*A. plantarius* Clerck, 1757” the earliest taxonomic discovery of any species of *Dolomedes* predates Linnaeus’ system of nomenclature by a year. The genus name *Dolomedes* dates back to Latreille (1804) who established it for the “wolf spiders” with a second eye arrangement differing from *Lycosa* Latreille, 1804. According to Latreille (1804), *Dolomedes* was equivalent to “*Les coureuses*” of Walckenaer (1802), a group of spiders that contained “*Araneus mirabilis* Clerck, 1757” = *Pisaura mirabilis* (Clerck, 1757) and “*Aranea marginata* De Geer, 1778” = *Dolomedes fimbriatus* (Clerck, 1757). Although not specified in Latreille’s catalogue, it is generally believed that *D. fimbriatus* is the type species of *Dolomedes*.

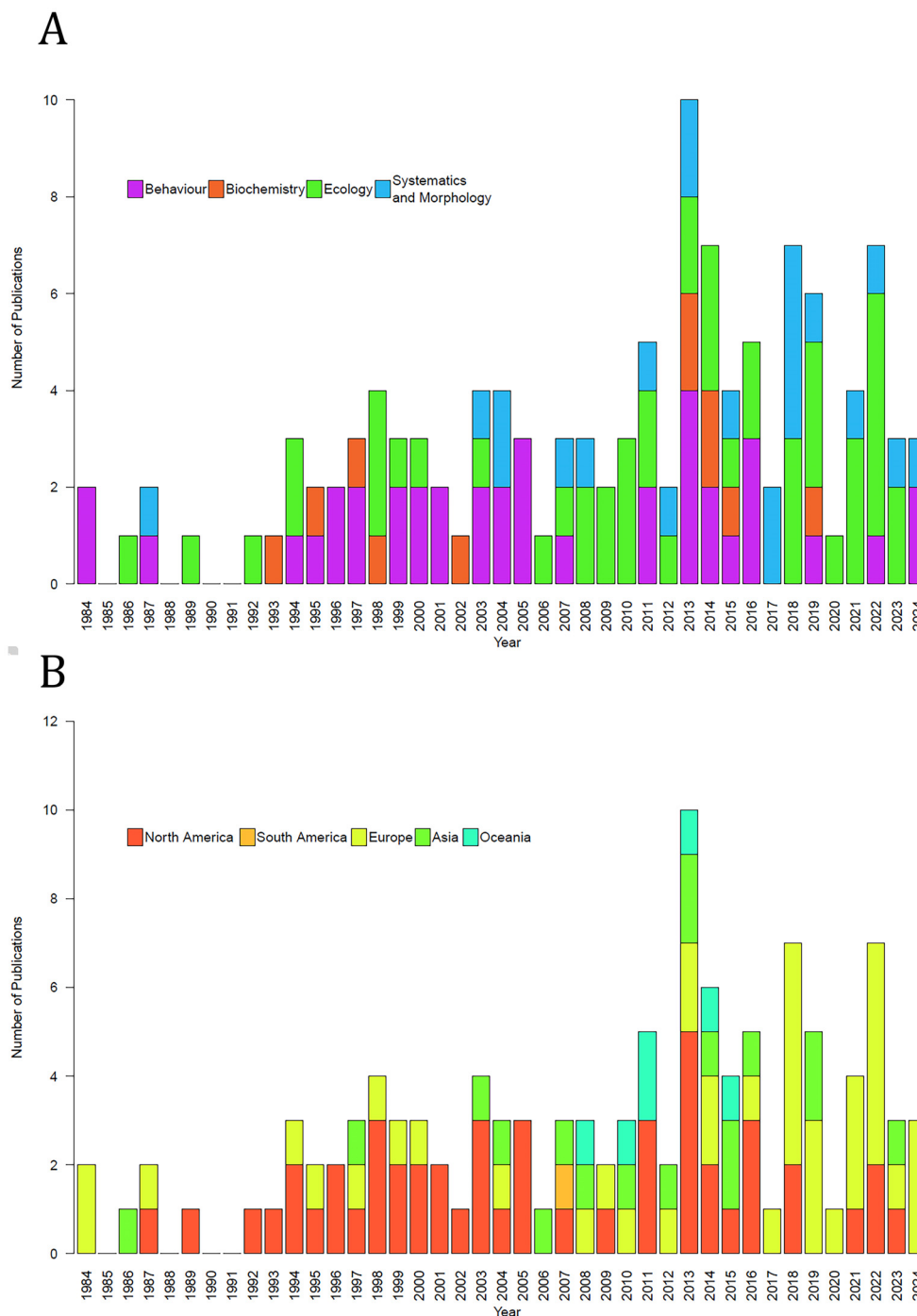


FIGURE 3 Number of *Dolomedes* related research by years, from 1964 to present; with color codon highlighting different (A) research fields and (B) continents where the research was carried out.

Subsequent authors have described new *Dolomedes* species in a non-linear fashion (Figure 4A). Two bursts of taxonomic discovery in *Dolomedes* are evident, one between 1850 and 1950, and another from 2000 onwards. The leading taxonomists are Carl Friedrich Roewer (Roewer, 1955), Robert J. Raven, and Wendy Hebron (Raven and Hebron, 2018). The result of taxonomic discoveries is that *Dolomedes* species diversity is well documented in North America, Europe, Japan, Australia, and New Zealand, but remains

poorly known in regions like Africa and Southeast Asia (Figure 4B). Thus, despite recent species discovery, many unknown pockets of species diversity are likely yet to be uncovered, particularly in the Old-World tropics (Yu and Kuntner, 2024). Depending on location, *Dolomedes* are commonly referred to as fishing or raft spiders. Herein, we use the colloquial names suggested in Yu et al. (2024), where the dolomedid family are the raft spiders, while *Dolomedes* specifically are called fishing spiders.

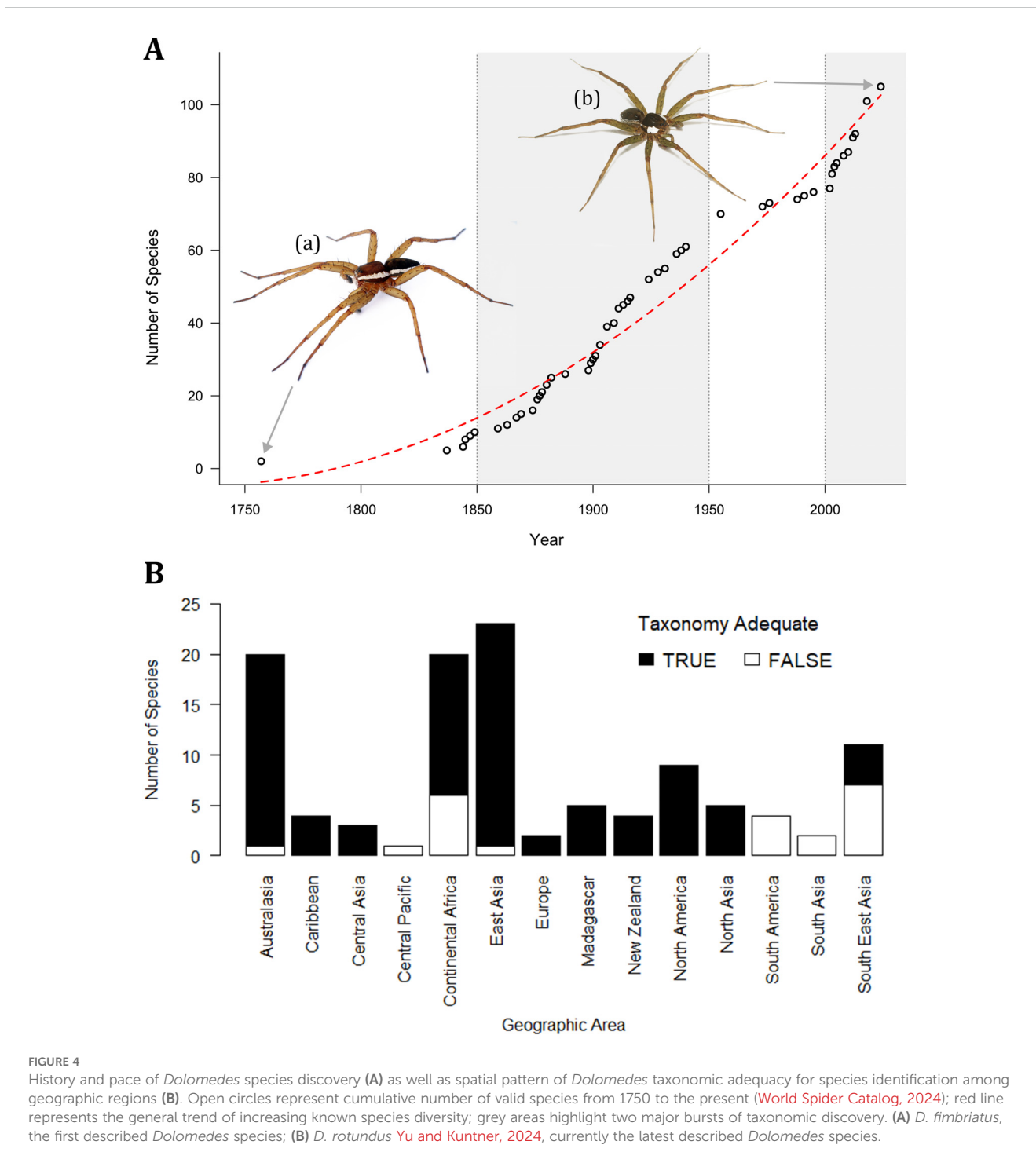


FIGURE 4 History and pace of *Dolomedes* species discovery (A) as well as spatial pattern of *Dolomedes* taxonomic adequacy for species identification among geographic regions (B). Open circles represent cumulative number of valid species from 1750 to the present (World Spider Catalog, 2024); red line represents the general trend of increasing known species diversity; grey areas highlight two major bursts of taxonomic discovery. (A) *D. fimbriatus*, the first described *Dolomedes* species; (B) *D. rotundus* Yu and Kuntner, 2024, currently the latest described *Dolomedes* species.

2.2 General morphology

For a species-rich genus, the morphology of *Dolomedes* is remarkably conserved. *Dolomedes* has a carapace that is longer than wide (Supplementary Figure S1A) with the posterior half slightly higher than the eye region (Supplementary Figure S1B). *Dolomedes* have eight eyes in two rows, with the posterior eye row strongly recurved while the anterior row is straight or weakly re/procurved (Supplementary Figure S1C). The posterior lateral eyes are fully separated from the anterior lateral eyes (Supplementary Figure

S1C). The abdomen of *Dolomedes* is oval with no modifications. *Dolomedes* legs are prograde and usually unmodified (but see Supplementary Figure S2). The fourth leg is the longest, followed by the second or the first leg while the third leg is the shortest.

Dolomedes are well known for their iconic body coloration with distinct white lateral bands, patches, or spots on carapace and/or abdomen over a dark background. This color pattern is uniform in some species (e.g., *D. mizhoanus* Kishida, 1936, *D. hydatostella* Yu and Kuntner, 2024, *D. rotundus* Yu and Kuntner, 2024) but can also show intraspecific variation in females (e.g., *D. raptor* Bösenberg

and Strand, 1906, and *D. horishanus* Kishida, 1936) or in both sexes (e.g., *D. fimbriatus*, *D. plantarius* (Clerck, 1757), *D. kalanoro* Silva and Griswold, 2013, *D. pegasus* Tanikawa, 2012, and *D. sulfureus* L. Koch, 1878; Supplementary Figure S3) (Tanikawa, 2003, Tanikawa, 2012; Tanikawa and Miyashita, 2008; Baillie et al., 2019; Serita, 2019; Yu and Kuntner, 2024). Several species uniformly lack this typical *Dolomedes* coloration in both sexes (e.g., *D. bedjanic* Yu and Kuntner, 2024). In *D. sulfureus*, three coloration morphs are known (Supplementary Figure S3; after Tanikawa and Miyashita, 2008). Although the function of the typical *Dolomedes* white lateral bands is unexplored, studies in *D. raptor* have linked them to foraging (Lin et al., 2015; Tso et al., 2016) (see Diet & Predation Behavior) and male mating success (Lin et al., 2015) (see Reproductive Behavior). The mechanism(s) behind *Dolomedes* color variation has only been studied in *D. plantarius*. Baillie et al. (2019) investigated the proportion of banded and non-banded offspring from 47 broods with their parents of different color phenotypes. They showed that presence/absence of white lateral bands was controlled by a single-gene system where the banded allele was dominant.

All *Dolomedes* species exhibit moderate female-biased sexual size dimorphism (SSD) with the ratio of female to male linear size (= SSD) between 1.00 and 1.88 (see Supplementary Table S1). Exceptions are *D. tenebrosus* Hentz, 1844, *D. okefinokensis* Bishop, 1924, and *D. raptoroides* Zhang et al., 2004 with SSD ratios 2.40, 2.46, and 2.46, respectively (Carico, 1973; Zhang et al., 2004; Silva et al., 2015). The extreme SSD (eSSD; Kuntner and Coddington, 2020) in these species may be indicative of phenotypic adaptations in males that relate to reproduction (see Reproductive Behavior).

2.3 Reproductive morphology

In spiders, genital anatomy provides critical taxonomic evidence to define species boundaries (Eberhard and Huber, 2010; Foelix, 2010). However, genital anatomy is conserved across *Dolomedes*, providing only limited species diagnostics. As the degrees of intraspecific variation vary in different groups of *Dolomedes*, combinations of diagnostic characteristics change even among closely related species (Yu and Kuntner, 2024). In this section, we describe the general anatomy of female epigynum and male pedipalp partially following Sierwald's (1989, 1990) nomenclature. However, our knowledge of the precise interactions of anatomical parts of male and female genitals is currently too preliminary to allow speculation of their precise reproductive function.

