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A review of the reproductive habitat preferences and conservation challenges of a rare, transient, and ecologically restricted darner dragonfly: *Rhionaeschna mutata*

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Rhionaeschna mutata is a rare North American dragonfly that is considered a species of concern or threatened throughout its range. It is most widely distributed in the eastern USA, but recent adult records indicate that its range extends further north and west than previously known. Effective conservation planning for rare species requires understanding their habitat requirements, and no comprehensive characterization of this species' reproductive habitat has previously been conducted. We conducted a review to synthesize information from records throughout this species' range and identified a narrow set of conditions that describe *R. mutata* reproductive habitat: small, heavily vegetated, fish-free ponds with a wooded riparian edge and with sphagnum present. While this habitat type may formerly have been widespread across this species' native range, anthropogenic activities have likely resulted in loss and increased fragmentation of *R. mutata* reproductive habitat. Our review also revealed that this species is transient or ephemeral, collected at a site one year and absent in subsequent years. Effective conservation planning for ecologically restricted odonates, such as *R. mutata*, requires consideration of multiple anthropogenic activities that threaten species' ability to persist.

Keywords: Odonata; *Rhionaeschna mutata*; rare species; habitat requirements; habitat specialist; conservation; Aeshnidae

Introduction

Extinction rates among North American freshwater fauna are disproportionately high relative to terrestrial species (Ricciardi & Rasmussen, 1999). Freshwater taxonomic groups vary in their vulnerability, with snails (61%) and mussels (48%) being the most threatened and odonates (8%) among the least (Clausnitzer et al., 2009; Wilcove & Master, 2005). This gap in extinction threat is likely linked to the semi-aquatic life-history and dispersal abilities of Odonata, whose ranges are not confined to watershed boundaries. Odonata that are most vulnerable to extinction tend to be those with limited dispersal and colonization abilities due to morphological constraints on their movement or close dependence on a narrow set of habitat conditions (Foster & Soluk, 2004; Korkeamäki & Suhonen, 2002; Purse, Hopkins, Day, & Thompson, 2003). Effective conservation planning for rare species requires understanding of their habitat requirements, dispersal

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behaviors, and geographic distribution. Yet, these are not well documented for many Odonata, particularly for their aquatic life-stage.

Rhionaeschna mutata (Hagen; family: Aeshnidae) is considered a species of concern or threatened throughout its range (Brunelle & deMaynadier, 2005; NatureServe, 2018). NatureServe ranks this species G4 globally (i.e. apparently secure: uncommon but not rare; some cause for long-term concern due to declines or other factors), and subnationally it is listed as critically imperiled (S1), imperiled (S2), or vulnerable (S3) in all states and provinces where the species has been ranked (NatureServe, 2018).[1] This species appears to have a small global distribution, confined to the northeastern USA and southern Canada. However, due to its rarity, the exact geographic extent of its range is uncertain. At the time of Walker's (1912) monograph on North American *Aeshna*, it was known only from Indiana, Ohio, Massachusetts, and Pennsylvania (Walker, 1912). A map of collection sites published by Beatty and Beatty (1969) documents its presence in a few additional locations, all confined within the eastern USA and southern Ontario (approximately 35–43°N, 70–85°W; Figure 1). As collection efforts of Odonata have intensified over the past few decades, more occurrences of this species have been documented throughout northeastern North America (Abbott, 2006–2018). Recent records of this species in
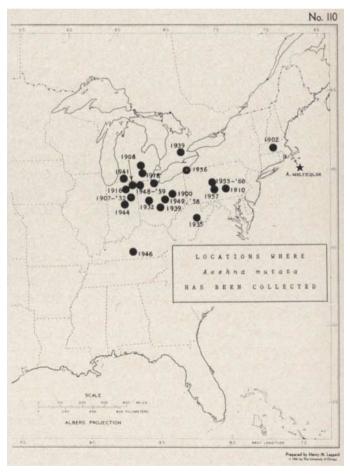

Figure 1.   Known geographical distribution of *Rhionaeschna mutata*, pre-1969. Image reprinted from Beatty and Beatty (1969). Evolution and speciation in the subgenus Schizuraeschna, with observations on *Aeshna* (*Schizuraeschna*) *mutata* Hagen (Odonata). *Proceedings of the Pennsylvania Academy of Science, 43*, 147–152. This image is used by permission of The Pennsylvania State University Press.

