

Parasitic Infestation Patterns of Water Mites (*Arrenurus spp.*) on Odonata Species in North African Freshwater Habitats

Houda KHEDIR^{1*}

Abdallah AOUADI^{2, 3}

Sihem SEDDIK⁴

¹Department of Biology, Laboratory of Sciences and Technology of water and Environment, Mohamed Cherif Messaadia University, Souk-Ahras, ALGERIA

²Department of Biology, Faculty of Nature and Life Sciences, Chadli Bendjedid University, El Tarf, ALGERIA

³Laboratoire de Conservation des Zones humides, 8 Mai 1945 Université, Guelma, ALGERIA

⁴Department of Biology, Laboratory of Terrestrial and Aquatic Ecosystems, Mohamed Cherif Messaadia University, Souk-Ahras, ALGERIA

e-mails: ¹h.khedir@univ-soukahras.dz, ²a.aouadi@univ-eltarf.dz, ⁴s.sidik@univ-soukahras.dz

ORCID IDs: ¹0009-0003-3737-9747, ²0000-0002-3259-7396, ⁴0009-0005-4794-1777

*Corresponding author

ABSTRACT

This study investigates the parasitic relationship between water mites and Odonata species in a lotic environment in Souk Ahras, analyzing 27 species including both Zygoptera and Anisoptera. Over a two-year period, we recorded 744 parasitic larvae on 110 individuals belonging to four Zygoptera species: *Platycnemis subdilatata* (Selys, 1849), *Coenagrion caerulescens* (Fonscolombe, 1838), *Coenagrion mercuriale* (Charpentier, 1840), and *Ischnura graellsii* (Rambur, 1842). Generalized linear model revealed significant differences in infestation levels based on species and body parts, while sex differences were not significant. *P. subdilatata* exhibited the highest infestation rate of 2.74%, accounting for 75 infested individuals. In contrast, *C. caerulescens*, *C. mercuriale*, and *I. graellsii* showed lower prevalence rates of 1.28%, 1.01%, and 0.95%, respectively. Mites were predominantly found attached to the thorax, probably because it provides better survival chances and more favorable conditions for larval development. Our findings highlight a strong host preference by water mites, indicating that only certain damselflies serve as hosts, thus contributing to the understanding of parasitism dynamics in freshwater ecosystems.

Keywords: Odonates, Lotic environment, Souk Ahras, Parasitic larvae, Infestation, Damselflies.

Khedir, H., Aouadi, A., & Seddik, S. (2025). Parasitic infestation patterns of water mites (*Arrenurus spp.*) on Odonata species in North African freshwater habitats. *Journal of the Entomological Research Society*, 27(1), 139-149.

Received: October 23, 2024

Accepted: February 14, 2025

INTRODUCTION

Host-symbiont interactions are fundamental ecological relationships that shape biodiversity and ecosystem dynamics. These interactions exist along a continuum, ranging from mutualism, where both organisms benefit, to parasitism, where one organism benefits at the expense of the other (Newman, Gillis, & Hager, 2021). Although viewed negatively, parasites can benefit other species, influence food web complexity, and affect community composition. They also contribute to ecosystem energy budgets thus underscoring their importance for conservation and public health (Hatcher, Dick, & Dunn, 2012). In freshwater ecosystems, parasitic interactions involving aquatic insects, particularly Odonata, provide notable examples of these ecological dynamics. The Odonata not only fulfill crucial ecological functions but also serve as valuable bioindicators of environmental health (Miguel, Oliveira-Junior, Ligeiro, & Juen, 2017). Their prominence in scientific literature contrasts with that of other important aquatic insect groups, such as Coleoptera, Ephemeroptera, Plecoptera, and Trichoptera, which are often underrepresented (Kohler, 2008). This underscores the significant focus on Odonata in understanding host-parasite dynamics and their implications for the health of freshwater ecosystems.

Odonates are primarily ectoparasitized by Ceratopogonidae, such as *Forcipomyia paludis* (Martens et al., 2008), and water mites (Hydrachnidia), particularly from the families Hydryphantidae and Limnocharidae, during the imago stage. In contrast, Arrenuridae generally parasitize odonate immature stages (Smith & Oliver, 1986). These parasites depend on odonates for both nutritional resources and habitat throughout their life cycles (Andrew, Thaokar, & Verma, 2012). Specifically, water mites use odonates as hosts to feed on their haemolymph and to achieve sexual maturation during the adult (imago) stage of the host (Forbes & Robb, 2008).