The female epigyne of *Dolomedes* is either round, triangular, or pentagonal, but some Australian species have lateral extensions (Raven and Hebron, 2018). The epigyne is highly sclerotized and separated into two lateral lobes by the middle field with usually two membranous windows (Figure 5A). The median field windows in some species (e.g., *D. plantarius*) merge into a larger transparent part while in others (e.g., *D. scriptus* Hentz, 1845) are small and indistinct. Some species from Africa (*D. actaeon* Pocock, 1903 and *D. straeleni* Roewer, 1955), Madagascar (*D. kalanoro*), and Australia (e.g., *D. briangreenei* Raven and Hebron, 2018) have one or two ventral protrusions on their median field (Roewer, 1955; Raven and Hebron, 2018; Yu and Kuntner, 2024). The margins of the median

field and lateral lobes together form two longitudinal epigynal folds that posteriorly lead to the copulatory openings (Figures 5A–C). A looped copulatory duct inserts into a spermathecal base, which connects to a small knob-, horn-, or bulb-shaped head of spermatheca via an indistinct stem. The remainder of spermathecal bases are long, curved, or spiraled, ending with short and flat fertilization ducts (Figures 5B–D). Two species, *D. tenebrosus* and *D. okefinokensis* have unique epigyna (Carico and Holt, 1964) with their median fields lacking membranous windows and their copulatory openings distinctly wider (Figure 5E) (Carico, 1973; Sierwald, 1989). However, their vulvae nonetheless share the common *Dolomedes* gestalt (Figure 5F; see Carico, 1973; Sierwald, 1989). Considering that *D. tenebrosus* and *D. okefinokensis* are both eSSD, their unique epigynal anatomy could determine their mating behavior (Schwartz et al., 2013; see also Reproductive Behavior).

The *Dolomedes* male pedipalp has a U-shaped tegular ring consisting of the tegulum, its distal projection, and a membranous conductor (Figures 6A–C). Unlike pisaurids, *Dolomedes* does not have a distal tegular apophysis; instead, a round, sclerotized saddle sits at the lower center of the tegular ring and connects the tegulum and the subtegulum (Figure 6B). Retrolateral to the saddle sits the highly sclerotized median apophysis which can be hooked (but see *D. tenebrosus* and *D. okefinokensis*; Carico, 1973). A distal sclerotized tube of the apical division that attaches to the embolus, fulcrum, and the lateral subterminal apophysis is a dolomedid feature (Figure 6D; Sierwald, 1990; Yu et al., 2024). *Dolomedes* can be separated from other dolomedids by the embolus with one simple circular or semi-circular loop (but see *D. bistylus* Roewer, 1955) that neither passes the dorsal part of the palp nor extends to the tip of the cymbium (Raven and Hebron, 2018; Yu and Kuntner, 2024). *Dolomedes* palps feature an oval or triangular basal cymbial apophysis. Palpal tibia has a ventral and a retrolateral apophysis (Figures 6A–C). The former is highly conserved across the genus while the latter readily distinguishes species (but, see *D. minor* L. Koch, 1876: Vink and Dupérré, 2010; and *D. tenebrosus*: Carico, 1973). Lengths of the palpal tibia and the whole palp can additionally diagnose species (Tanikawa and Miyashita, 2008; Yu and Kuntner, 2024). When expanded, the left palpal organ rotates clockwise in ventral view. In *D. tenebrosus* the distal sclerotized tube rotates to the position between the tibia and the retrolateral tibial apophysis during mating (Sierwald and Coddington, 1988).

2.4 Phylogeny, evolution and genomics

Although *Dolomedes* has been traditionally classified in Pisauridae Simon, 1890 (World Spider Catalog, 2024), these clades are not each other's closest relatives. Instead, *Dolomedes* with related Oceanian genera has now been reclassified in Dolomedidae (Yu et al., 2024). In a pre-phylogenetic argumentation, Lehtinen (1967) already proposed the use of Dolomedidae, however, the family status for the clade has not been generally accepted due to conflicting topologies (Sierwald, 1990; Griswold, 1993; Zhang et al., 2004; Santos, 2007; Wheeler et al., 2017; Piacentini and Ramirez, 2019) but has recently regained phylogenetic attention (Albo et al., 2017; Hazzi and Hormiga, 2023; Kulkarni et al., 2023). Dolomedidae is now

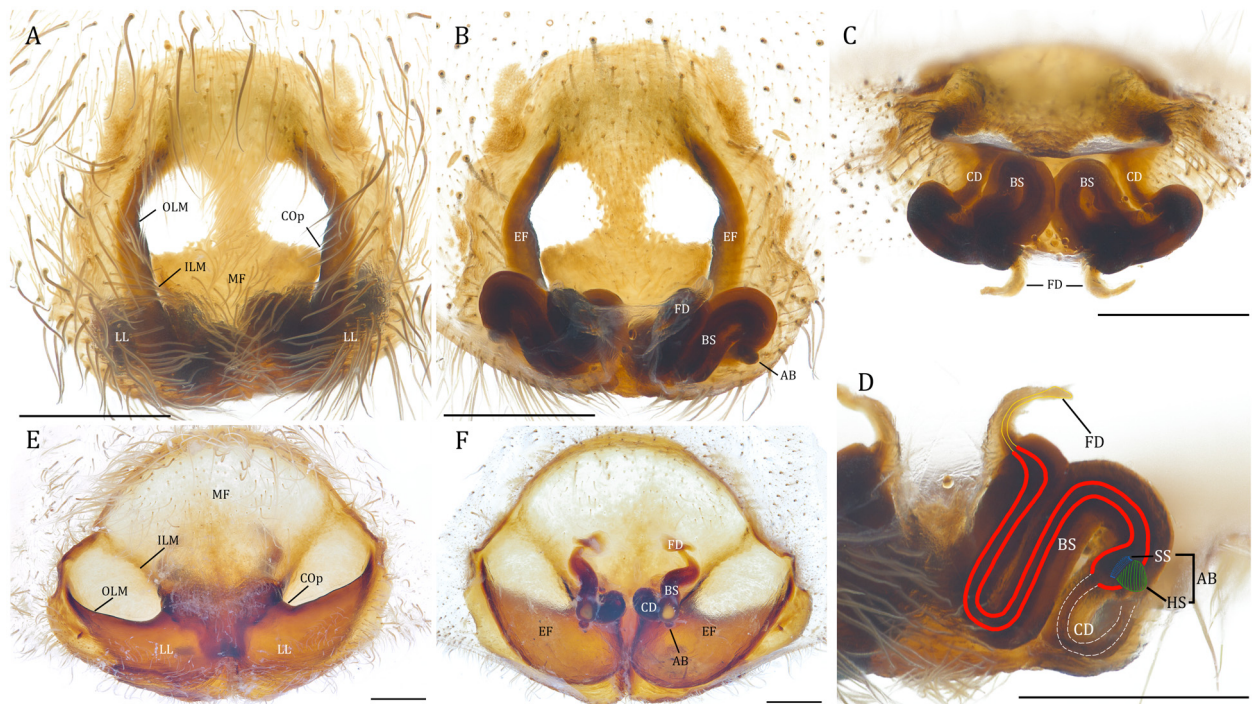


FIGURE 5
 (A–D), Female genitalia of *Dolomedes fimbriatus*, typical of *Dolomedes*: (A) epigyne, ventral view; (B) *idem*, dorsal view; (C) vulva, anterior view; (D) *idem*, posterior view with anatomic structures highlighted in colors: white dot lines, copulatory duct; red bold lines, base of spermatheca; blue dotted region, stem of spermatheca; green lined region, accessory bulb; yellow line, fertilization duct. (E, F), Female genital anatomy of *Dolomedes tenebrosus* Hentz, 1844, representing a unique genital morphology among *Dolomedes*: (E) epigyne, ventral view; (F) *idem*, dorsal view. AB, accessory bulb; BS, base of spermatheca; CD, copulatory duct; COP, copulatory opening; EF, epigynal fold; FD, fertilization duct; HS, head of spermatheca; ILM, interior margin of epigynal fold; LL, lateral lobe; MF, middle field; OLM, outer lateral margin of epigynal fold; SS, stem of spermathecae. Scale bars: 0.5 mm.

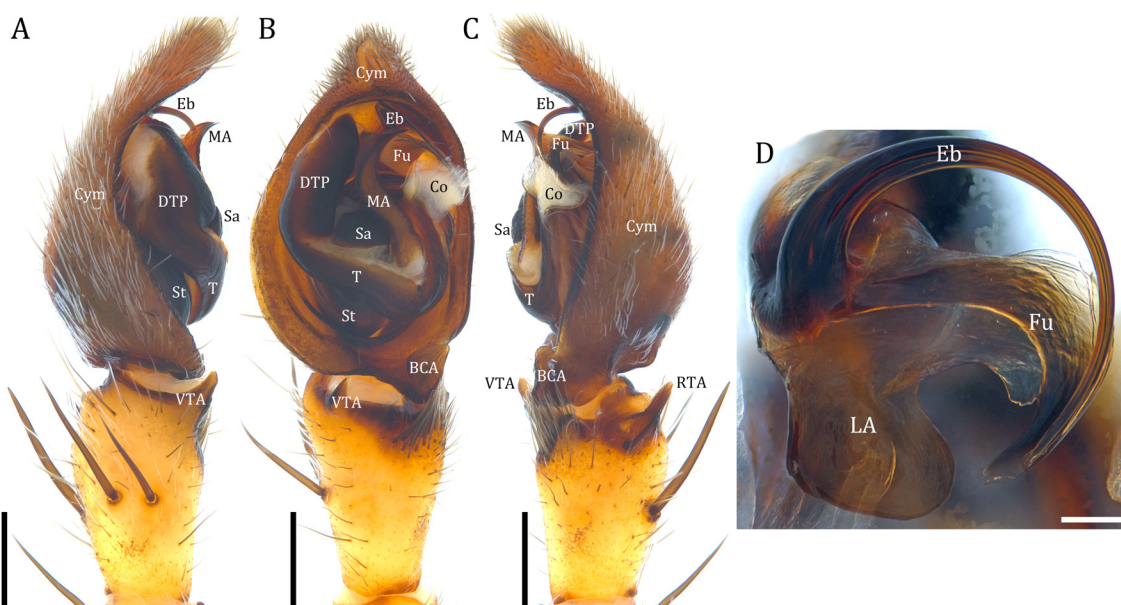


FIGURE 6
 Male pedipalp of *Dolomedes fimbriatus*, typical of *Dolomedes*: (A) left palp, prolateral view; (B) *idem*, ventral view; (C) *idem*, retrolateral view; (D) distal sclerotized tube of the apical division of the expanded right palp. BCA, basal cymbium apophysis; Co, conductor; Cym, cymbium; DTP, distal tegular projection; Eb, embolus; Fu, fulcrum; LA, lateral subterminal apophysis; MA, median apophysis; RTA, retrolateral tibial apophysis; Sa, saddle; St, subtegulum; T, tegulum; VTA, ventral tibial apophysis. Scale bars: A–C: 0.5 mm, D: 0.1 mm.

supported through a phylogenomic analysis of over half of *Dolomedes* species and pisaurid genera (Yu et al., 2024). This phylogeny vastly expands the prior understanding of phylogenetic relationships among *Dolomedes* species that has been limited to regional analyses focused on New Zealand (Vink and Dupérré, 2010), Japan (Ono, 2002; Tanikawa, 2003; Tanikawa, 2012; Tanikawa and Miyashita, 2008), and Madagascar (Yu and Kuntner, 2024). Currently, no fossil *Dolomedes* are known (Wunderlich, 2008; Magalhaes et al., 2020).

Among the most well-known semi-aquatic spiders, *Dolomedes* species are common model organisms in many study fields (see sections below). However, incomplete and conflicting *Dolomedes* phylogenies (see citations above) have hampered further studying the evolution of their remarkable lifestyles and related traits until very recently. Based on the phylogenomic data of more than half of the pisaurids genera and *Dolomedes* species, Yu et al. (2024) investigate the evolutionary shifts of lifestyles and the presence of a capture web, as well as the morphological traits accompanying a semi-aquatic lifestyle. Their results suggest that *Dolomedes* and dolomedids are ancestrally semi-aquatic with several independent reversals to a terrestrial lifestyle (see also Microhabitat use and preference and Locomotion & Dispersal); and ancestrally lacking a capture web without any reversals. Yu et al. (2024) also found that *Dolomedes* and other semi-aquatic dolomedid and pisaurid genera have wider carapaces than the terrestrial genera but with no differences in their legs. They proposed that semi-aquatic spiders need to be large enough to break through the water surface tension to forage under water.

A reference genome is currently available only for *D. plantarius* (GenBank GCA_907164885.2). At 2.8 Gb, its size is among the largest sequenced arachnid genomes (reviewed in Kuntner, 2022). The complete mitochondrial genome of *D. angustivirgatus* Kishida, 1933 has been sequenced with gene arrangement typical of mitochondrial genomes of Entelegynae spiders (Wang et al., 2020). Ten polymorphic microsatellite DNA loci were developed for *D. plantarius* for use in paternity studies and for analysis of population genetics (Ji et al., 2004). The newly available subgenomic data with ultraconserved elements of *Dolomedes* worldwide (Yu et al., 2024) will be useful, beyond phylogenomics, in efforts to generate new sets of microsatellites (Raposo do Amaral et al., 2015).

