

Aspects of reproductive biology and ecology of *Coenagrion mercuriale* at its southern range margin

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Coenagrion mercuriale is a threatened damselfly in most parts of its geographic distribution. It is listed as endangered in North Africa, where no data on its biology or ecology are available. This study aims to illustrate the reproductive behaviour and habitat preferences of adults in a population located in north-east Algeria, representing the southern limit of the species distribution. After emergence, adults spent 3 to 4 days away from the water to mature. Young mature individuals returned to the stream to mate, sometimes not far from their emergence site. The mean duration of copulation and oviposition were 20.08 ± 8.79 min (\pm SD) and 52.66 ± 12.17 min (\pm SD), respectively, separated by a short post-copulatory rest of 4.60 ± 2.02 min (\pm SD). Copulation duration was positively correlated with male body length while resting duration was positively related to copulation duration. Single males and breeding pairs preferred the same habitats, characterized by relatively dense and high in-channel bank vegetation, and a quite large stream bed, with a substrate which mainly consisted of clay and silt. A comparison of the reproductive behaviour and habitat preferences with a population located in the northern limit of the distribution range is presented and discussed.

Keywords: Odonata; damselfly; endangered; Algeria; reproductive behaviour; habitat preferences

Introduction

All species exist in a limited geographic range that varies in size and spatial structure. Species life history pattern changes in different parts of the range (Conover, 1992; Stearns, 1992). These environment-mediated responses are often referred to as plasticity, which can be detected not only in morphology but also in physiology and behaviour (Scheiner, 2002; Smith-Gill, 1983; Tanaka, 2004; Thompson, 1992; Van Buskirk, 2002; Van Buskirk & Arioli, 2005). In temperate regions, one might expect that population differences are more marked in the two latitudinal extremes of the geographic range because they face substantially different environmental conditions, mainly in temperature. Understanding the pattern of life history trait variation along a distribution range is crucial to determining how marginal populations are adapted to their local

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environment and what the consequences are of such adaptation on the population dynamics under climate change (Bridle & Vines, 2007).

Odonates are widespread and occupy all continents except the Antarctic. Globally, many species have a large distribution that covers a large part of a continent or even more. Therefore, they represent interesting model organisms to test latitudinal adaptations to local environment. However, this aspect has received little attention in the literature. There is evidence of latitudinal variation in body size in some damselflies in Europe (Hassall, Keat, Thompson, & Watts, 2014; Hassall, Thompson, & Harvey, 2009) in concordance with the temperature–size rule (Bergmann’s rule) which states that larger size is expected at higher latitudes due to lower temperatures (Atkinson & Sibly, 1997; Bergmann, 1847). In fact, unlike larvae from high latitudes, those from low latitudes display substantially higher growth rate resulting from physiological and behavioural differences (Śniegula, Nilsson-Örtman, & Johansson, 2012; Stoks, Swillen, & De Block, 2012). As a consequence, there is a latitudinal pattern in voltinism in temperate odonates, showing an increasing trend in generation time from south to north (Corbet, Suhling, & Soendgerath, 2006).

Coenagrion mercuriale is an Atlanto-Mediterranean damselfly of great conservation concern. Although it is globally listed as Near Threatened in the IUCN Red List, it is categorized as Endangered in several parts of its range (Boudot, 2006). Its geographic distribution is more continuous in Southern Europe and rather fragmented in the two latitudinal extremes, namely southern UK in the north and the Tell Atlas (North Africa) in the south (Grand, 1996). Although the core population occurs in south Europe, most detailed studies on the biology and ecology of the species have been carried out in the UK (Kerry, 2001; Purse & Thompson, 2002, 2003a, b, 2005; Rouquette & Thompson, 2005, 2007; Watts, Kemp, Saccheri, & Thompson, 2005).

Our study aims to document some aspects of the reproductive behaviour and habitat requirements of the species in a North African population where it is listed as endangered (Samraoui et al., 2010) and compare them to those reported by Purse and Thompson (2003a) and Rouquette & Thompson (2005) in the UK, in order to test whether latitude affects ecological and behavioural characteristics in two latitudinally distant populations.

Material and methods

Study site

The Seybouse River is 225 km long, located in north-east Algeria. It is formed by the confluence of oued Cherf and oued Bouhamdane in Medjez Amar and flows into the Mediterranean near Sidi Salem. Old Bridge Canal is an artificial shallow stream, 450 m long, that flows into the upstream part of the Seybouse, at Guelma (36°28' N, 7°22' E). *Coenagrion mercuriale* is restricted to the lower part of the stream where the study took place. The study population has not been recorded before in the Seybouse watershed odonate checklist, in which the species is listed rare (Khelifa et al., 2011). The bank vegetation is dominated by *Typha angustifolia*, *Cynodon dactylon*, *Solanum nigrum*, *Veronica anagallis-aquatica*, and *Scirpus holoschoenus*. In-channel plant species consisted of *Typha angustifolia*, *Lythrum junceum*, *Nasturtium officinale*, *Cyperus laevigatus distachyo* and *Mentha aquatica*. Beside *C. mercuriale*, reproductive populations of *Calopteryx haemorrhoidalis*, *Orthetrum nitidinerve*, *O. chrysostigma* and *O. coerulescens* thrived.