Water mites (Hydrachnidia) constitute a significant group within class Arachnida, with over 6,000 species described worldwide (Cook, 1974; Viets, 1987). The attachment body part of these larval mites on a host varies according to the host's morphology and the mite's phylogenetic background (Smith & Oliver, 1986; Smith, Cook, & Smith, 2001). This parasitic interaction can have significant effects on the host, thus affecting its health, behavior, and ecological roles, reducing body mass (Smith, 1988), causing tissue damage (Åbro, 1982), affecting developmental stability, and hindering fertility by obstructing sperm transfer to the male's secondary genitalia or interfering with copulation (Bonn, Gasse, Rolff, & Martens, 1996; Forbes, 1991; Forbes & Baker, 1991). In response, odonates can aggregate hemocytes at the punctured body part and produce melanotic encapsulations around the feeding tubes, immobilizing the mites, which become "deflated" (Nagel, Mlynarek, & Forbes, 2011). This response serves as a visible indicator of host resistance. The capacity of Odonates to resist parasitism and the difference in parasitism rate even between congeneric species (Worthen & Hart, 2016) highlight the complex interplay between ecological factors, such as the abundant host species and possible evolutionary adaptations in response to parasitism (Hasik, Ilvonen, Siepielski, & Murray, 2022). Larval water mites of the

Arrenurus genus actively seek their hosts during their larval stage (Ilvonen, 2018), timing their peak host-seeking activity to coincide with the emergence of preferred odonate hosts from the water (Michell, 1967; Smith, 1988). Upon locating a larval odonate, the water mite attaches itself and remains in place until the host emerges as an adult.

Once the odonate reaches maturity, the mite transfers from the larval exoskeleton, to the skin of the newly emerged adult (Mitchell, 1961). Individual Odonates can host over 400 mites simultaneously (Worthen & Turner, 2015), with mite infestation prevalence reaching 100% for certain species in specific habitats (Zawal & Buczyński, 2013). Several studies have demonstrated that ectoparasitism of Odonata species varies significantly, with some species showing greater susceptibility to infestation (Ilvonen, 2018) due to factors such as morphological and life history traits (Bunker et al., 2013), as well as environmental conditions like vegetation biomass and climatic stability (Da Silva, Poulin, & Guillermo-Ferreira, 2021).

To date, only one study has been conducted in North Africa that specifically addressing the parasitism of Odonata, with a focus on *Forcipomyia paludis* as a parasite (Boudot, Havelka, & Martens, 2019). Moreover, despite strong interest in odonate studies in Algeria, most research has focused on their taxonomic distribution (Samraoui & Corbet, 2000; Chelli & Moulai, 2019; Chelli, Moulai, & Djemai, 2020; Ait Taleb, Ali Ahmed Sadoudi, Bensidhoum, & Houhamdi, 2024), reproduction and life cycles (Samraoui, Bouzid, Boulahbal, & Corbet, 1998; Mellal, Bensouilah, Houhamdi, & Khelifa, 2018; Samraoui, Touati, & Samraoui, 2019), and responses to climate change and anthropogenic pressure (Hafiane et al., 2016; Khelifa, Mahdjoub, Baaloudj, Cannings, & Samways, 2021). Consequently, the parasitological aspects of these insects remain notably understudied, particularly in regions like North Africa. This gap in knowledge restricts our understanding of host-parasite interactions within freshwater ecosystems. Addressing this issue will enhance our understanding of the ecological roles of Odonates and their responses to environmental changes. This study aims to explore the prevalence, distribution, and infestation patterns of water mites (*Arrenurus* sp.) infestation in odonata species inhabiting the freshwater ecosystems of Souk Ahras (Algeria). Specifically, it aims to identify the Odonata species most affected by water mite parasitism, investigate differences in infestation patterns across various body parts (thorax, abdomen, wings), and assess potential differences in parasitism rates between male and female hosts. Furthermore, this research establishes a foundation for future investigations into the phenology and environmental factors influencing infestation rates.

MATERIALS AND METHODS

Study area and Sampling Method

Between January 2022 and August 2023, adult odonates were collected monthly from a lotic ecosystem in Souk Ahras, at eight sampling stations located at elevations ranging from 598 to 818 meters asl (Fig. 1). All odonate species observed within and around the water body, along a 100-meter transect, were recorded and identified using the field guide by Dijkstra & Lewington (2007). Mite larvae attached to each specimen

were carefully removed using fine histological tweezers and needles, then preserved in Eppendorf tubes containing Koenig's fluid (40 mL distilled water, 10 acetic acid, and 50 glycerin). After mite removal, the sampled individuals were released, and their subsequent flight was carefully monitored to ensure minimal harm.