2.5 Biogeography

Extant *Dolomedes* species are distributed globally (Figure 2). It is noteworthy, however, that South America seems to lack any *Dolomedes* diversity (the few catalogued names are ambiguous or refer to other spider groups), making it the only major continent, in addition to Antarctica, that is thought to lack *Dolomedes*. Furthermore, while some species such as *D. triton* (Walckenaer, 1837), *D. fimbriatus*, and *D. plantarius* are widespread across continents, others such as *D. orion* Tanikawa, 2003 (Okinawa Island) and *D. schauinslandi* Simon, 1899 (Chatham Island archipelago) are narrow island endemics.

Dolomedes is a relatively distal clade on the spider tree of life (Wheeler et al., 2017; Kulkarni et al., 2023). The origin of the genus is hypothesized in the Cenozoic, between 16 and 9 (mid-Miocene)

million years ago (Yu et al., 2024). This relatively recent origin of *Dolomedes* implies that climate oscillations in the Cenozoic (Zachos et al., 2001) may have driven its diversification. Considering that the current distribution patterns of *Dolomedes* include most continents, glacial cycles and land bridges might also have shaped their distribution patterns. Although the origin and the biogeographic history of *Dolomedes* have not been directly tested, preliminary hypotheses can be derived. Considering i) the known sister relationship with the New Caledonian *Bradystichus* Simon, 1884 (Wheeler et al., 2017; Piacentini and Ramirez, 2019; Kulkarni et al., 2023); ii) the monophyly of Dolomedidae containing *Dolomedes* and Australian relatives (Raven and Hebron, 2018; Yu et al., 2024); and iii) the highest *Dolomedes* contemporary species richness in East Asia, one can hypothesize that *Dolomedes* might have originated from either Australasia or Eastern Eurasia.

3 Ecology

3.1 Microhabitat use and preference

Dolomedes inhabit most freshwater-related habitats, each species preferring specific microhabitats with varying flexibility (Figure 7) (Carico, 1973; Jordan et al., 1994; Tanikawa and Miyashita, 2008; Ono, 2009; Vink and Dupérré, 2010; Dickel et al., 2022; Yu and Kuntner, 2024). In regions where multiple species cohabit, they distinctly differentiate their habitat usage (Carico, 1973; Vink and Dupérré, 2010; Dickel et al., 2022). By summarizing the literature, the major differences in habitat preferences among cohabiting *Dolomedes* are: 1) vegetation structure near and above water bodies, 2) velocity and depth of water bodies, and 3) distance to the water bodies. Aside from picking different aquatic microhabitats, we found at least eight species that do not engage water bodies frequently and can inhabit terrestrial habitats away from water (e.g., forest understory, open bushes, or tree trunks; see Supplementary Table S1). These more terrestrial species are found on separate landmasses, including New Zealand (*D. minor* (Figure 1C) and *D. schauinslandi*: Vink and Dupérré, 2010), North America (*D. tenebrosus* (Figure 1H) and *D. albineus* Hentz, 1845: Carico, 1973; Guarisco, 2010), and East Asia (*D. sulfureus* (Figure 1I), *D. silvicola* Tanikawa and Miyashita, 2008, *D. nigrimaculatus* Song and Chen, 1991, and *D. zatsun* Tanikawa, 2003: Tanikawa, 2003; Tanikawa and Miyashita, 2008; Ono, 2009; Chae et al., 2023). These instances of terrestrial lifestyle have, according to the phylogeny, evolved independently (Yu et al., 2024).

The apparent high degree of microhabitat specialization may play a role in limiting heterospecific interactions and matings, even in regions where multiple species are common. Indeed, introgression has only been recorded once between two New Zealand species (Vink and Dupérré, 2010; Lattimore et al., 2011). Cytochrome *c* oxidase subunit I (COI) haplotypes clearly assignable to *D. aquaticus* Goyen, 1888 were present in specimens of *D. minor*, however, the reverse situation is unknown (Vink and Dupérré, 2010; Lattimore et al., 2011). This introgression has only been identified from the southern quarter of the South Island of New Zealand despite the two species also occurring sympatrically elsewhere. It is unknown why

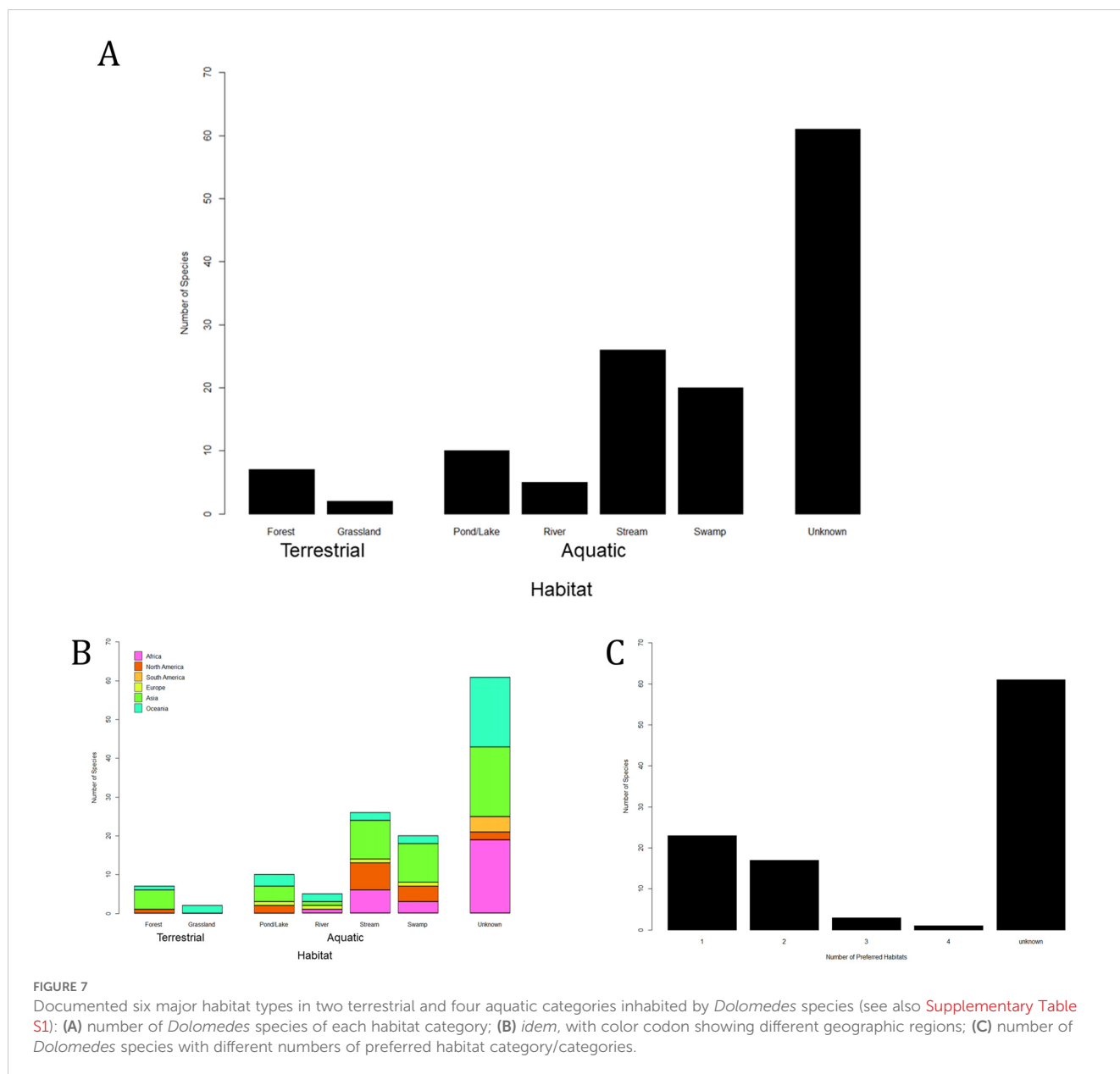


FIGURE 7 Documented six major habitat types in two terrestrial and four aquatic categories inhabited by *Dolomedes* species (see also [Supplementary Table S1](#)): **(A)** number of *Dolomedes* species of each habitat category; **(B)** *idem*, with color codon showing different geographic regions; **(C)** number of *Dolomedes* species with different numbers of preferred habitat category/categories.

introgression only occurs one way in these two species and why it appears to be geographically limited, but it may have something to do with species-specific microhabitat use and/or flexibility. Studies examining microhabitat use and mating behavior in these species will surely shed light on this intriguing pattern.

As a genus well known for its semi-aquatic lifestyle, terrestrial *Dolomedes* species raise questions about adaptations to land versus water. [Tanikawa and Miyashita \(2008\)](#) compared two terrestrial species – *D. sulfureus* and *D. silvicola* – to their semi-aquatic sisters and found that the terrestrial species have relatively longer first legs. A comparative analysis over the breath of *Dolomedes* phylogeny, however, has rejected an overall validity of this hypothesis but instead found that semi-aquatic spiders at higher hierarchical levels are larger-bodied ([Yu et al., 2024](#)). Empirical studies that focus on hydrophobic structures, mechanisms, and behavior related to locomotion on and under water (e.g., claw tuft functional morphology, the ability to dive across species) as well as resilience

to dehydration are now needed to elucidate the differences between semi-aquatic and terrestrial species.

3.2 Phenology

Although there is information on the population dynamics across seasons for a few *Dolomedes* species (e.g., *D. triton*: [Zimmermann and Spence, 1998](#)), most species accounts of phenology can only be estimated according to notes on collections or from anecdotal evidence. Although *Dolomedes* can be found throughout the year, they are most commonly observed during the mating season. Most *Dolomedes* seem to be nocturnal (*D. minor*, *D. aquaticus*: [Williams, 1979a](#); *D. orion*: [Baba et al., 2019](#); *D. raptor*: [Tso et al., 2016](#)), however, North American and European species are active during the day (e.g. *D. scriptus*: [Scott et al., 2016](#); *D. fimbriatus* and *D. plantarius*: [Heldingen, 1993](#); *Dolomedes* sp.: [Nyffeler and Pusey, 2014](#)).

The reproductive season for northern hemisphere species typically spans May to October (Carico, 1973; Guarisco, 2010; Nakajo, 2024), while southern hemisphere species reproduce between September to May, peaking in December and January (Vink and Dupérré, 2010). Many species overwinter as juveniles, though adults have also been found during these months (Carico, 1973; Zimmermann and Spence, 1998; Guarisco, 2010; Nakajo, 2024; Miyashita, 1986).

Many species require one to two years of development and live for several seasons (Schmidt, 1957; Zimmermann and Spence, 1998; Nakajo, 2024). This varies not only between species, but also within species. For example, in *D. sulfureus*, juveniles will overwinter once or twice to reach maturity depending on hatching time. Such differences in overwintering strategy might relate to the cessation of juvenile growth under short daylight conditions (Miyashita, 1986). Maturation time can also differ between the sexes, which may relate to variation in SSD. For example, Nakajo (2024) suggests male *D. raptor* require a year to mature, while the much larger females may need two additional years. Sex ratios in *Dolomedes* can fluctuate over the season, shifting from male-biased to female-biased, likely due to mating behavior, including sexual cannibalism and spontaneous male death (Zimmermann and Spence, 1992; Schwartz et al., 2013). Furthermore, protandry, or the patterns of males maturing before females, appears common (*Dolomedes tenebrosus*: Schwartz et al., 2013; *D. triton*: Johnson, 2004, Johnson, 2005). We lack data on population sex-ratio and seasonality for most species, yet this information is crucial for understanding aspects of their biology, especially as it relates to reproduction and mating systems.

3.3 Predators and parasitoids

Dolomedes are known to be important to nutrient flow in riparian systems (Collier et al., 2002), through their role as predators of aquatic invertebrates and vertebrates. However, their role as prey, and therefore as nutrient transfer to higher trophic levels is poorly documented.

There are sporadic references to *Dolomedes* as prey to generalist predators. These include little blue heron (*Egretta caerulea*) (Carico, 1973), frogs (Suter, 2003; Loc-Barragán et al., 2017), fish (Figiel and Miller, 1994), owls (Lindsay and Ordish, 1964), and *Parasteatoda tepidariorum* cobweb spiders, documented with *D. tenebrosus* and *D. albineus* specimens in their webs (Guarisco, 2010). *Dolomedes fimbriatus* and *D. striatus* Giebel, 1869 occasionally fall prey to the purple pitcher plant (*Sarracenia purpurea*) when using it as a refuge and hunting ground, although even newly emerged spiderlings can avoid pitcher plant predation (Leech and Buckle, 1987; Zander, 2016). Carico (1973) suggested that sphecoid wasps hunt *Dolomedes*, but this predation appears rare, with only occasional instances by generalist species (Krombein, 1979; Polidori et al., 2007). Furthermore, Carico (1973) speculated that visual predators must be important to multiple *Dolomedes* species given their cryptic coloration which helps them blend into their respective habitats.

The New Zealand fernbird (*Megalurus punctatus*) is a notable predator of *Dolomedes*, feeding on all three mainland New Zealand species (Harris, 1986; Parker, 2002). Fernbirds partially specialize in *Dolomedes*, taking spiderlings from nursery webs for their nestlings and consuming adult females (Forster and Forster, 1999; Parker, 2002). Bird predation is assumed to influence habitat selection in *Dolomedes triton*, with higher population densities forming in habitats with more potential refuges from bird and fish predators (Jordan et al., 1994). This suggests bird predation affects the behavior and habitat selection of many *Dolomedes* species, driving them to remain inconspicuous. The impact of bird predation on spiders varies by spider family (Gunnarsson, 2007), presenting the need for more research on its effects on *Dolomedes*. Future studies should examine how bird predation influences *Dolomedes* microhabitat selection and activity cycles to better understand its role in shaping their behavior.