Nova Scotia (Cook & Bridgehouse, 2005), Quebec (Mochon, 2015), northern New York (Abbott, 2006–2018), Maine (Brunelle, 1999), Vermont (Abbott, 2006–2018), and Minnesota (DuBois et al., 2015) indicate that this species' distribution extends further west and north than previously known. Whether these records indicate a northward expansion of its range, possibly linked to warming climate, or simply reflect more intensive survey efforts is unclear.

The species (formerly *Aeshna mutata*) was reclassified in 2003 to a genus of primarily tropical dragonflies. While the majority of *Rhionaeschna* species reside in South America, *R. mutata* is one of only five congenerics found in North America and the only one with an eastern North American range. This species is of particular conservation concern due to its taxonomic distinctiveness within its known range (White, Hunt, Schlesinger, Corser, & deMaynadier, 2015). The only other *Rhionaeschna* species whose range is known to marginally overlap with *R. mutata* is *R. multicolor*; the western edge of the known range of *R. mutata* overlaps with the eastern edge of the known range of *R. multicolor* in Minnesota and Wisconsin (Abbott, 2006–2018).

The cause of this species' rarity throughout its range is not understood. As a member of Aeshnidae, a family that includes the largest dragonfly species in North America, it is amongst the strongest fliers of odonates. Its mobility and dispersal ability is therefore unlikely to be constrained by morphology. We hypothesize that the rarity of *R. mutata* correlates to its reproductive habitat specificity. It has been demonstrated that Odonata with very specific habitat requirements may only be found in a small number of waterbodies even within water-rich regions (Hassall & Thompson, 2008). No comprehensive characterization of *R. mutata* reproductive habitat requirements has previously been conducted. Here, we present a review of *R. mutata* habitat characteristics and address some of the challenges of conservation planning for this rare species.

Characterization of *Rhionaeschna mutata* breeding habitat

We queried a wide range of sources in our review of *R. mutata* reproductive habitat characteristics. Peer-reviewed publications that include detailed descriptions of *R. mutata* habitat are few, therefore we included field guides and state agency reports, in addition to peer reviewed literature, in our review. We also contacted natural resource managers in states and provinces within this species' range to gather reproductive habitat descriptors. Additionally, we consulted citizen science websites, including Odonata Central, a database that maps and records the distribution of dragonflies in North America, for records of *R. mutata* (Abbott, 2006–2018). Odonata Central records that include detailed descriptions of locations where the specimens were collected were included in our habitat characterization. For each source we recorded the type, year, location, and habitat characteristics described. Sources are cited by source-type in Appendix 1. In total, we identified 63 sources describing *R. mutata* reproductive habitat characteristics: 29 records from Odonata Central, six published field guides, six state agency published reports, eight citizen science websites, six peer-reviewed papers, three peer-reviewed books, and personal communications with natural resource managers in five states (Virginia, Kentucky, Rhode Island, New York, Maine).

A relatively narrow range of conditions characterizing *R. mutata* reproductive habitat was revealed by our review (Table 1). This species breeds in small/shallow, heavily vegetated ponds with a preference for those that are fish-free, although this association is not obligate. They prefer waterbodies that have a wooded riparian edge. They have a tendency to breed in "boggy" ponds with a sphagnum fringe, indicating a possible association with acidic water. Additionally, they seem to prefer semi-permanent waterbodies, although they may not be restricted to a temporary hydroperiod. One study noted their ability to persist in low-water years, possibly indicating

Table 1.   *R. mutata* breeding habitat characteristics identified from a review of sources reporting habitat information within this species' known range. Characteristics named in $\geq 10\%$ of sources are reported here (see Appendix 1 for full list).