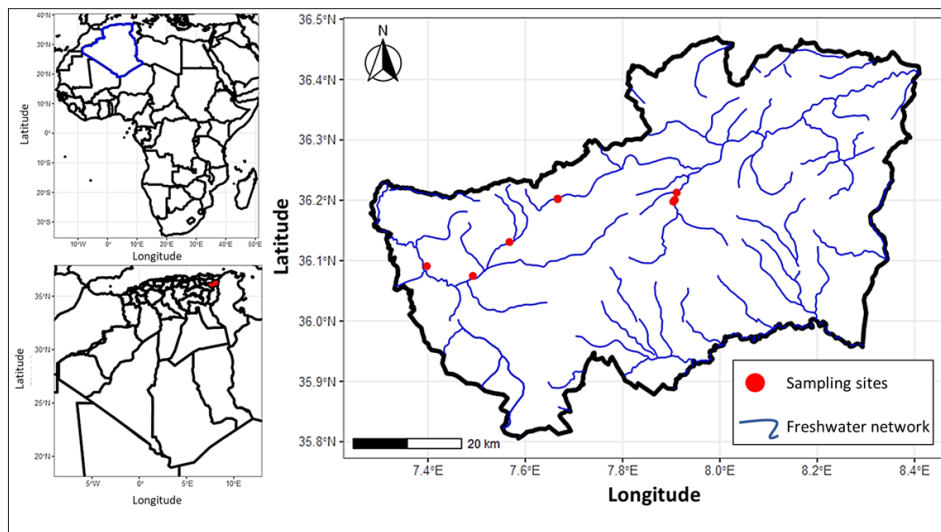


Figure 1. Study area location.

Data Analysis

The prevalence of infestation was calculated as the proportion of parasitized individuals relative to the total number of individuals analyzed (parasitized individuals/total individuals analyzed \times 100). In addition, to determine whether mite counts varied by species, sex, or body part, a generalized linear model (GLM) with a negative binomial distribution and a log link function was performed using the *glm.nb* function from the MASS package (Ripley et al., 2013) to account for overdispersion. Afterwards, post hoc analysis for category differences was performed using the *glht* function from the multcomp package (Hothorn et al., 2016).

RESULTS

Over the two-years period, a total of 27 species, belonging to 7 families were analyzed, 744 parasitic larvae of water mites were found on 110 (♀ and ♂) specimens representing four species of Odonata from the suborder Zygoptera. Our results showed that, *P. subdilatata* was the most infested species, with 75 individuals observed carrying larval water mites on their bodies (Fig. 2). This species exhibited the highest prevalence among those infested, at 2.74%. The second most infested species was *C. caerulescens*, which was recorded with 13 infested individuals and a prevalence rate of 1.28%. Lastly, *C. mercuriale* and *I. graellsii* had the lowest prevalence with, 1.01% and 0.95%, respectively. Only 11 parasitized individuals of each species were encountered during the survey (Table 1).

Parasitic Infestation Patterns of Water Mites (Arrenurus spp.) on Odonata

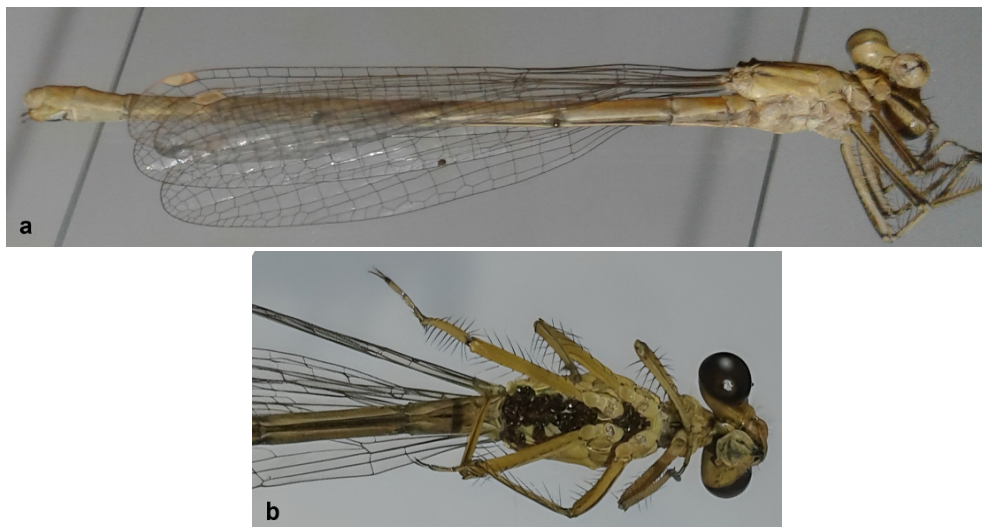


Figure 2. Presence of aquatic mites (*Arrenurus*) on different body parts of *Platycnemis subdilatata*, a) abdomen and wings, b) thorax.

Table 1. Details of mite-Infested Odonates: Prevalence, sex distribution, and body localization of Infestation (numbers indicate mites per body part).

Odonata species	Parasitized individuals	Prevalence of infestation (%)	Part of host's body			Specimens parasitized by sex	
			Abdomen	Thorax	Wings	♀	♂
<i>Platycnemis subdilatata</i>	75	2.74	17	657	3	41	34
<i>Coenagrion mercuriale</i>	11	1.01	1	11	1	4	7
<i>Coenagrion caerulescens</i>	13	1.28	2	21	1	8	5
<i>Ischnura graellsii</i>	11	0.95	2	28	0	5	6

Mite counts were significantly influenced (Table 2) by odonate species and body part, whereas differences between sexes were not significant.