Predatory fish also indirectly affect *Dolomedes*. While anecdotal evidence found fish eating semi-aquatic spiders (Jordan et al., 1994), experimental evidence shows that direct effects of fish predation are limited. In experimental pools, bluegill sunfish presence reduced average *D. triton* body size but not population size, suggesting avoidance strategies or competition for prey (Figiel and Miller, 1994). *Dolomedes triton* escape behavior is ineffective against simulated trout (*Oncorhynchus mykiss*) attacks (Suter and Gruenwald, 2000a) implying fish predation on *Dolomedes* is a relatively minor evolutionary factor. Similar studies, however, are needed in other *Dolomedes* species.

Dolomedes have numerous defense mechanisms against predation. Touch and vibration are most important in threat detection, with vision being used only secondarily, if at all (Williams, 1979a; Suter, 2003). When under threat, *Dolomedes* can use their rapid locomotion to escape. Williams (1979a) found that New Zealand *Dolomedes* tend to escape by either submerging under water or dropping to the ground (see also Locomotion & Dispersal). However, *D. dondalei* Vink and Dupérré, 2010 will run onto the surface of rivers, even allowing the current to take it further downstream. This species is also more difficult to disturb, indicating it could rely more on crypsis than escape behavior (Williams, 1979a). *Dolomedes triton* also has specialized escape behavior against frog attack, involving leaping away from the surface of the water. This behavior was tested against two frog species under laboratory conditions, and when the *Dolomedes* deployed this behavior, they mostly escaped predation (Suter, 2003). The behavior is effective in the wild, as Krupa (2002) found *Dolomedes* make up only a small proportion of frog gut contents.

Dolomedes are also preyed upon by parasitoid pompilid wasps, as evidenced by prey records in North America, Europe, New Zealand and Eastern Russia (Richards and Hamm, 1939; Harris, 1999; Kurczewski and Edwards, 2012; Kurczewski and Kiernan, 2015; Kurczewski et al., 2017; Kochetkov and Loktionov, 2019), laboratory evidence of pompilid predation on *Dolomedes* in Japan (Shimizu, 1992), as well as assumed interactions in Ireland (O'Hanlon and O'Connor, 2021) and India (Rajmohana, 2017). Pompilids often rob nests of other species, leading to *Dolomedes* becoming prey for pompilids that do not hunt them directly

(Harris, 1999). Wasps hunt *Dolomedes* predominantly by visual cues (Shimizu, 1992) but can also utilize their antennae to follow scent trails left by spiders (Harris, 1987; Harris, 1999), and then paralyze the spider with venom. At least one case is noted of a *Dolomedes* resisting capture by biting a wasp (Kurczewski and Edwards, 2012). After paralysis, the spider is dragged back to the wasp's nest. The hydrophobic nature of *Dolomedes* can be used by wasps to ride them as rafts, sometimes propelling themselves along the water using their wings (Evans and Yoshimoto, 1962; Shimizu, 1992; Kurczewski and Edwards, 2012). Eggs are laid on the spider, after which *Dolomedes* can be large enough to sustain a wasp larva through several early instars (Harris, 1999).

Generally, Pompilidae target spiders based on their ecology, but there is also evidence of specialization on *Dolomedes*. In New Zealand, nests of the introduced Australian *Cryptochelius australis* were found to have large numbers of *Dolomedes*. However, there are also reports of this species preying upon *Miturga* and *Ulidon* spiders (Harris, 1999; Martin, 2012). In North America, *Anoplius depressipes* is a specialist on Dolomedidae and Pisauridae, predominantly targeting *Dolomedes*, though in some cases hunting *Pisaurina mira* (Kurczewski and Edwards, 2012; Kurczewski and Kiernan, 2015; Kurczewski et al., 2017). *Anoplius depressipes* are also adapted to walk across water and dive to capture their prey (Evans and Yoshimoto, 1962; Roble, 1985; Kurczewski and Edwards, 2012). These traits are shared with *Anoplius eous*, however, while laboratory data shows this species to specialize on *Dolomedes*, it seems to hunt *Pardosa pseudoannulata* (Lycosidae) in the wild (Iwata, 1939; Shimizu, 1992). Details of pompilid predation and other predation on *Dolomedes* can be found in Table 1.

Mantis lacewings (Mantispidae) are also spider-specific parasitoids (Kaston, 1938). Unlike the above-mentioned wasps, mantispid larvae target spider eggs by "hitchhiking" on spiders then entering their egg sacs when the female spiders are laying eggs (Haug et al., 2018). So far, direct record of Mantispidae parasitizing *Dolomedes* is only known from a female *D. bedjanic* from Madagascar, where Yu and Kuntner (2024) found a mantispid larva in the spider's epigastric furrow.

3.4 Conservation

Despite their ecological importance, spiders are rarely the focus of conservation programmes (Milano et al., 2021) but wetlands, where many *Dolomedes* are located, are estimated to have decreased between 33% and 87% since the 18th Century (Davidson, 2014; Hu et al., 2017). Wetlands provide vital ecological services, including temperature regulation, pollution filtering, and surface runoff control (Zedler and Kercher, 2005). Unfortunately, these vital habitats face significant degradation from urbanization, agriculture, pollution, and climate change (Davidson, 2014; Hu et al., 2017). Monitoring organisms like spiders can help gauge the impact of human activities on these crucial habitats.

Two species of *Dolomedes* are of current conservation interest; *D. plantarius* from Europe and *D. schauinslandi* from the Chatham Islands of New Zealand. The former is rated as "vulnerable" on the IUCN Red List (World Conservation Monitoring Centre, 1996) while the latter is classified as "At Risk: Relict" in New Zealand (Sirvid et al., 2021).

Dolomedes plantarius is one of the most widespread *Dolomedes* species, distributed from Siberia to Britain and from the Apennines to Scandinavia (World Spider Catalog, 2024). However, the species prefers very specific habitats which are in general well-vegetated open water bodies with low velocity (Dickel et al., 2022), such as lowland rivers, bogs, fens, and oxbows (Smith, 2000; Van Helsdingen, 2005; Duffey, 2012). *Dolomedes plantarius* is considered threatened by habitat loss and degradation caused by human activities (Smith, 2000; Duffey, 2012; Milano et al., 2021). Although our knowledge of their distribution ranges remains largely incomplete, recent estimations and modeling of their suitable habitats (Leroy et al., 2013; Leroy et al., 2014; Monsimet et al., 2020; Milano et al., 2022) show that *D. plantarius* is under more pressure from climate and land use changes than *D. fimbriatus*. Compared to *D. fimbriatus*, *D. plantarius* exhibits narrower habitat preferences as well as poorer ability of both waterborne and airborne long-distance dispersal (Monsimet et al., 2020; Monsimet et al., 2022; see also Locomotion & Dispersal). Overall, the distribution ranges of *D. plantarius* are estimated to decrease and shift northward following the trends of global temperature rising (Leroy et al., 2013; Leroy et al., 2014; Monsimet et al., 2020; Milano et al., 2022).

Dolomedes plantarius is listed in the national Red Lists of 13 European countries with nine of them protecting the species and its habitats by law (see Milano et al., 2021). The United Kingdom (UK) is the only country that applies further actions in protecting *D. plantarius* (Smith, 1996, Smith, 2000, Smith, 2005¹; Duffey, 2012; Smith et al., 2013). There are only three disjunct natural populations of *D. plantarius* left in the UK (Duffey, 2012). Therefore, the species is suggested to be highly vulnerable with urgent need of conservation action to prevent local extinction. Habitat restoration work and regular census of *D. plantarius* at Lopham Fen National Nature Reserve has occurred since 1991 to prevent degradation of current water bodies and create new habitats (Smith, 1996, Smith, 2000, Smith, 2005¹). Although long-term monitoring suggests that the population sizes of *D. plantarius* vary drastically across years, progressive vegetation restoration at the site has allowed considerable expansion of the population over the last decade (Smith, 2005¹; Smith, 2020). In addition, the conservation framework of *D. plantarius* in the UK also includes translocation. Starting in 2010, Smith et al. (2013) launched the translocation project of *D. plantarius* aiming to expand its populations from three to 12 in the UK following the IUCN protocols. By 2021, the translocation project had successfully increased the *D. plantarius* populations from three to seven (Milano et al., 2021).

Unlike *D. plantarius*, the degradation of wetlands does not explain the decline of *D. schauinslandi*, found in forest and scrublands away from waterways on three small islands in the Chatham Island archipelago (Hokoreoro/Rangatira/South East, Maung'Re/Mangere, and Houruakopara) in New Zealand. It was previously found on Rangihau/Rangiauria/Pitt Island before going extinct in the early 1900s (Vink and Dupérré, 2010) and was likely also found on Rēkohu/Wharekauri/Chatham Island.

1 Smith, H. (2005). Fen raft spider recovery project: report for redgrave and lopham fen 2001–2005 (Unpublished report to Natural England). Available at: https://www.dolomedes.org.uk/conservation/Redgrave_Lopham_Fen.

TABLE 1 Overview of records and studies about predators that prey on *Dolomedes* species.

Predator Taxonomic Group	Predator	Recorded Prey	Specialist or Generalist	Region	Method of Study	References
Bird	Little blue heron <i>Egretta caerulea</i>	<i>Dolomedes triton</i>	Generalist	North America	Gut contents	Carico, 1973
	New Zealand fernbird <i>Megalurus punctatus</i>	<i>Dolomedes minor</i> , <i>D. aquaticus</i> , <i>D. dondalei</i>	Specialist – uses spiderlings to feed nestlings	New Zealand	Behavioral observations	Forster and Forster, 1999; Harris, 1986; Parker, 2002
	Morepork <i>Ninox novaeseelandiae</i>	<i>Dolomedes</i> sp.	Generalist	New Zealand	Gut contents	Lindsay and Ordish, 1964
Frog	Bullfrogs <i>Rana catesbiana</i>	<i>Dolomedes triton</i>	Generalist	North America	Laboratory experiments, Gut contents	Krupa, 2002; Suter, 2003
	Green frogs <i>Rana clamitans</i>	<i>Dolomedes triton</i>	Generalist	North America	Laboratory experiments	Suter, 2003
	Ferrer's Leopard Frog <i>Lithobates forreri</i>	<i>Dolomedes</i> sp.	Diet unknown, but likely generalist	North America	Behavioral observations	Loc-Barragán et al., 2017
Fish	Bluegill sunfish <i>Lepomis macrochirus</i>	<i>Dolomedes triton</i>	Generalist	North America	Laboratory experiment	Figiel and Miller, 1994
Spider	Cobweb spider <i>Parasteatoda tepidariorum</i>	<i>Dolomedes tenebrosus</i> , <i>D. albineus</i>	Generalist	North America	Observations from webs	Guarisco, 2010
Pitcher plant	Purple pitcher plant <i>Sarracenia purpurea</i>	<i>Dolomedes fimbriatus</i> , <i>D. striatus</i>	Generalist (predation assumed to be uncommon)	North America, Europe	Collection from pitcher plants	Leech and Buckle, 1987; Zander, 2016
Pompilid wasps	<i>Anoplius eous</i>	<i>Dolomedes saganus</i> , <i>D. sulfureus</i>	Specialist in laboratory, but hunts <i>Pardosa pseudoannulata</i> in wild	Japan	Laboratory experiments, field observations	Iwata, 1939; Shimizu, 1992
	<i>Anoplius (Anoplius) depressipes</i>	<i>Dolomedes scriptus</i> , <i>D. striatus</i> , <i>D. tenebrosus</i> , <i>D. triton</i> , <i>D. vittatus</i>	Specialist, but will also hunt <i>Pisaurina mira</i>	North America	Behavioral observations	Evans and Yoshimoto, 1962; Kurczewski and Edwards, 2012; Kurczewski and Kiernan, 2015; Kurczewski et al., 2017; Roble, 1985;
	<i>Anoplius (Anoplius) sundukovi</i>	<i>Dolomedes</i> sp.	Insufficient information	Eastern Russia	Behavioral observation	Kochetkov and Loktionov, 2019
	<i>Anoplius (Lophopompilus) atrox</i>	<i>Dolomedes</i> sp., <i>D. scriptus</i> , <i>D. tenebrosus</i> , <i>D. vittatus</i>	Generalist	North America	Behavioral observations	Krombein, 1979; Kurczewski and Edwards, 2012; Kurczewski and Kiernan, 2015; Kurczewski et al., 2017
	<i>Anoplius (Lophopompilus) samariensis</i>	<i>Dolomedes</i> sp.	Generalist	Japan	Prey records	Evans and Yoshimoto, 1962
	<i>Arachnospila scelestus</i>	<i>Dolomedes</i> sp.	Generalist	North America	Behavioral observation, prey records	Evans and Yoshimoto, 1962; Krombein, 1979; Kurczewski and Kiernan, 2015

(Continued)