Habitat characteristics	Number (and percent) of sources (N = 63) naming characteristic
Spatterdock (yellow) waterlily	27 (43%)
Heavily vegetated	21 (33%)
Boggy (sphagnum/peat)	20 (32%)
Wooded riparian edge	19 (30%)
Fish-free	18 (29%)
Shallow/small	11 (18%)
Semi-permanent	8 (13%)
White waterlily	6 (10%)

drought hardiness, similar to its congeneric *R. multicolor* which persists in much more arid regions (Shiffer & White, 1995). As indicated by their name, they are also associated with spatterdock waterlily (aka yellow waterlily; *Nuphar variegatum* or *Nuphar advena*); however, this association does not appear to be obligate. They also are associated with other emergent macrophytes, such as White Waterlily (*Nymphaea odorata*).

Most of the characteristics that describe optimal reproductive habitat for this species are inter-related. *R. mutata* is similar to other members of Aeshnidae in its association with fish-free waterbodies (Schilling, Loftin, & Huryn, 2009b). Aeshnidae are top predators in permanent fish-free waterbodies (McPeek, 1990, 1998). Like other large, active macroinvertebrates, their conspicuousness makes them particularly vulnerable to fish predation, and they thrive in water-bodies where fish are absent (Crowder & Cooper, 1982; Schilling et al., 2009b; Werner & McPeek, 1994). It is well documented that fish predation directly impacts larval odonates, with some species more vulnerable than others (Crowder & Cooper, 1982; Johansson & Brodin, 2003; Johnson & Crowley, 1980; McPeek, 1998; Morin, 1984a; Pierce, Crowley, & Johnson, 1985; Schilling, Loftin, & Huryn, 2009a; Torben, Goran, & Suhling, 2010). The success of large, preda-tory macroinvertebrates in fish-free habitats is likely linked not only to the absence of direct fish predation on their nymphs, but also indirectly to the lack of competition with fish for common prey (Morin, 1984b). In fact, fish ponds can act as ecological "sinks" for dragonflies (Sigutova, Sigut, & Dolny, 2015).

The association of *R. mutata* with acidic water and ponds with a sphagnum fringe is similar to other aeshnids, such as *Aeshna tuberculifera*, that have also shown associations with low pH and boggy conditions (Nikula, Loose, & Burne, 2003; Paulson, 2011; Pollard & Berrill, 1992). One reason that these species are acidophilic may be linked to their preference for fish-free habitats; this may be an indirect effect mediated through fish predators that do not persist in low pH environments (Johansson & Brodin, 2003; Magnuson et al., 1998; Rychla, Benndorf, & Bucyński, 2011). Odonata are known to use indirect cues for habitat selection, and it is pos-sible that acidophilic plants, such as sphagnum, are used as oviposition cues for fish absence (Corbet, 1999). Similarly, the preference of *R. mutata* for small/shallow semi-permanent ponds is likely also associated with the exclusion of fish from these habitats due to occasional dry-ing and winter anoxia (Magnuson et al., 1998). Others have suggested that freshwater insects, including Odonata, with larval stages that are sensitive to fish predation select small waterbodies for oviposition as a fish-predator avoidance mechanism (Bohenek, Pintar, Breech, & Resetaris, 2017; Johansson & Brodin, 2003).

Small, shallow ponds are also more likely to be heavily vegetated, another key *R. mutata* habitat characteristic. Their attraction to heavily vegetated ponds is likely linked to oviposition behavior. Females oviposit on spatterdock stems, undersides of spatterdock leaves, and in other

aquatic and emergent vegetation as well as in shoreline mud (Beatty & Beatty, 1969; Dunkle, 2000; Nikula et al., 2003; Opler, 1985). Shallow ponds have an extended littoral zone, and thus provide an abundance of oviposition sites. Despite their common name (Spatterdock Darner), our review indicates that *R. mutata* is not restricted to ponds with spatterdock waterlily. They are also successful in ponds with different types of emergent macrophytes, including white waterlily (*Nymphaea odorata*) and pond weed (*Potamogeton* spp.). Finally, the preference of *R. mutata* to breed in ponds with a wooded riparian edge may be associated with the provision of emergence sites by downed branches and trees. Preferences for emergence supports within a species have been documented for other Anisopterans (Corbet, 1999; Worthen, 2010). When *R. mutata* was first documented in Minnesota, exuviae were collected mainly on the underside of sticks and logs along the shoreline (R. Lawrenz, personal observation).