Table 2. Results of generalized linear model (GLM) with negative binomial error distribution to compare parasite abundance among Odonate species, body part, and sex.

	Df	Sum Sq	F value	P-value
(Intercept)		-2.67	-6.35	<0.001 ***
Species	3	25.55	4.02	<0.001 ***
Body part	2	420.26	99.19	<0.001 ***
Sex	1	0.34	0.16	0.56

In the four odonate species infested with mite, mite abundance differed significantly between *P. subdilatata* and the other three species. Specifically, *P. subdilatata* exhibited significantly higher mite abundance compared to *C. caerulescens* (Estimate = 1.3489, $Z = 3.801$, $p < 0.001$), *C. mercuriale* (Estimate = 1.4936, $Z = 3.776$, $p = 0.00103$), and *I. graellsii* (Estimate = 1.0356, $Z = 2.837$, $p = 0.02265$). However, there were no significant differences in mite abundance among *C. caerulescens*, *C. mercuriale*, and

I. graellsii ($p > 0.05$) (Fig. 3). Mite abundance also varied significantly across different body parts (Fig. 4). Mite abundance on the thorax was significantly higher than on the abdomen (Estimate = 3.45, $Z = 12.83$, $p < 0.001$), while the wings had significantly fewer mites compared to both the abdomen (Estimate = -1.2560, $Z = -2.594$, $p = 0.024$) and the thorax (Estimate = -4.7114, $Z = -10.83$, $p < 0.001$).

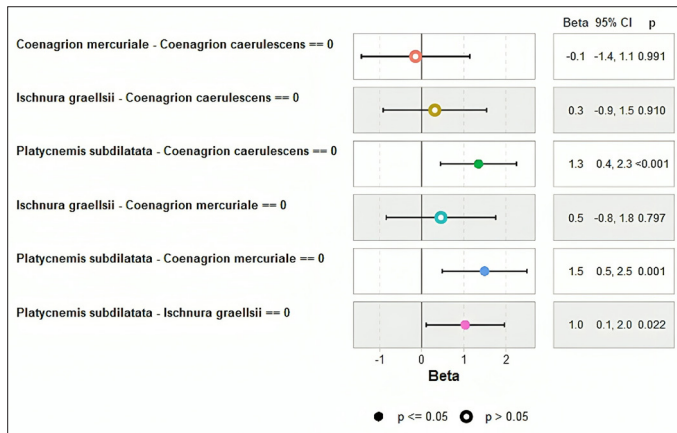


Figure 3. Multiple Comparison of odonate species in terms of mite count. Confidence Intervals not crossing zero on the x-axis Indicate a significant difference.

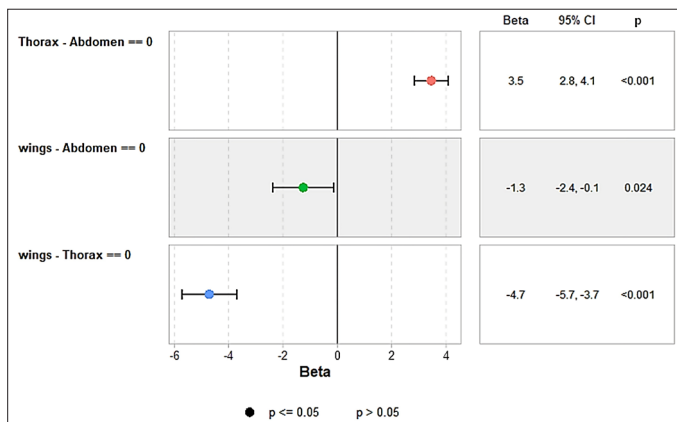


Figure 4. Multiple Comparison of body parts in terms of mite count. Confidence Intervals not crossing zero on the x-axis Indicate a significant difference.

DISCUSSION

Literature indicates a strong taxonomic preference of Arrenurid mites for parasitizing Diptera and Odonata (Rolff, 2001), with the genus *Arrenurus* being specialized in parasitizing odonata (Smith, 1988). This paper provides new insights into odonata hosts of parasitic larvae from the *Arrenurus* genus in lotic environments of Northern Africa, where no data had previously been reported for four damselfly species (*P. subdilata*, *C.*

Parasitic Infestation Patterns of Water Mites (Arrenurus spp.) on Odonata

caerulescens, *C. mercuriale*, and *I. graellsii*). In general, our results agree with other studies, which show that zygopterans are more frequently infected than anisopterans (Conroy & Kuhn, 1977; Davids, 1997; Zawal, 2004; 2006; Ilvonen, 2018; Janra & Herwina, 2021).