TABLE 1 Continued

Predator Taxonomic Group	Predator	Recorded Prey	Specialist or Generalist	Region	Method of Study	References
Pompilid wasps	<i>Cryptocheilus australis</i>	<i>Dolomedes minor</i> , <i>Dolomedes</i> spp.	Specialist, but also preys on <i>Miturga</i> and <i>Ulidon</i>	New Zealand (but species native to Australia)	Behavioural observations, nest contents	Harris, 1999; Martin, 2012
	<i>Entypus fulvicornis</i>	<i>Dolomedes tenebrosus</i>	Generalist	North America	Behavioural observations	Kurczewski et al., 2017
	<i>Entypus unifasciatus unifasciatus</i>	<i>Dolomedes albineus</i> , <i>D. tenebrosus</i>	Generalist	North America	Behavioural observations	Kurczewski and Edwards, 2012; Kurczewski and Kiernan, 2015; Kurczewski et al., 2017
	<i>Priocnemis (Priocnemissus) minorata</i>	<i>Dolomedes tenebrosus</i>	Generalist	North America	Behavioural observations	Krombein, 1979; Kurczewski and Kiernan, 2015; Kurczewski and Kurczewski, 1972
	<i>Priocnemis (Trichocurgus) monachus</i>	<i>Dolomedes aquaticus</i> , <i>D. minor</i>	Generalist	New Zealand	Nest contents	Harris, 1999
	<i>Priocnemis (Trichocurgus) nitidiventris</i>	Unidentified New Zealand mainland <i>Dolomedes</i>	Generalist	New Zealand	Nest contents	Harris, 1999
	<i>Sphictostethus fugax</i>	<i>D. minor</i>	Generalist	New Zealand	Nest contents	Harris, 1999
	<i>Sphictostethus nitidus</i>	<i>D. aquaticus</i> , <i>D. dondalei</i> , <i>D. minor</i>	Generalist, but preys on large spiders including <i>Dolomedes</i>	New Zealand	Nest contents	Harris, 1999
	<i>Tachypompilus ferrugineus ferrugineus</i>	<i>Dolomedes albineus</i> , <i>D. scriptus</i> , <i>D. tenebrosus</i>	Generalist	North America	Behavioural observations	Krombein, 1979; Kurczewski and Edwards, 2012; Kurczewski and Kiernan, 2015; Kurczewski et al., 2017
<i>Tachypompilus jerrugineus</i>	<i>Dolomedes</i> sp.	Generalist	North America	Laboratory experiments	Evans and Yoshimoto, 1962	
Sphecid wasps	<i>Sceliphron caementarium</i>	<i>Dolomedes</i> sp.	Generalist	North America	Prey records	Krombein, 1979
	<i>Sceliphron spirifex</i> or <i>S. caementarium</i> (owner of nest unknown)	<i>Dolomedes fimbriatus</i>	Generalist	Europe	Nest contents	Polidori et al., 2007
Mantis lacewing	Mantispidae gen. sp.	<i>Dolomedes bedjanic</i>	Unknown	Madagascar	Prey records	Yu and Kuntner, 2024

Despite being a threatened species, little is known about its biology, making it an obvious subject for conservation genomics and ecology research. In particular, understanding the interacting effects of dispersal behavior, impacts of invasive predators, habitat availability and quality, prey availability, and climate change are essential for the future of this species.

It is unlikely that these two species are the only *Dolomedes* affected by global change, but understanding the impacts of anthropogenic pressures is difficult when we lack diagnosis of

threat status for most species. A relatively new research avenue involves studying the effects of heavy metals and pharmaceuticals on aquatic spiders as bioindicators of waterway pollutants. For example, Ortega-Rodriguez et al. (2019) found that an unidentified *Dolomedes* had the highest methylmercury concentration among numerous shoreline spiders, likely reflecting their aquatic prey diet. Given their close proximity to water and ease of observation, using *Dolomedes* as bioindicators of a range of anthropogenic impacts provides a fruitful avenue for future research.

4 Behavior

4.1 Sensory physiology

Given that many *Dolomedes* species hunt on water, a strong focus of their sensory physiology has been the detection of waterborne prey. Prey detection and stimulus discrimination has been well-investigated in *D. triton* (Bleckmann and Barth, 1984; Bleckmann and Rovner, 1984; Bleckmann and Bender, 1987; Bleckmann and Lotz, 1987; Bleckmann et al., 1994; Suter, 2003) as well as in *D. okefinokensis* (Bleckmann et al., 1994). *Dolomedes* can locate prey using different environmental cues, with artificially generated water surface waves showing the highest spider responsiveness, followed by airborne vibrations (Bleckmann and Rovner, 1984; Bleckmann and Barth, 1984). Notably, visual stimuli were shown to trigger spider reactions in a few cases as well (Bleckmann and Rovner, 1984).

Dolomedes are likely to detect water surface waves using lyriform organs (a slit organ on the metatarsus of the legs; Figure 8A) and airborne vibrations using trichobothria (long, thick sensilla; Figure 8B). Studies have shown that spiders are attracted to stimuli with an irregular mix of low and high frequencies, including those about 30–40 Hz (Bleckmann and Barth, 1984; Bleckmann and Lotz, 1987). In comparison, wind generated surface waves rarely exceed 10 Hz (Bleckmann and Rovner, 1984). Sensory abilities and reactions to wave sources also seem to differ between species, as shown in a comparative study on *D. fimbriatus* and *D. triton* (Bleckmann and Barth, 1984). *Dolomedes fimbriatus* has a larger error angle (i.e., the spider is less accurate in targeting the wave source) and is slower than *D. triton* (Bleckmann and Barth, 1984). Both the lyriform organ and trichobothria were shown to be crucial to minimize the error angle when spiders move towards or escape from a wave source (Bleckmann and Rovner, 1984; Suter, 2003). The morphology and ultrastructure of *Dolomedes* sensory structures is only briefly touched on by a few studies. For New Zealand species mechanoreceptive sensilla and contact-chemoreceptors have been discussed (Williams, 1979a), but never described in further detail. There is much room for comparative studies on sensory systems across *Dolomedes*, especially focused on terrestrial versus water-associated species.

Dolomedes, like the majority of spider groups, are thought to have rather poor vision. Nonetheless, *Dolomedes* use visual cues during predation and presumably also during courtship (Roland and Rovner, 1983; Bleckmann and Barth, 1984). *Dolomedes triton*, for example, was found to run slower and shorter distances towards prey when blinded (Bleckmann and Barth, 1984). They also appear able to focus light under water, because the surrounding body hairs capture a thin air layer (Williams, 1979a). However, the extent to which they might use vision underwater, and whether this varies across species, has yet to be explored.

There are detailed descriptions of the architecture of the eyes of *D. aquaticus* and other New Zealand *Dolomedes* species (Blest and Day, 1978; Williams, 1979b) as well as the tapetum lucidum (a light-reflecting layer inside the eye) of *D. tenebrosus*, *D. triton*, *D. scriptus*

and *D. vittatus* Walckenaer, 1837 (Benson and Suter, 2013). But apart from those studies, there has been little work done on the anatomy of the visual system. To our knowledge, no studies have explored the processing pathways of the primary and/or secondary eyes of any *Dolomedes* species. Such a study would be interesting, as major differences were recently discovered in the central nervous system of primarily web building versus cursorial spiders. While cursorial species possess prominent higher order processing centers (mushroom bodies) and visual neuropils, web builders have those regions reduced or absent, however their leg neuropils are proportionally larger (Steinhoff et al., 2023). We would predict *Dolomedes* central nervous system patterns to be like those described in other cursorial species, but detailed neuroanatomical studies are needed.

4.2 Locomotion and dispersal

Given their often-close connection with water, *Dolomedes* are highly capable of moving across its surface (Figure 9A). Early research explored their patterns of locomotion across terrestrial versus water surfaces (multiple species: Ehlers, 1939; *D. fimbriatus*: Barnes and Barth, 1991; *D. triton*: Shultz, 1987) and comparative studies suggest that *Dolomedes* are specialized for water locomotion (Shultz, 1987; Barnes and Barth, 1991; Stratton et al., 2004).

Two types of water surface gaits have been described – rowing (*D. triton*: McAlister, 1960; Shultz, 1987; *D. plantarius*: Gorb and Barth, 1994; Suter and Gruenwald, 2000a, Suter and Gruenwald, 2000b) and galloping or running (Figure 9B; *D. triton*: Suter and Wildman, 1999; *D. plantarius*: Gorb and Barth, 1994); the latter of which tends to be associated with prey capture (*D. plantarius*: Gorb and Barth, 1994). Rowing *Dolomedes* can reach speeds of <0.27m/s (reviewed in Suter, 1999) and involves the use of leg pairs II and III in synchrony while legs I and IV are motionless and held parallel to the direction of movement. Galloping is much faster, with individuals moving more than 0.4m/s, and involves leg pairs I, II, and III moved in synchrony (reviewed in Stratton et al., 2004). Numerous studies have explored the posture, gait, and rowing behavior of *Dolomedes* on different substrates and/or on water with different viscosity and depth (e.g., *D. aquaticus*: Campbell et al., 2014; *D. triton*: Shultz, 1987; *D. fimbriatus*: Barnes and Barth, 1991) while others have explored their hydrophobicity and escape responses across water (*D. aquaticus* and *D. minor*: Williams, 1979a).

In 2004, Stratton and colleagues greatly expanded our understanding of spider locomotion on water by conducting a comparative study exploring water-surface locomotion from 249 spider species across 42 families. Trechaleidae Simon, 1890 and Pisauridae (at the time, containing *Dolomedes*) were the only focal families to show a monomorphy for both a hydrophobic surface (remaining dry and completely above the water surface) and movement by rowing. All five *Dolomedes* species tested (*D. albineus*, *D. tenebrosus*, *D. triton*, *D. gertschi* Carico, 1973, and *D. vittatus*) demonstrated rowing and the genus was used as the standard against which other species were compared (Stratton et al., 2004). A specialized rowing gait was hypothesized to have evolved at least 4 times independently, with hydrophobicity

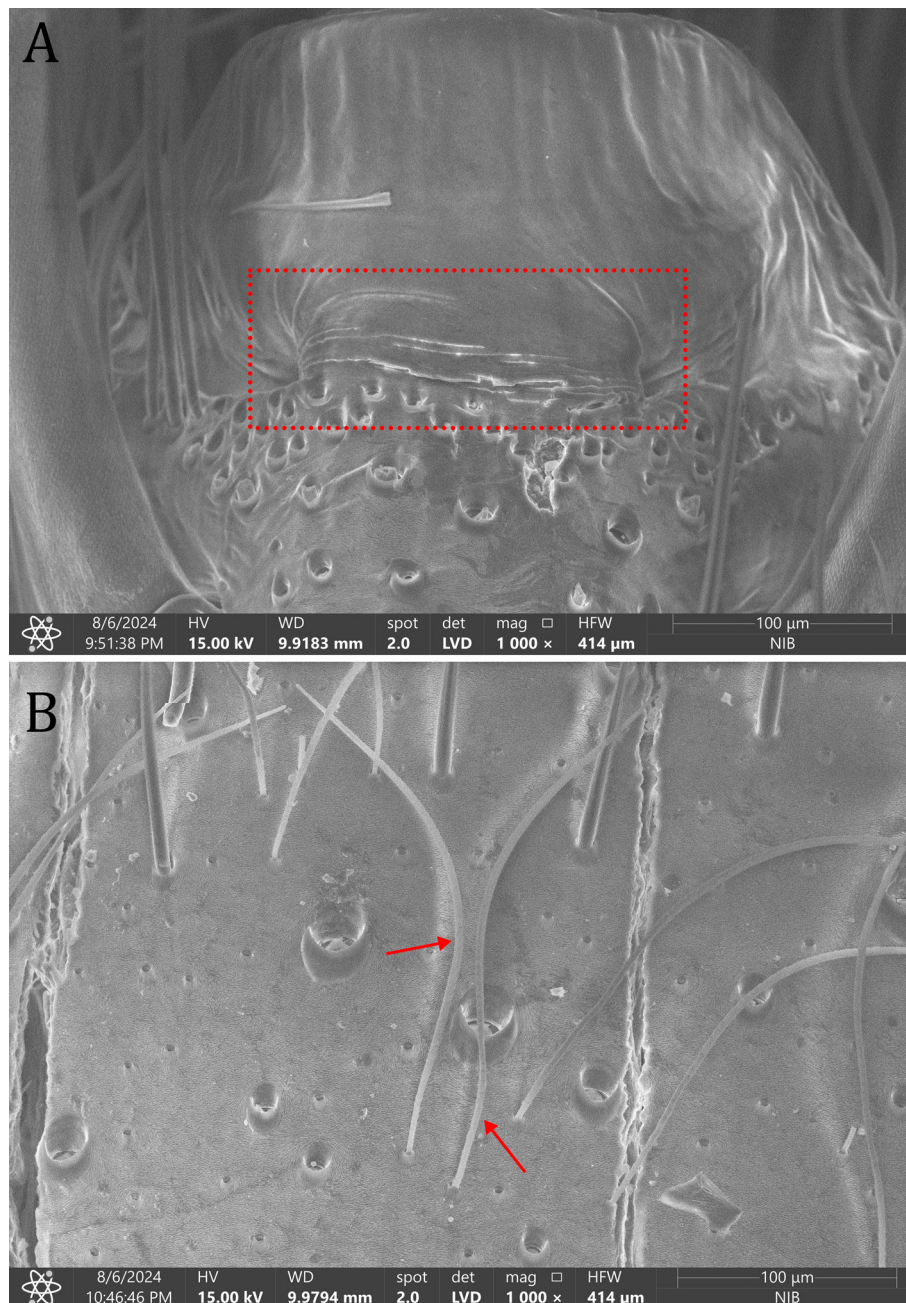


FIGURE 8

Vibration sensing organs in *Dolomedes*: (A) a lyriform organ of *Dolomedes fimbriatus* (highlighted in red) on the apical dorsal part of metatarsus of leg I; (B) trichobothria of *Dolomedes angustivirgatus* Kishida, 1933 (red arrows) on the basal ventral part of metatarsus of leg IV.

suggested to be a preadaptation to aquatic gaits. Rowing behavior, however, was hypothesized to have evolved once at the base of the clade that includes Pisauridae (containing *Dolomedes*), Lycosidae and Trechaleidae. The specialized gait of pisaurids is facilitated by dimple distortion, drag, generation of vortices, and the hydrophilic hairs (Suter, 2013). The results of Stratton et al. (2004) aligned with the latest study (Yu et al., 2024) suggesting that the semi-aquatic lifestyle is ancestral to Dolomedidae, Pisauridae, Lycosidae, and Trechaleidae. Considering our knowledge of the aquatic movement patterns is limited to a few *Dolomedes* species, an expanded investigation across a broader range of *Dolomedes* species would

allow a more nuanced understanding of the evolution of water-surface locomotory gaits and associated traits.