A transient species

Very few observations of persistent *R. mutata* populations have been documented (e.g. Shiffer & White, 2014). Many state and provincial records of this species (25% of sources) indicate that this species' distribution is locally restricted (or rare), with adults observed at a small number of sites and few reproductive ponds confirmed with exuviae and/or nymph collection. Sources indicate that this species is transient or ephemeral, with adults collected at a site one year and absent in subsequent years (Appendix 1). Sources that have documented reproduction with nymphs and/or exuviae also indicate transience of the species. For example, a breeding population was documented with nymph and exuviae collection in two small, fish-free kettle ponds in the St. Croix River Valley, Minnesota in 2009–2015 (DuBois et al., 2015). This was first record of this species in the region, and documents the furthest northwest population in the species' known range. However, numbers of *R. mutata* in the two breeding ponds declined in 2013–2014. Intensive systematic survey efforts of nymphs, exuviae, and adults in 2015 and 2016 in the same breeding ponds and several other nearby waterbodies with similar habitat characteristics have revealed no further evidence of *R. mutata* in the region (Schilling E.G. and Lawrenz, R., unpublished data). Whether the species has gone locally extinct or undetected by survey efforts is uncertain, but points to the challenge of conservation planning for a species whose distribution and abundance seems to vary widely from year to year.

This species' transience and its preference for fish-free habitats corroborates the findings of Van Allen, Rasmussen, Dibble, Clay, and Rudolf (2017) that dragonfly communities are more stable through time and space in ponds with fish as top predators, whereas dragonfly communities in fish-free ponds show higher levels of species turnover (Van Allen et al., 2017). Variability in dragonfly abundance and species composition in fish-free lakes may be linked to the vagility of taxa associated with this habitat type. Amongst the strongest fliers of Odonates, aeshnids are highly mobile as adults. Some aeshnid species, such as *Anax junius*, are known to migrate long distances on a continental scale, which is believed to be a key dispersal mechanism for colonizing new habitats (May, 2012). Dispersal may be particularly important for dragonflies that rely on fish-free habitats. While there are many types of fish-free habitats, those that are small and shallow tend to have a more variable hydroperiod, dependent on precipitation patterns, than deeper fish-free waterbodies with a permanent hydroperiod (Brönmark & Hansson, 2005; Stoks & McPeek, 2003). Many small, shallow ponds experience occasional late season drying and winter anoxia, environmental factors that ensure fish absence but that may also result in local extirpation of dragonfly populations for species that cannot withstand drying (Magnuson et al., 1998; Stoks & McPeek, 2003). This habitat instability likely favors dispersal and dragonfly reproduction in several different waterbodies across the landscape to ensure persistence on a regional scale (May, Gregoire, Gregoire, Lubertazzi, & Matthews, 2017). Correspondingly,

lentic dragonflies are known to be stronger dispersers than lotic species, as lentic habitats are less persistent over time than lotic habitats (Corbet, 1999; Hof, Brändle, & Brandl, 2006; Hof et al., 2012). Interestingly, the dispersal ability of lentic species and their adaptation to more variable habitats is thought to result in larger ranges, wider ecological preferences, and ultimately confer a lower extinction risk relative to lotic species (Clausnitzer et al., 2009). The rarity of *R. mutata* does not fit this paradigm. Odonata that are habitat specialists, like *R. mutata*, are more prone to changes in environmental conditions than habitat generalist, and thus are more prone to experiencing local extinction (Korkeamäki & Suhonen, 2002).

Conservation challenges

Ultimately, the availability of suitable reproductive habitat will dictate whether *R. mutata* will persist on a landscape scale. Waterbodies exhibiting the conditions that we identified as ideal *R. mutata* reproductive habitat may historically have been widespread throughout this species' range. The abundance of small lakes and ponds across the landscape is high relative to larger waterbodies, and many small waterbodies in North America are isolated from the surface hydrology network (Downing, 2010; Hill, Weber, Debbout, & Leibowitz, 2018). Hydrological isolation is correlated with fish absence (due to the lack of natural routes of colonization by fish); therefore, the number of fish-free ponds distributed across the landscape was likely historically high (Magnuson et al., 1998; Schilling, Loftin, DeGoosh, Huryn, & Webster, 2008). However, humans have historically undervalued small waterbodies, and the ecological integrity of this habitat type has become increasingly threatened due to anthropogenic activities.