The fact that parasitism was found only in damselflies and not in dragonflies is likely linked to the longer larval period of dragonflies compared to that of damselflies, as well as their lower population density (Rivas-Torres & Cordero-Rivera, 2024), which increases the opportunity for mites to find their hosts. Additionally, damselflies are generally found living around water bodies for most of their lives, which increases the likelihood that water mites can return to water as soon as their parasitic phase ends. Among zygopterans, we recorded interspecific variation in water mite infestation, with prevalence ranging from 0.95% in *Ischnura graellsii* to 2.74% in *Platycnemis subdilatata*, which also had the highest number of infested individuals (75). Although infestation levels were generally low across species, *P. subdilatata* showed the greatest recorded prevalence, albeit only slightly higher compared to other species. Possibly affected by the sheer abundance of the latter species in the study area, this may be due to specific biological factors. However, this result should be interpreted with caution, as the sample size is not large enough to draw definitive conclusions. Further research is necessary to determine whether these parasitic preference patterns hold with larger sample sizes.

Water mite parasitism is influenced by both environmental factors (e.g., dissolved oxygen, conductivity, pH, and air temperature) and host traits (e.g. body mass) (LoScerbo, Farrell, Arrowsmith, Mlynarek, & Lessard, 2020; da Silva et al., 2021; Hasik & Siepielski, 2022). In the water mite literature, numerous reports evaluate the differential parasitism of host sexes. Robb & Forbes (2006); Zawal (2004, 2006); Zawal & Dyatlova (2008); Baker, Mill, & Zawal (2008); Andrew et al. (2012) and Janra & Herwina (2021) have indicated clear preferences for the infestation of female hosts. This preference has also been observed in *Ceriatrion tenellum* (Andrés & Cordero, 1998). Female odonates oviposit in or near water, which increases their exposure to aquatic environments and, consequently, to water mites. Alternatively, specific behaviors exhibited by female odonate, such as their habitat preferences or activity patterns, may also increase their susceptibility to mite infestations. Therefore, attachment to female odonates could be advantageous for larval water mites to complete their life cycle.

However, this biased sexual imbalance was not confirmed in the present study, likely due to the low infestation rate, which may have limited the statistical power to detect such differences. Likewise, Rolff (2000); Zawal & Buczyński (2013); Ilvonen, Kaunisto, & Suhonen (2016) reported the absence of such differences. This is because mites attach to their hosts while immature, without considering the sexual differences that appear later (Ilvonen et al., 2016). Paul, Khan, & Herberstein (2022) proposed that sex-related disparities in infestation rates across species might stem from unique differences in body condition, shaped by both sexual and developmental factors. However, the results obtained did not provide clear answers, and analyzing a large dataset from various environments is essential to determine whether parasites exhibit a preference for the sex of their hosts.

Our data clearly indicate a preference for mites to attach to different body parts of their hosts. It is not surprising that mites attach more frequently to the ventral surface of the thorax than to the abdomen or wings. According to Zawal & Buczyński (2013), this preference may stem from the reduced mortality of parasites located on this body region (the legs of the odonates protect parasites from mechanical harm) or from the sequence in which parasites occupy different body areas (the thorax being the primary tagma of the body that is more conducive to inhabiting and emerges first from the exuvium). Generally, the first abdominal segments are inhabited when no more space is available on the thorax. In accordance with the present results, Zawal (2004, 2006) reported that the thorax of *Enallagma cyathigerum*, *Pyrrhosoma nymphula*, *Coenagrion puella* and *Coenagrion pulchellum* serves as a nearly exclusive host for *Arrenurus* larvae. This finding was also supported by Baker, Mill, & Zawal (2007) for *Coenagrion puella*, with an attachment rate of 82.3%. On the other hand, abdominal attachment sites have been documented for *Lestes sponsa*, *Platycnemis pennipes* and *Ischnura elegans*. However, in *Erythromma najas*, both the thorax and abdomen were equally affected (Zawal, 2004, 2006). Previous data on wing attachment have also been noted by Cassagne-Mejean (1966), Åbro (1982), Pavlyuk (1981, 1989), Davids (1997), and Zawal & Jaskula (2008) for two Anisoptera species: *Sympetrum fonscolombii* and *Sympetrum meridionale*.

In conclusion, this study provides new insights into the infestation of water mite (*Arrenurus* sp.) in Odonata species in Souk Ahras. The highest prevalence was observed in *P. subdilatata*. The thorax was parasitized more frequently than the abdomen and wings, and no significant differences were found between male and female hosts. These findings enhance our understanding of parasitism in freshwater ecosystems. Further research is needed to investigate how host phenology, environmental factors, and life-history traits influence infestation patterns, as well as the long-term effects of parasitism on Odonata populations and ecosystem health.

CONFLICT OF INTEREST

All authors have declared that there is no conflict of interest regarding publication of this article.