Dolomedes triton has also been observed “sailing” by extending and elevating its anterior pair of legs and letting the wind carry it across the water’s surface (Deshefy, 1981). Another distinct form of sailing involves the spider lifting its body above the water surface by extending and depressing all of its legs (Suter, 1999). Controlled studies of this elevated posture reveal that it is a cheap form of locomotion but comes at the cost of reduced control of directionality (Suter, 1999). Expanding biomechanical and behavioral studies of sailing to other *Dolomedes* species, potentially with a focus on



FIGURE 9

Aquatic locomotion in *Dolomedes*: (A) *D. plantarius* (Clerck, 1757) floating on water; (B) *D. plantarius* "running" on water; (C) *D. plantarius* diving under water; (D) *D. aquaticus* Goyen, 1888 diving under water.

locomotion across distinct bodies of water (e.g., fast flowing versus stagnant) could provide information regarding the evolution of mechanisms of unique locomotion.

In addition to moving across water, many *Dolomedes* species can submerge underwater (Figures 9C, D) in response to predation risk, by exploiting air bubbles created by hydrophobic hairs spread across their body. Submergence tests revealed that *D. triton* individuals would dive under water and remain there voluntarily from 4–30 minutes, with at least one individual remaining responsive underwater for more than 3 hours (McAlister, 1960). Similarly, *D. aquaticus* can stay submerged for up to 30 minutes (Forster and Forster, 1973). *Dolomedes triton* appeared to require solid support structures to break through the water surface both on entry and exit (McAlister, 1960; Williams, 1979b) and similar observations of the requirement of a substrate for submergence were seen in New Zealand's *Dolomedes* (presumably *D. minor*, *D. aquaticus*, and *D. dondalei*: Williams, 1979a). Interestingly, McAlister noted that *D. vitattus* (referred to as *D. urinator* Hentz, 1845) exhibits a different exit behavior (McAlister, 1960), which sounds similar to some of the feeding positions of *D. dondalei* (Williams, 1979a) – remaining largely submerged with one or two legs protruding above the water. Given observations of distinct exit behavior, comparative work across species exploring the biomechanics of submergence and re-emergence might provide insights into the evolution of related morphologies – e.g., size variation.

To disperse, spiders can actively walk over short-distances or passively travel over longer-distances by ballooning, like many spiderlings do after their first molts in their nursery web (Bell et al., 2005; Vink and Dupérré, 2010; Frost et al., 2013; Monsimet

et al., 2022). Species-level differences have been found too: for example, *Dolomedes fimbriatus*, a species with less habitat specialization, demonstrated a higher propensity for long-distance dispersal (both airborne and waterborne), while the more habitat specialized *D. plantarius* was more likely to engage in waterborne rowing (Monsimet et al., 2022). In the field, quantified distances of dispersal are lacking for any species. Studies aimed at *Dolomedes* dispersal distance and patterns could provide insight into the likelihood of establishment for species of conservation concern, such as *D. plantarius* and *D. schauinslandi*, in newly restored habitats or for translocation. Such studies could also inform hypotheses about the global distribution of *Dolomedes*.

Little is known about individual movement patterns in most *Dolomedes* species. In *D. triton*, a field survey using marked individuals found that adult females moved more than juveniles, but their movement reduced again once they produced egg sacs (Kreiter and Wise, 1996). This increase in movement with adulthood was presumed to be associated with more active, versus passive, hunting in adult females, but could also relate to distinct age or size-related predation pressure. To fully understand the natural history of *Dolomedes*, we require additional information on species-specific movement and dispersal patterns.

4.3 Diet and predation behavior

Like most spiders, *Dolomedes* are opportunistic predators with broad diets (Figure 10), although invertebrates seem to make up



FIGURE 10

Diet of *Dolomedes*: (A) *D. schauinslandi* Simon, 1899 feeding on a Wētā; (B) *D. raptor* eating a katydid; (C) female *D. triton* (Walckenaer, 1837) cannibalizing a male; (D) *D. mizhoanus* Kishida, 1936 eating a mosquito fish; (E) *D. plantarius* having captured a newt; (F) *D. raptor* feeding on a freshwater prawn.

most of their catch (Figures 10A, B). In *D. triton*, semi-aquatic and aquatic insects and spiders form most of their diet, dominated by Hemiptera, Odonata and Diptera (Zimmermann and Spence, 1989). Similarly, *D. dondalei* and *D. aquaticus* primarily consume aquatic insects, especially Diptera (mostly tipulids), Trichoptera and Ephemeroptera. An isotope analysis confirmed that aquatic insects are a key component of *Dolomedes* diet, although this varied between sites (Collier et al., 2002). Cannibalism can also form a significant portion of *Dolomedes* diet (Figure 10C; e.g. Greenwood et al., 2010). For example, in *D. triton* conspecifics formed about 5% of their diet (Zimmermann and Spence, 1989). The diet of terrestrial *Dolomedes* species (e.g. *D. schauinslandi*; Figure 10A) is less known, but presumably comprises of terrestrial invertebrates. Even in semiaquatic species, small juveniles may forage on vegetation away from the water that larger juveniles and adults rely on (Zimmermann and Spence, 1998). The extent to which *Dolomedes* feed on aquatic versus terrestrial prey may be important in their roles as bioindicators as well as in their susceptibility to distinct forms of environmental contamination.

Dolomedes do not limit their diet to small invertebrates, capturing the attention of biologists and arachnophobes alike with their predation of vertebrates, including fish (Figure 10D; Williams, 1979a; Nyffeler and Pusey, 2014), lizards (Eversole, 2022), amphibians (frogs, tadpoles, toads, and newts; Figure 10E; Moore and Townsend, 1998; Cabrera-Guzmán et al., 2015), bats (Leivers et al., 2021), as well as large freshwater crustaceans (Figure 10F;

Kosuge and Sasaki, 2002; Baba et al., 2019). A review by Nyffeler and Pusey (2014) reports observations of fish predation in the wild across 11 *Dolomedes* species. It seems appropriate to refer to *Dolomedes* as fishing spiders given widespread fish predation in the genus.

Adult *Dolomedes* spiders forego capture webs, opting instead to position themselves motionless to sit and wait for their prey to walk or float by. A characteristic behavior of semi-aquatic *Dolomedes* is to dangle their anterior legs over water surfaces in anticipation of prey floating past (Williams, 1979a). They will pursue prey, but only after initial detection (Williams, 1979a) and they do not actively hunt throughout the landscape, in contrast to roaming predators. *Dolomedes* use their chelicerae to inject venom, which immobilizes and kills prey, followed by extraintestinal digestion, some species transport prey to land after capture (Forster and Forster, 1973; Williams, 1979a; Uzenbaev and Lyabzina, 2009). Meal completion in *D. minor* can range from 10 to 30 minutes from prey capture, depending on prey size (Forster and Forster, 1973).

The use of body coloration in prey capture has also been suggested to help *Dolomedes* forage. For example, female *D. raptor* use distinct white patches of hairs on their legs to lure prey (Tso et al., 2016), while bright white stripes on male cephalothorax provide a similar function for prey attraction (Lin et al., 2015). Several other *Dolomedes* similarly possess such distinct leg patches in females (e.g. *D. horishanus* and *D. hydatostella*) or cephalothorax stripes in males (e.g. *D. fimbriatus*, *D. rotundus*),

with related species lacking them, offering a valuable system to determine the prevalence of luring and compare prey capture techniques in this group.

Given that *Dolomedes* are able to take down vertebrates that can be many times larger than the spider itself, there has been significant interest in the function and biochemical properties of the venom for a handful of species – *D. fimbriatus* (Uzenbaev and Lyabzina, 2009; Kozlov et al., 2014) *D. mizhoanus* (Jiang et al., 2013; Li et al., 2014; Xu et al., 2015), *D. sulfureus* (Wang et al., 2013; Xu et al., 2015), and *D. okefinokensis* (McCormick et al., 1993; Meinwaldt and Eisnert, 1995). Bioactivity assays have shown that *Dolomedes* venom has a neurotoxic effect, causing disorientation, altered movement, and ultimately the death of prey (Li et al., 2014). Venoms of several *Dolomedes* species have been analyzed using mass spectrometry (McCormick et al., 1993; Meinwaldt and Eisnert, 1995; Wang et al., 2013; Li et al., 2014) and transcriptomics (Kozlov et al., 2014; Xu et al., 2015; Jiang et al., 2013). These studies document the diversity and structure of venom polypeptides, aid in reconstructing the evolutionary history of spider venom, and contribute to our understanding of venom function. *Dolomedes* venom seems to be of special interest in the potential for neurochemical and neurotherapeutic drug development, particularly because they can prey upon vertebrates, which suggests their venom contains neurotoxins that are targeted for vertebrate nervous systems (Li et al., 2014).

4.4 Reproductive behavior

Dolomedes courtship behavior (Figure 11A) has received less attention compared to other spider groups that show conspicuous behavior (see for a review: Huber, 2005) – e.g., the numerous colorful jumping spiders that engage in complex dances (reviews: Richman and Jackson, 1992; Elias et al., 2012; Nelson, 2023) or wolf spiders like the genus *Schizocosa* Chamberlin, 1904 which have conspicuous ornaments combined with complex songs and dances and whose study has contributed significantly to our understanding of complex multimodal signaling (Starrett et al., 2022 and references therein). *Dolomedes* lack obvious secondary sexual traits, sensational courtship or extensive silk use during courtship, all traits which have been observed in other spider taxa (e.g., some nephilids (Zhang et al., 2011) and pisaurids (Anderson and Hebets, 2016) (reviewed in Scott et al., 2018)). As such, there has been little research on the relationship(s) between reproductive behavior such as courtship and mating success in *Dolomedes*.

Early studies on *D. scriptus* and *D. triton* showed that female silk contains sex pheromones, which aid as chemical cues for males who follow female draglines (Kaston, 1936; Roland and Rovner, 1983), inducing courtship displays. These pheromones are probably emitted from the female's integument to the surrounding water, which may help males locate potential mating partners (Roland and Rovner, 1983). The species-specificity of pheromones

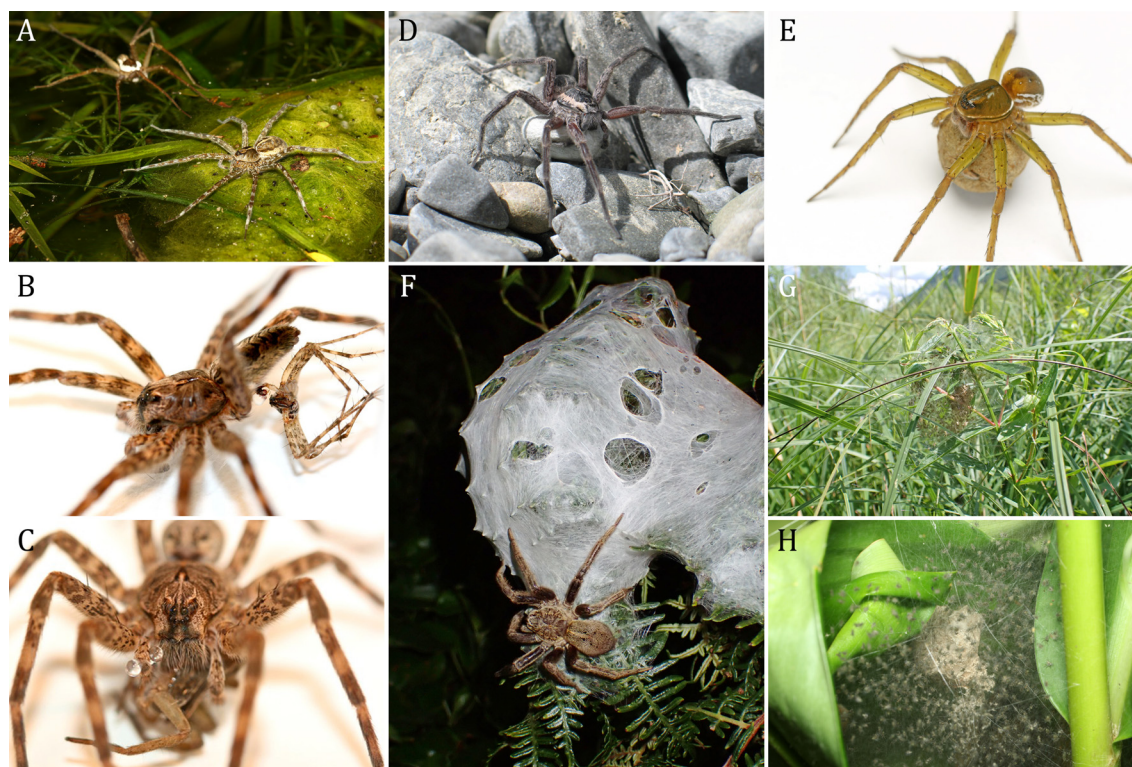


FIGURE 11

Reproductive behavior of *Dolomedes*: (A) male *D. mizhoanus* (left) approaching a female (right); (B) copulation in *D. tenebrosus*, showing a male (right) having spontaneously died after inserting his left palp; (C) female *D. tenebrosus* cannibalizing a male; (D) female *D. aquaticus* carrying her egg sac; (E) female of an unknown *Dolomedes* species from Madagascar carrying her egg sac; (F) female *D. schauinslandi* guarding her nursery web; (G) nursery web of *D. fimbriatus* housing the spiderlings; (H) spiderlings of *D. raptor* in the nursery web.

and/or the potential for airborne signals/cues remain unexplored in *Dolomedes*.