Studies of *R. mutata* dating back to the early 1900s have called for the protection of woodland ponds from agriculture and development (Williamson, 1921). Unfortunately, the pace of anthropogenic environmental change has only accelerated since these early studies, and small waterbodies in the northern hemisphere have become increasingly threatened. Humans disrupt natural barriers to fish migration into hydrologically isolated ponds via fish stocking and hydrological alterations, resulting in fewer fish-free waterbodies distributed across the landscape (Hanson et al., 2005; Rahel, 2007; Schilling et al., 2009a). Research shows that shallow lakes are particularly vulnerable to shifting stable states from clear to turbid water as a result of fish introductions and upland agricultural practices that cause nutrient loading (Hobbs et al., 2014). This shift in water quality and accompanying differences in the dominant primary producers (planktonic versus macrophytic) in turbid versus clear shallow lakes can have a dramatic effect on macroinvertebrate communities, although impacts on odonates have not yet been studied (Nolby, Zimmer, Hanson, & Herwig, 2015). Additionally, deforestation threatens the integrity of both upland and aquatic habitats, and forest fragmentation can limit movement of adult Odonata between suitable habitat patches (Jonsen & Taylor, 2000). Finally, accumulating evidence suggests that climate change, especially rising global temperature, is affecting Odonata. Shifts in distributional range and phenology, as well as community reorganization, have been documented (Bush, Theischinger, Nipperess, Turak, & Hughes, 2013; Flenner & Sahlén, 2008; Hassall & Thompson, 2008; Hassall, Thompson, French, & Harvey, 2007; Hickling, Roy, Hill, & Thomas, 2005; Ott, 2001). In particular, species inhabiting small, shallow ponds may be especially prone to experiencing the effects of warming climate, due to the smaller thermal mass in these waterbodies than in larger, deeper lakes (Matthews, 2010).

Thus, there are multiple human stressors that are likely impacting the quality and distribution of *R. mutata* reproductive habitat throughout its range. And, we suggest that the apparently stochastic and rare occurrence of this species across its range is linked not only to its habitat specificity, but also an overall decline in suitable habitat. These factors combined make conservation planning challenging for this rare and transient species. Additionally, defining ecological

requirements for Odonata to inform conservation planning is ideally based on evidence of repro-
duction, due to the potential for painting a misleadingly broad picture of a species' ecological
niche when only adult records are used (Patten, Bried, & Smith-Patten, 2015). However, most
records of *R. mutata* are one-time observations of adults (Beatty & Beatty, 1969). We found few
studies that document repeated adult records at a pond (Montgomery, 1947; Shiffer & White,
1995) and even fewer that document emergence (e.g. with exuviae) or examine for the pres-
ence of nymphs (DuBois et al., 2015). This points to the challenge of conservation planning for
Odonata in general; data on reproductive habitat preferences are scarce relative to adult presence
(Patten et al., 2015). We acknowledge that our inclusion of adult records to indicate reproductive
habitat preferences may result in criteria that are too course, possibly preventing us from discern-
ing even more idiosyncratic requirements of this species. However, our review provides the most
comprehensive synthesis of known habitat associations of *R. mutata* to date. The habitat criteria
that emerge from our review (small, heavily vegetated, fish-free ponds with a wooded riparian
edge and with sphagnum present) may be used as a guide for selecting potentially suitable ponds
as candidate waterbodies to conserve in order to confer protection to this species.

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Supplementary data

Supplemental data for this article can be accessed here https://doi.org/10.1080/13887890.2018.1554513

Note

1. Connecticut (S2), Illinois (S2), Indiana (S1S2), Iowa (S1), Kentucky (S1S2), Maryland (S1), Massachusetts (S3),
   Michigan (SNR), Missouri (SNR), New Hampshire (S1), New Jersey (S3), New York (S2), Ohio (S2), Pennsylva-
   nia (S1), Rhode Island (S2), Tennessee (S3S4), Vermont (S1), Virginia (S2), West Virginia (S1), Wisconsin (S1),
   and Ontario (S1)

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