REFERENCES

- Åbro, A. (1982). The effect of parasitic water mite larvae (*Arrenurus* spp.) on zygopteran imagoes (Odonata). *Journal of Invertebrate Pathology*, 39(3), 373-381.
- Ait Taleb, L., Ali Ahmed Sadoudi, D., Bensidhoum, M., & Houhamdi, M. (2024). Altitudinal pattern of Odonata diversity in Kabylia (Algeria): a contrasting pattern in lotic and lentic habitats. *Aquatic Insects*, 45(4), 1-13. <https://doi.org/10.1080/01650424.2024.2329550>.
- Andrés, J. A. & Cordero, A. (1998). Effects of water mites on the damselfly *Ceragrion tenellum*. *Ecological Entomology*, 23(2), 103–109. <https://doi.org/10.1046/j.1365-2311.1998.00125.x>
- Andrew, R.J., Thaokar, N., & Verma, P. (2012). Ectoparasitism of Anisopteran dragonflies (Insecta: Odonata) by water mite larvae of *Arrenurus* spp (Arachnida: Hydrachnida: Arrenuridae) in Central India. *Acarina*, 20(2), 194-198.

Parasitic Infestation Patterns of Water Mites (Arrenurus spp.) on Odonata

- Baker, R.A., Mill, P.J., & Zawal, A. (2007). Mites on Zygoptera - with particular reference to *Arrenurus* species, selection sites and host preferences. *Odonatologica*, 36(4), 339-347.
- Baker, R.A., Mill, P.J., & Zawal, A. (2008). Ectoparasiting water mite larvae of the genus *Arrenurus* on dragonfly *Coenagrion puella* (Linnaeus) (Zygoptera: Coenagrionidae). *Odonatologica*, 37(3), 193-202.
- Bonn, A., Gasse, M., Rolff, J., & Martens, A. (1996). Increased fluctuating asymmetry in the damselfly *Coenagrion puella* is correlated with ectoparasitic water mites: implications for fluctuating asymmetry theory. *Oecologia*, 108(4), 506-598.
- Boudot, J.P., Havelka, P., & Martens, A. (2019). The biting midge *Forcipomyia paludis* as a parasite of Odonata in North Africa (Diptera: Ceratopogonidae). *Notulae Odonatologicae*, 9(4), 125-172. <https://doi.org/10.5281/zenodo.3539758>.
- Bunker, B.E., Janovy Jr, J., Tracey, E., Barnes, A., Duba, A., Shuman, M., & Logan, J.D. (2013). Macroparasite population dynamics among geographical localities and host life cycle stages: Eugregarines in *Ischnura verticalis*. *The Journal of parasitology*, 99(3), 403-409. <https://doi.org/10.1645/GE-3137.1>.
- Cassagne-Mejean, F. (1966). Contribution à l'étude des Arrenuridae (Acari, Hydrachnellae) de France. *Acarologia*, 8, 1-186.
- Chelli, A. & Moulai, R. (2019). Ecological characterization of the odonatofauna in lotic and lentic waters of northeast Algeria. *Annales de la Société entomologique de France* (NS). 55(5), 430-445.
- Chelli, A., Moulai, R., & Djemai, A. (2020). Does the Tichi Haf dam construction affect dragonfly and damselfly (Odonata: Insecta) assemblages of the Boussellam watercourse (central north Algeria)? A preliminary study. *Zoology and Ecology*, 30(30), 37-47.
- Conroy, J.C. & Kuhn, J.L. (1977). New annotated records of Odonata from the province of Manitoba with notes on their parasitism by larvae of water mites. *The Manitoba Entomologist*, 11, 27-40.
- Cook, D.R. (1974). Water mite genera and subgenera. *Memoirs of American Entomological Institute*, 21, 1-860.
- Da Silva, G.G., Poulin, R., & Guillermo-Ferreira, R. (2021). Do latitudinal and bioclimatic gradients drive parasitism in Odonata? *International Journal for Parasitology*, 51(6), 463-470.
- Davids, C. (1997). Watermijten als parasieten van libellen. *Brachytrom*, 1(2), 51-55.
- Dijkstra, K-D.B. & Lewington, R. (2007). *Guide des Libellules de France et d'Europe*. Delachaux et Niestlé, Paris, France. 320 p.
- Forbes, M.R. (1991). Ectoparasites and mating success of male *Enallagma ebium* damselflies (Odonata: Coenagrionidae). *Oikos*, 60(3), 336-342.
- Forbes, M.R. & Baker, R.L. (1991). Condition and fecundity of the damselfly, *Enallagma erbi* (Hagen): the importance of ectoparasites. *Oecologia*, 86(3), 335-341.
- Forbes, M.R. & Robb, T. (2008). Testing hypotheses about parasite-mediated selection using odonate hosts. In A. Córdoba-Aguilar (Ed.). *Dragonflies and damselflies: model organisms for ecological and evolutionary research* (pp. 175-188). Oxford, UK: Oxford University Press.
- Hafiane, M., Hamzaoui, D., Attou, F., Bouchelouche, D., Arab, A., Alfarhan, A.H., & Samraoui, B. (2016). Anthropogenic impacts and their influence on the spatial distribution of the Odonata of wadi el Harrach (north-central Algeria). *Revue d'Écologie*, 71(3), 239-249.
- Hasik, A.Z. & Siepielski, A.M. (2022). A role for the local environment in driving species-specific parasitism in a multi-host parasite system. *Freshwater Biology*, 67(9), 1571-1583.
- Hasik, A.Z., Ilvonen, J.J., Siepielski, A.M., & Murray, R.L. (2022). Odonata immunity, pathogens, and parasites, in Córdoba-Aguilar, C., Beatty, C., Bried, J. (eds), *Dragonflies and Damselflies: Model Organisms for Ecological and Evolutionary Research*, 2nd edn. <https://doi.org/10.1093/oso/9780192898623.003.0006>
- Hatcher, M.J., Dick, J.T., & Dunn, A.M. (2012). Diverse effects of parasites in ecosystems: linking interdependent processes. *Frontiers in Ecology and the Environment*, 10(4), 186-194.