Though courtship behavior likely varies in intensity, duration and specific expression between species, all investigated species share common features. The first phase of male courtship usually includes a series of leg movements (visual and vibratory modalities), which are often referred to as “leg-waving”, “tapping” and “jerking” (Kralj-Fišer et al., 2016). Next, males touch the female on their legs and abdomen (Carico, 1973; Roland and Rovner, 1983; Sierwald and Coddington, 1988; Arnqvist, 1992; Lin et al., 2015). In *D. fimbriatus*, male courtship was found to vary with female traits – females with lower body weight received less intense male courtship and were more likely to remain unmated (Kralj-Fišer et al., 2016). To date, however, no information exists regarding the relationship between courtship duration and/or complexity and male mating success. Male coloration appears to play a significant role in female mating decisions. For instance, in *D. raptor*, females are more likely to reject and even attack males that lack the species-typical white stripes (Lin et al., 2015). Female mate choice based on other visual or vibratory cues/signals has not received much attention in other *Dolomedes*, but they are worth investigating further, especially in conjunction with studies on their sensory ecology and physiology.

Female responses to courting males are quite variable among species. In *D. scriptus* and *D. triton*, females may respond to courting males with their own courtship behavior, such as “drumming” and “leg waving” (Roland and Rovner, 1983; Schoenberg et al., 2022), while females of *D. fimbriatus* react either by attacking the male or staying motionless in a receptive body position (Arnqvist, 1992), similar to the motionless female *D. tenebrosus* (Sierwald and Coddington, 1988). Males mount females usually facing the opposite direction and start inserting their pedipalps for sperm transfer (Sierwald and Coddington, 1988; Arnqvist, 1992; Schoenberg et al., 2022). The motionless state of females is reminiscent of the quiescence described in other spiders (reviewed in Cargnelutti et al., 2023) and would be interesting to explore further.

The duration of copulation as well as the number of pedipalps used for insertions varies across *Dolomedes* species. Copulation duration (male mounting female and inserting pedipalp/s) can be rather short (e.g., a few seconds in *D. vittatus*, *D. triton*, and *D. fimbriatus*: Carico, 1973; Arnqvist, 1992) or relatively long (on average 22 minutes in *D. tenebrosus*: Schwartz et al., 2014; though most of this time involves the male’s body hanging from the female

as his heart slowly stops beating). The pattern of pedipalp use (one or both) varies between but also within species (Schmidt, 1957; Carico, 1973; Johnson, 2001; Schoenberg et al., 2022; Sierwald and Coddington, 1988; Arnqvist, 1992; Schwartz et al., 2013). Quantifying the relationship between copulation duration, number of pedipalps being used and sperm transfer, as well as disentangling the roles of each sex in copulation duration, will help us understand the observed variation and the potential role of sexual selection and sperm competition in influencing these evolutionary patterns.

4.5 Mating systems

In *Dolomedes* we observe great variation in species-specific patterns of female and male mating rates (i.e. mating systems; Table 2). At one extreme end of the spectrum we find *D. tenebrosus*, a species in which females will mate with up to three males while males will die in 100% of first matings (spontaneous male death; Figure 11B), making them strictly monogynous (Schwartz et al., 2013, Schwartz et al., 2014). At the other end of the spectrum, *D. fimbriatus*, *D. scriptus* and *D. triton* males mate with multiple females, making them polygynous (Arnqvist and Henriksson, 1997; Johnson, 2001; Kralj-Fišer et al., 2016; Schoenberg et al., 2022). Since both sexes have paired genitalia, males can potentially inseminate the same female twice, inserting both pedipalps in different openings. There is also evidence of high individual variation within the same population in a female’s number of mates (Arnqvist and Henriksson, 1997; Johnson, 2001; Kralj-Fišer et al., 2016; Schoenberg et al., 2022). Details of mating and cannibalism rates for previously studied species are summarized in Table 2.

The spontaneous death by male *D. tenebrosus* provides an intriguing example of monogyny (including terminal investment strategies) (for examples from other spiders and social insects see: Boomsma et al., 2005; Schneider and Fromhage, 2010; Jaffé et al., 2014) and provides a system in which to test hypotheses of the evolution of this mating system. In *D. tenebrosus*, the male’s death coincides with his consumption by the female, which has been shown to benefit both sexes through higher offspring quantity and quality (Schwartz et al., 2016). Various life history traits linked to monogyny are also observed in *D. tenebrosus* – i.e., a male-biased sex ratio and eSSD (Fromhage et al., 2007; Miller, 2007; Wilder and

TABLE 2 Overview of mating system and sexual cannibalism in four *Dolomedes* species.

Species	Mating rate females	Mating rate males	Sexual cannibalism	References
<i>Dolomedes fimbriatus</i>	monoandrous – biandrous	probably monogynous – bigynous	rare – frequent	Arnqvist and Henriksson, 1997; Kralj-Fišer et al., 2016; Fisher and Price, 2019
<i>Dolomedes triton</i>	probably monoandrous	probably monogynous	frequent	Zimmermann and Spence, 1989; Johnson, 2005; Johnson and Sih, 2005
<i>Dolomedes scriptus</i>	monoandrous	53% of males mated multiply	common	Schoenberg et al., 2022
<i>Dolomedes tenebrosus</i>	polyandrous	monogynous	always	Schwartz et al., 2014

Rypstra, 2008; Schwartz et al., 2013). To fully leverage *Dolomedes* mating system evolution, more data on the mating systems and life history traits of additional species is needed for comparative analyses. Research on *D. scriptus* (Schoenberg et al., 2022), *D. tenebrosus* (Schwartz et al., 2013, Schwartz et al., 2014) and *D. triton* (Wojcicki, 1992) provide a good start, but such a diverse genus offers a wealth of further species to contribute to a comprehensive comparative study.

4.6 Sexual cannibalism and female aggression

Female aggression, often resulting in precopulatory and postcopulatory sexual cannibalism (consuming a mate before, during or after copulation; reviewed in Burke, 2024), is present in many *Dolomedes* species and significantly impacts mating rates and population dynamics (*D. fimbriatus*: Arnqvist, 1992; *D. triton*: Johnson, 2005b; Johnson and Sih, 2005; *D. scriptus*: Fisher and Price, 2019; Schoenberg et al., 2022). Numerous hypotheses have been proposed to explain sexual cannibalism (Figures 10C, 11C; reviewed in Burke, 2024), and a few have been tested with *Dolomedes*. Using *D. fimbriatus*, for example, Arnqvist and Henriksson (1997) found no evidence for Newman and Elgar (1991) idea that pre-copulatory sexual cannibalism represents a female's assessment of a male's value as a sperm donor versus a prey item, as female foraging history did not influence likelihood of cannibalism. An alternative hypothesis – the “aggressive spillover hypothesis” – was discussed in the same publication by Arnqvist and Henriksson (1997). They proposed that high female aggression towards males may stem from selection for a general predatory aggressive syndrome that is beneficial in a foraging context but potentially costly in a mating context. The aggressive spillover hypothesis has been tested in two *Dolomedes* species that showed mixed results. While a study on *D. fimbriatus* did not find evidence of a correlation between female foraging aggression and aggression toward courting males (Kralj-Fišer et al., 2016), a study on *D. triton* showed that foraging aggression was positively correlated with increased sexual cannibalism, feeding rate, larger adult size, boldness towards a threat and higher fecundity (Johnson and Sih, 2005). Further research exploring relationships between aggression and reproductive behavior are necessary to discern the potential role of female aggression in influencing reproductive strategies across *Dolomedes* and the potential for sexual cannibalism to be a sexually selected trait (Burke, 2024).

There are also interesting first insights into the existence of consistent among-individual differences in aggressiveness (i.e. “personality” traits) in *Dolomedes* and their correlation to sexual behaviors. In *D. fimbriatus*, for example, female voracity towards prey might be considered an intrinsic personality trait, but not aggression towards mates, as females adjusted their aggressive responses towards courting males based on the male's size relative to their own (Kralj-Fišer et al., 2016). In contrast, *D. triton* female aggression levels were consistent across contexts, with *D. triton* females showing positive behavioral correlations between foraging voracity, sexual cannibalism tendency, and boldness in response to

predation risk (Johnson and Sih, 2005, Johnson and Sih, 2007). Given the heightened interest in animal personality and behavioral syndromes in the last decades (see for example: Réale et al., 2007; Sih et al., 2015; MacKinlay and Shaw, 2023), *Dolomedes* could be a useful taxon to address questions related to the extent to which certain behavior is fixed per individual (i.e., a personal trait) or context dependent.

Previous experience also influences cannibalistic behavior in *Dolomedes*. Specifically, works on *D. triton*, *D. scriptus*, and *D. fimbriatus* found females to be significantly more aggressive to courting males if already mated (Zimmermann and Spence, 1989, Zimmermann and Spence, 1992; Johnson, 2001; Kralj-Fišer et al., 2016; Schoenberg et al., 2022). In *D. triton*, females that cohabited with adult males were more likely to subsequently cannibalize males during courtship encounters later in life (Johnson, 2004). Furthermore, levels of SSD also impact the probability of a female cannibalizing a male – i.e., when size differences were minimal, male *D. fimbriatus* and *D. triton* had a higher chance of evading female attacks (Johnson, 2005; Johnson and Sih, 2005; Kralj-Fišer et al., 2016). These latter results are consistent with the idea that female aggression towards males is non-selective with cannibalism being contingent upon the female's physical power relative to the male's defensive capability (Wilder and Rypstra, 2008; Roggenbuck et al., 2011).

In contrast to pre-copulatory sexual cannibalism, post-copulatory sexual cannibalism occurs after sperm transfer, making it possible for males to receive a fitness benefit from being cannibalized. Such a benefit was observed for both sexes in *D. tenebrosus* as females that cannibalized males after copulation produced more offspring that were higher in mass and survived longer than the offspring of females who consumed a similarly sized cricket (Schwartz et al., 2016). To date, it is unknown whether this benefit is specific to the consumption of male *D. tenebrosus*, or simply to the consumption of a new prey type. It is also unknown whether similar fitness benefits are present from post-copulatory sexual cannibalism in other *Dolomedes* species. *Dolomedes tenebrosus* is an eSSD species and has received attention because the male's terminal investment strategy of obligate death following sperm transfer makes the males complicit in their own cannibalism (Schwartz et al., 2013, Schwartz et al., 2014). Complicity in sexual cannibalism has not yet been observed in other *Dolomedes* species. It remains unclear what, if any, mechanisms of post-copulatory sexual selection are at play in this system, but future studies exploring the potential for sperm competition and cryptic female choice are likely to reveal interesting patterns across species.

4.7 Parental investment

Dolomedes parental care is strictly maternal. Upon oviposition, female *Dolomedes* create a silken egg sac, holding it tight in their chelicerae, with their pedipalps extended over the front, and a silk dragline attached to their spinnerets (Figures 11D, E; Comstock, 1912). The egg sacs of *D. triton* have a unique, highly hydrophobic outer layer, allowing them to submerge their egg sacs (Correa-Garhwal et al., 2019). The egg sac exudes a buoyant force while submerged, resulting in the female exerting more pressure to

remain underwater (McAlister, 1960), away from potential threats. Egg sacs are highly protected by the female and difficult to remove without tearing the lining of the egg sac (Johnson and Sih, 2007). Even unmated females have been observed guarding unfertilized egg sacs, however unfertilized egg sacks are also frequently consumed (Schmidt, 1957; Arnqvist, 1992; Fisher and Price, 2019). The only time a female will let go of her egg sac is to forage, after which she will resume carrying the egg sac (Forster and Forster, 1973). A study by Johnson and Sih (2007) found a significant negative correlation between a female’s boldness in guarding her egg sac and her body condition, denoting the importance of foraging to the cost of parental care. As with most topics discussed thus far, data on parental investment come from only a handful of species, leaving open the possibility of variation across the genus in parental investment.

A general timeline of reproduction for some common *Dolomedes* species is within Table 3. Female *Dolomedes* will travel with their egg sacs until close to hatching (Comstock, 1912). Spiderlings hatch within the egg sac as they are being carried (Forster and Forster, 1973). Near the time of the spiderlings’ first molt, the female constructs her nursery web and deposits the egg sac (Carico, 1973; Forster and Forster, 1973; Vink and Dupérré, 2010). She will tear open the egg sac using her chelicerae, releasing her offspring into the nursery web (Figures 11F–H; Comstock, 1912; Nicholas et al., 2011). In New Zealand, nursery webs of *D. minor* are more easily seen than the spiders. These distinctive nursery webs appear as little white purses, often on the tips of shrubs (Forster and Forster, 1973). On the other hand, in some species like *D. fimbriatus* nursery webs are less distinct, being made of sparser silk (Figure 11G) and persist for a shorter time. The placement of nursery webs by some female *Dolomedes* is purposeful and habitat specific. A study by Kreiter and Wise (1996) found a preference for placing nursery webs in *Juncus effusus* and structurally similar *Juncus*-like vegetation. Similarly, Dickel et al. (2022) found that *D. plantarius* showed a strong association with *Carex* sp. and that distance to water was a significant factor of web placement.

Parental care in *Dolomedes* does not end at hatching, as females are infamous for fiercely guarding their young. If a threat approaches the nursery web, the female will aggressively approach

and may be prompted to bite (Comstock, 1912). Much of the research on female aggression has addressed its benefits to female fecundity, but no studies have investigated the benefits of female aggression to offspring survival post-hatching.

5 Discussion

Although the genus *Dolomedes* boasts over 100 species, our review has revealed that detailed studies on most species are scarce. Our current understanding is predominantly shaped by knowledge of just four species from Europe and North America – *D. fimbriatus*, *D. plantarius*, *D. triton*, *D. tenebrosus*, although studies on several Asian (e.g., *D. sulfurerus*) and New Zealand (e.g., *D. aquaticus*) species are expanding (Figure 12). We particularly noticed an absence of research in Africa and Australia, where there is clearly much to learn. Regardless, our review has compiled rich insight into the biology of this genus. Our key conclusion is that *Dolomedes* spiders are an exceptional model group for exploring a wide range of ecological, evolutionary and conservation questions. With their near-global distribution and highly diverse ecology and behavior, *Dolomedes* make themselves available for collaborative and comparative research opportunities. Furthermore, their impressive size, ease of collection, and straightforward handling and rearing enhance their appeal to researchers.

5.1 Systematics and morphology

We uncovered numerous avenues for further investigation regarding the systematics and morphology of *Dolomedes*. The recent placement of *Dolomedes* within the newly resurrected Dolomedidae family (Yu et al., 2024) marks a significant advancement in our understanding of their systematics, but many questions remain. Prioritizing the phylogenetic testing of the monophyly and the nomenclatural validity of Dolomedidae with increased taxon sampling is essential, along with clarifying their biogeographic history. If Miocene climatic oscillations have shaped their trait evolution and diversification, then *Dolomedes* can inform

TABLE 3 General timelines for *Dolomedes* parental care behaviors and reproductive output. Some oviposition times may differ slightly depending on region.

Species	Oviposition	Time to hatch from egg sac	Average clutch size	Lifetime number of egg sacs	References
<i>Dolomedes minor</i>	September to April	5 weeks	Unknown	Unknown	Forster and Forster, 1973; Vink and Dupérré, 2010
<i>Dolomedes aquaticus</i>	November to March	5 weeks	300	Unknown	Forster and Forster, 1973; Greenwood et al., 2010; Connolly n.d.
<i>Dolomedes tenebrosus</i>	June, early July	4 weeks	1,873	1–2	Guarisco, 2010; Schwartz et al., 2013
<i>Dolomedes triton</i>	Unknown	3–4 weeks	768	1–3	Guarisco, 2010; Kreiter and Wise, 1996; Spence et al., 1996
<i>Dolomedes albineus</i>	Early July	3 weeks	362	Unknown	Guarisco, 2010
<i>Dolomedes scriptus</i>	Mid-June	3 weeks	558	Unknown	Comstock, 1912; Kaston, 1938; Carico, 1973; Guarisco, 2010

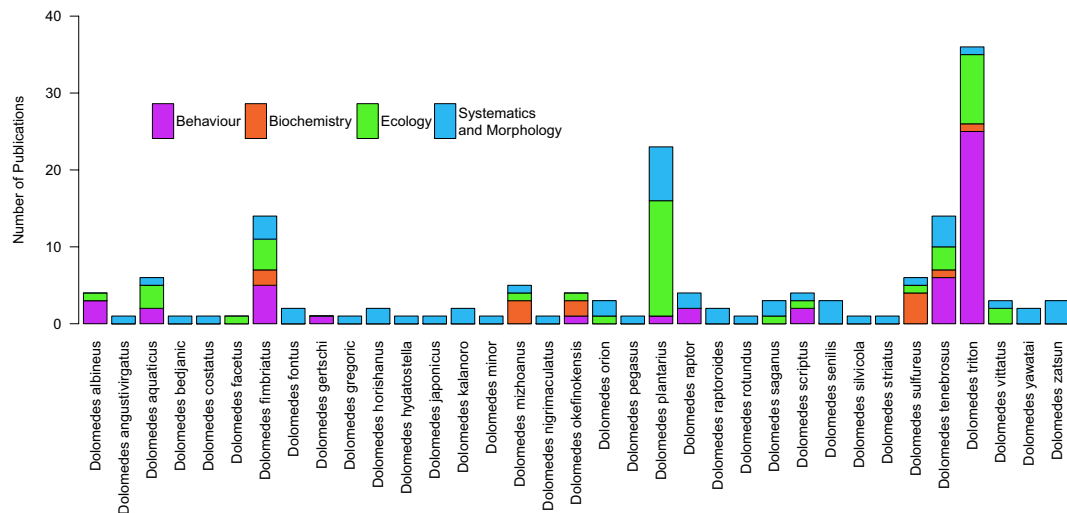


FIGURE 12

Number of research papers focusing on different *Dolomedes* species with color codon highlighting different research fields.

us of future biotic responses to global change. Expanding taxonomic descriptions to understudied regions (central Africa, Madagascar, India, Southeast Asia, and Oceania) is crucial for a more balanced understanding of their diversity. Further taxonomic discoveries will facilitate reconstruction of a more complete species-level phylogeny, strengthening evolutionary analyses, classification decisions and biogeographic reconstruction. Furthermore, the few South American *Dolomedes* are likely misplaced, leaving a continent curiously devoid of these almost globally distributed creatures – a biogeographic puzzle possibly explained by competition from earlier-arriving, semi-aquatic spiders.

We identified several unknowns regarding *Dolomedes* morphology. One key question is the adaptive function of color pattern variation within and among species. A comparative study mapping the occurrence of white lateral bands and their functions across species would provide valuable insights into the selective pressures driving and maintaining this variation. Studies on *D. raptor* suggest these bands play roles in both foraging and mate choice (Lin et al., 2015; Tso et al., 2016), but the extent to which this applies to other species is unknown. Furthermore, studies incorporating within-species variation would be powerful for untangling proximate and ultimate causes of polymorphism in body color patterns. Another set of morphological questions concerns the functional implications of divergent genital morphology in species, such as *D. tenebrosus* and *D. okefinokensis*, which also exhibit other traits such as eSSD and unusual mating systems. We suspect that this variation is driven by sexual conflict over mating optima, including gametic competition and choice, and look forward to future studies exploring these possibilities.

5.2 Ecology

The ecology of *Dolomedes* offers opportunities for insight into the interface between aquatic and terrestrial ecosystems and

associated adaptations. Apparent microhabitat specialization coincident with indications of recent divergence (Yu et al., 2024) suggests that microhabitat specificity may have influenced diversification in *Dolomedes*; a hypothesis that requires testing. Numerous opportunities also exist to explore potential adaptations to aquatic versus terrestrial lifestyles, especially studies that focus on populations that vary in their aquatic/terrestrial lifestyle and/or species that change their microhabitat use throughout their life.

Often found at the boundary between freshwater and terrestrial ecosystems, *Dolomedes* are ideal for testing the effects of anthropogenic pressures on behavior, ecology and morphology. Early evidence suggests *Dolomedes* can serve as bioindicators of heavy metals in waterways (Ortega-Rodriguez et al., 2019) but there is significant potential to explore the impacts of a wider range of pollutants, including agrichemicals, pharmaceuticals and excess nutrients, on these key ecosystem predators and their prey. Additionally, many *Dolomedes* are found along urban-rural gradients, offering a natural transect to tease apart the pollutant impacts. Furthermore, the effects of global change on the behavioral ecology of animals are a rapidly growing area of research (Wong and Candolin, 2015). One area of interest has been the effect of pollutants on aquatic animal behavior, especially signaling and communication (reviewed in Saaristo et al., 2018). Although *Dolomedes* have yet to be studied from this perspective, observable courtship and reproductive behavior make them ideal candidates. They would also be a good taxon to explore for targeted citizen science data projects, like iNaturalist, for documenting distributions and diets (see Powell et al., 2021).

Seasonal variation in maturation times and sex ratios across *Dolomedes* makes them a potential model system for exploring the relationship between life history and reproductive traits. Sex ratios, for example, are theoretically and empirically linked to SSD across animals and often, to extreme reproductive behavior (Kuntner and Coddington, 2020). The causes and consequences of these

relationships, however, remain obscure and require testing in a system with a strong hypothesis of evolutionary relationships coincident with species-level variation. We now have the former requirement (Yu et al., 2024), but unfortunately, the number of species for which we have behavioral and ecological data remains dismally low.

The often-high abundance and large size of *Dolomedes* make them inviting prey for birds and hosts for the growing larvae of pompilid wasps. The pattern of generalists and specialists in pompilid wasp parasitism observed in New Zealand and the USA likely varies in other regions, especially areas of high *Dolomedes* diversity such as Africa or Asia. Knowledge of prey for many pompilid species in Britain and Ireland are missing (O'Hanlon and O'Connor, 2021), and in New Zealand, there is call for more thorough documentation of pompilid prey (Thompson, 2020) as it may provide insight into species-level divergence in morphology, microhabitat use, and other behavior. Furthermore, the importance of predation pressure in microhabitat choice, phenology, activity cycles, and more remain to be explored. Such information will be especially informative when elucidating the conservation status of species and populations and when developing interventions that might mitigate their conservation risk.

These large spiders are not only prey, but are presumably important predators in their aquatic and terrestrial environments as well. Future directions related to their importance as predators could include molecular gut content analyses through metabarcoding to examine their role in ecosystems, including their potential role in controlling pest species.

5.3 Behavior

Fishing spiders have fascinated scientists for decades with their ability to move on water and detect surface vibrations. The literature on *Dolomedes* sensory capabilities is extensive, yet incomplete and provides a great basis for follow-up studies on sensory physiology, especially studies that compare across species with different lifestyles and those that focus explicitly on vision as well as sensory processing. Future research could also explore the biomechanics of submerging and re-emerging from water, and biomimetic studies of artificial water-surface locomotion may inspire innovative robotic designs.

Many opportunities exist to further investigate parental care behavior in *Dolomedes*. Studies could explore the metabolic or biomechanical costs of taking an egg sac underwater and how the tradeoff between reduced foraging and increased offspring survival during nursery web guarding varies by female size and species. Spence et al. (1996), for example, found that food availability increasingly restricts fecundity in *D. triton* as size increases.

Given our collective expertise in behavioral ecology, we identify *Dolomedes* as an excellent taxon for studying reproductive behavior, particularly sexual cannibalism. Investigating more species could help test hypotheses about the evolution and function of both pre- and post-copulatory cannibalism (Burke, 2024). While the role of aggressive spillover in pre-copulatory cannibalism remains uncertain (Johnson and Sih, 2005; Kralj-Fišer et al., 2013; Kralj-Fišer et al., 2016), there is substantial evidence that post-copulatory sexual cannibalism is adaptive, even for males (Schwartz et al., 2016). It would be valuable

to address how sexual selection relates to sexual cannibalism rates and whether any other *Dolomedes* species shows male complicity in cannibalism. *Dolomedes* have also been at the forefront of personality research, as female aggression in foraging is highly repeatable and sometimes correlated with sexual aggressiveness. Additional research topics could include the role of sexual selection on sperm competition, paternal investment, and mating systems. Most current studies on reproductive behavior of spiders focus on web-building families. Studying *Dolomedes*, a free-roaming predator, will broaden our understanding of mating behavior and its dependence on other behavioral ecology and life-history traits.

Author contributions

K-PY: Writing – original draft, Writing – review & editing. ZR: Writing – original draft, Writing – review & editing. JK: Writing – original draft, Writing – review & editing. SC: Writing – original draft, Writing – review & editing. CV: Writing – original draft, Writing – review & editing. JJ: Writing – original draft, Writing – review & editing. SK-F: Writing – original draft, Writing – review & editing. MK: Writing – original draft, Writing – review & editing. EH: Writing – original draft, Writing – review & editing. CP: Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/frchs.2024.1501653/full#supplementary-material>

SUPPLEMENTARY FIGURE S1

General somatic characteristics of *Dolomedes* featuring female *D. fimbriatus* (A) habitus, dorsal view; (B) *idem*, lateral view, red arrows showing the height

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- SUPPLEMENTARY FIGURE S2
Leg modifications and extra bristles (red arrows) in male *Dolomedes*: (A) *D. triton*, leg IV; (B) *D. vittatus* Walckenaer, 1837, leg IV; and (C) *D. horishanus*, leg IV. Scale bars: 1 mm.
- SUPPLEMENTARY FIGURE S3
Intraspecific variation of body coloration in *Dolomedes sulfureus*: (A) female, white banded morph; (B) female, dark/white band absent morph; (C) female, mottled brown morph; (D) male, white banded morph; (E) male, dark/white band absent morph.
- SUPPLEMENTARY TABLE S1
Valid *Dolomedes* species with known distribution ranges, habitat preferences, and SSD (as female to male size ratio). See attached excel file.
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