- Hothorn, T., Bretz, F., Westfall, P., Heiberger, R.M., Schuetzenmeister, A., Scheibe, S., & Hothorn, M. T. (2016). Package 'multcomp'. Simultaneous inference in general parametric models. Project for Statistical Computing, Vienna, Austria, 1-36.
- Ilvonen, J.J., Kaunisto, K.M., & Suhonen, J. (2016). Are sexes equally parasitized in damselflies and dragonflies? *Oikos*, 125 (3), 315-325. <https://doi.org/10.1111/oik.02437>.
- Ilvonen, J.J. (2018). A comparative study of parasitism in insects: Why some odonata species have parasites and others do not? Doctoral Thesis in Biology (Finland: University of Turku).
- Janra, M.N. & Herwina, H. (2021). *Parasitism on Riparian Dragonflies (Odonata) at Biology Education and Research Forest*, Universitas Andalas. <https://doi.org/10.1088/1755-1315/757/1/012083>.
- Khelifa, R., Mahdjoub, H., Baaloudj, A., Cannings, R.A., & Samways, M.J. (2021). Effects of both climate change and human water demand on a highly threatened damselfly. *Scientific reports*, 11(1), 7725.
- Kohler, S.L. (2008). The ecology of host-parasite interactions in aquatic insects. In *Aquatic insects: challenges to populations* (pp. 55-80). Wallingford UK: CABI.
- LoScerbo, D., Farrell, M.J., Arrowsmith, J., Mlynarek, J., & Lessard, J.-P. (2020). Phylogenetically conserved host traits and local abiotic conditions jointly drive the geography of parasite intensity. *Functional Ecology*, 34(12), 2477-2487.
- Mellal, M.K., Bensouilah, M., Houhamdi, M., & Khelifa, R. (2018). Reproductive habitat provisioning promotes survival and reproduction of the endangered endemic damselfly *Calopteryx exul*. *Journal of Insect Conservation*, 22(3), 563-570.
- Martens, A., Ehmann, H., Peitzner, G., Peitzner, P., & Wildermuth, H. (2008). European Odonata as hosts of *Forcipomyia paludis* (Diptera: Ceratopogonidae). *International Journal of Odonatology*, 11(1), 59-70.
- Miguel, T.B., Oliveira-Junior, J.M.B., Ligeiro, R., & Juen, L. (2017). Odonata (Insecta) as a tool for the biomonitoring of environmental quality. *Ecological Indicators*, 81, 555-566.
- Mitchelle, R. (1961). Behavior of the larvae of *Arrenurus fissicornis* Marshall, a water mite parasitic on dragonflies. *Animal Behavior*, 9(3/4), 220-224. [https://doi.org/10.1016/0003-3472\(61\)90012-4](https://doi.org/10.1016/0003-3472(61)90012-4).
- Michelle, R. (1967). Host exploitation of two closely related water mites. *Evolution*, 21(1), 59-75. <https://doi.org/10.1111/j.1558-5646.1967.tb00130.x>.
- Nagel, L., Mlynarek, J.J., & Forbes, M.R. (2011). Immune response to nylon filaments in two damselfly species that differ in their resistance to ectoparasitic mites. *Ecological Entomology*. 36(6): 736-743. <https://doi.org/10.1111/j.1365-2311.2011.01323.x>.
- Newman, J.A., Gillis, S., & Hager, H.A. (2021). Costs, benefits, parasites and mutualists: The use and abuse of the mutualism–parasitism continuum concept for Epichloë fungi. *bioRxiv*, 2021-04. <https://doi.org/10.1101/2021.04.21.440766>.
- Paul, S., Khan, M.K., & Herberstein, M.E. (2022). Sexual and developmental variations of ecto-parasitism in damselflies. *PLoS ONE*, 17(7), e0261540.
- Pavlyuk, R.S. (1981). Parasitological studies of dragonflies (Insecta, Odonata) stored in entomological collections. *Vestnik Zoologii*, 2, 90-92 [in Russian].
- Pavlyuk, R.S. (1989). Dragonfly parasites. In Belyshev, B.F., Haritonov A.Yu., Borisov C. N., Spuris Z.D., Mazohin-Porshnyakov, G.A., Mokrushov, P.A., Pavlyuk, R.S., Pritykina, L. N., Ryazanova, G.I., Shalopenok, E.S., Pisanenko, A.D., Suhacheva, G.A., Haritonova, I.N., Zaika, V.V. & Francevich, L.I (Eds), *Fauna i ekologiya strekoz [Fauna and ecology of dragonflies]* (pp.118-141). Nauka, Novosibirsk [in Russian].
- Ripley, B., Venables, B., Bates, D.M., Hornik, K., Gebhardt, A., Firth, D., & Ripley, M.B. (2013). Package 'mass'. *Cran r*, 538, 113-120.
- Rivas-Torres, A. & Cordero-Rivera, A. (2024). A review of the density, biomass, and secondary production of odonates. *Insects*, 15(7), 510. <https://doi.org/10.3390/insects15070510>
- Robb, T. & Forbes, M.R. (2006). Sex biases in parasitism of newly emerged damselflies. *Ecoscience*, 13(1), 1-4.
- Rolf, J. (2000). Water mite parasitism in damselflies during emergence: two hosts, one pattern. *Ecography*, 23, 273-282.

Parasitic Infestation Patterns of Water Mites (Arrenurus spp.) on Odonata

- Rolff, J. (2001): Invited Review. Evolutionary Ecology of Water mite-insect interactions: a critical appraisal. Stuttgart, Arch. *Hydrobiol*, 152, 353-368.
- Samraoui, B., Bouzid, S., Boulahbal, R., & Corbet, P.S. (1998). Postponed reproductive maturation in upland refuges maintains life-cycle continuity during the hot, dry season in Algerian dragonflies (Anisoptera). *International Journal of Odonatology*, 1(2), 119-135.
- Samraoui, B. & Corbet, P.S. (2000). The odonata of numidia, northeastern algeria part I status and distribution. *International Journal of Odonatology*, 3(1), 11-25.
- Samraoui, B., Touati, L., & Samraoui, F. (2019). Slow and steady wins the race: Life cycle and seasonal regulation of *Gomphus lucasii* (Odonata: Gomphidae). *Odonatologica*, 48(3-4), 229-246.
- Smith, I.M. & Oliver, D.R. (1986). Review of parasitic associations of larval water mites (Acari Parasitengona: Hydrachnida) with insect hosts. *The Canadian Entomologist*, 118, 407-472.
- Smith, B.P. (1988). Host-parasite interaction and impact of larval water mites on insects. *Annual Review of Entomology*, 33, 487-507. <https://doi.org/10.1146/annurev.en.33.010188.002415>.
- Smith, I.M., Cook, D.R., & Smith, B.P. (2001). Water mites (Hydrachnida) and other arachnids. In Thorp, J.H. & Covich, A.P (eds), *Ecology and Classification of North American Freshwater Invertebrates* (pp. 551-659). Academic Press, San Diego.
- Viets, K.O. (1987). Die Milben des Süßwassers (Hydrachnellae und Halacaridae [part], Acari.II: Katalog). In *Sonderbände des Naturwissenschaftlichen Vereins Hamburg*, 8, 1-1012.
- Worthen, W.B. & Turner, L.H. (2015). The effects of odonate species abundance and diversity on parasitism by water mites (*Arrenurus* spp.) testing the dilution effect. *International Journal of Odonatology*, 18, 233-248.
- Worthen, W.B., & Hart, T.M. (2016). Resistance to *Arrenurus* spp. parasitism in odonates: patterns across species and comparisons between a resistant and susceptible host. *Journal of Insect Science*, 16(1), 37.
- Zawal, A. (2004). Parasitizing of dragonflies by water mite larvae of the genus *Arrenurus* in the neighbourhood of Barlinek (NW Poland). *Zoologica Poloniae*, 49, 37-45.
- Zawal, A. (2006). Phoresy and parasitism: water mite larvae of the genus *Arrenurus* (Acari: Hydrachnida) on Odonata from lake Binowskie (NW Poland). *Biological Letters*, 43, 257-276.
- Zawal, A. & Dyatlova, E.S. (2008). Parasitizing on damselflies (Odonata: Coenagrionidae) by water mite (Acari: Hydrachnida) larvae from Odessa province (Southwestern Ukraine). *Natura Montenegrina*, 7, 453-462.
- Zawal, A. & Jaskula, R. (2008). First data of parasitizing on *Sympetrum meridionale* (Sélys) by *Arrenurus* (Hydrachnida, Acari) larvae from Montengro. *Natura Montenegrina*, 7, 354-359.
- Zawal, A. & Buczyński, P. (2013). Parasitism of Odonata by *Arrenurus* (Acari: Hydrachnida) larvae in the Lake Świdwie, nature reserve (NW Poland). *Acta Parasitologica*, 58, 486-495.