Breeding parameters

Mature individuals were marked daily with alphanumeric codes on the left hind wing with paint markers from 9 April 2013 to 20 May 2013 along a 120-m transect, from 09:00 to 16:00. Body

and wing length were measured to the nearest 0.01 mm with digital callipers. Some teneral were also marked in order to determine the maturation period, and, given that their emergence location was recorded, natal dispersal was estimated. To reduce damage on the teneral soft wings and body, they were kept in cages for six hours before marking and released in their original location. The entire reproductive episode (copulation, post-copulatory resting, and oviposition) was surveyed and timed to the nearest second based on the method adopted by Purse & Thompson (2003a). The percentage of time devoted to the actual oviposition was also estimated.

Habitat preferences

The study area was divided into 12 contiguous 10 m-sections labelled with flags. Eight environmental parameters were estimated in each section, namely bank and in-channel vegetation height and density, water velocity, stream width, stream depth, emergence stone density and substrate type. For each variable, five different sampling points were selected and then the mean was calculated. Vegetation height (from the water surface to the tip of the stand) and stream width and depth were measured to the nearest centimetre with a 5 m decameter. Emergent stone and vegetation density were estimated with a 1 × 1 m quadrat. The main component of the stream bed substrate was classified as gravel-sand, sand-silt, or clay-silt using the Wentworth Scale (Allan, 1995).

Statistical analyses

All statistical analyses were conducted with R software (R project 3.0.1). Spearman correlation tests were conducted to assess potential relationship between copulation duration and male body and wing length, and between resting and copulation duration and the latter morphological traits. One-sample *t*-tests were carried out to compare the duration of the different reproductive stages with those presented by Purse & Thompson (2003a). In order to determine habitat requirements of the adults (males and breeding pairs) a principal component analysis (PCA) was carried out with the package Vegan (Oksanen et al., 2013) based on eight environmental factors and the number of males and reproductive pairs daily recorded in the 12 sections. Principal component (PC) scores were grouped based on the Bray–Curtis dissimilarity index using substrate type (Beals, 1984). Values are mean ± standard deviation (SD).

Results

Pre- and post-maturation behaviour

Of the 43 teneral that were marked, only 12 individuals were recaptured. Among the recaptures, six (two males and four females) were recorded in a reproductive state i.e. copulation in males and oviposition in females. The minimum maturation period was three and four days for males and females, respectively. The mean distance of natal dispersal was 12.5 ± 3.53 m (*n* = 2) and 35 ± 18.25 m (*n* = 4) in males and females, respectively. Mean daily apparent sex ratio was highly male biased (7.01:1, *n* = 30).

Table 1 presents the duration of the different stages of a reproductive episode. The entire reproductive episode lasted 78.20 ± 12.37 min. Mean copulation duration was 20.08 ± 8.79 min and it was positively correlated with male body length (*R* = 0.47, *p* = 0.04) but not with wing length (*R* = 0.32, *p* = 0.18). After each copulation, breeding pairs rested for a mean duration of 4.60 ± 2.02 min (1.3–8.7 min, *n* = 14). Resting duration was significantly positively

Table 1. Characteristics of reproductive behaviour of *C. mercuriale* in Algerian and British populations.

Duration	Algeria (present study)			UK (Purse & Thompson, 2003a)			<i>t</i> -test (<i>p</i> -value)
	Mean ± SD	Range	<i>n</i>	Mean ± SD	Range	<i>n</i>	
Copulation (min)	20.08 ± 8.79	6–41.5	18	24.1 ± 2.4	15.0–40.0	9	0.06
Resting (min)	4.60 ± 2.02	1.3–8.7	14	13.3 ± 3.5	3.0–39.0	9	< 0.0001
Ovi./search (min)	52.66 ± 12.17	34.5–73	9	30.5 ± 5.5	8.3–58.0	9	0.0006
Per cent ovi. (%)	51.22 ± 18.30	27–85	9	50.1 ± 8.5	23.5–100	9	0.85
Total episode (min)	78.20 ± 12.37	64.55–103	7	69.9 ± 16.0	43–130.4	5	0.07

Notes: 'Ovi./search' refers to time allocated to both oviposition and oviposition site searching. 'Per cent ovi.' refers to percentage of time allocated to actual oviposition.

Table 2. Eigenvalues, percentage of variance explained, and eigenvectors of the principal component analysis of habitat requirements of *C. mercuriale*. Eigenvectors higher than 0.35 are indicated in bold.

	PC1	PC2
Eigenvalue	6.49	1.74
Percentage of variance (%)	59.04	15.83
Males	0.28	0.11
Breeding pairs	0.22	0.14
Bank vegetation density (%)	0.33	-0.31
Bank vegetation height (cm)	0.31	-0.39
In-channel vegetation density (%)	0.36	0.13
In-channel vegetation height (cm)	0.35	0.18
Water depth (cm)	-0.19	-0.49
Water width (cm)	0.33	-0.01
Water velocity (m.s)	0.34	0.3
Emergent stones (%)	0.19	0.57
Substrate	0.33	0.1

correlated to copulation duration ($R = 0.59$, $p = 0.02$), but not to body length ($R = -0.01$, $p = 0.96$) or wing length ($R = 0.43$, $p = 0.12$). Oviposition duration (including searching time) had a mean of 52.66 ± 12.17 min but only $51.22 \pm 18.30\%$ of time was devoted to actual oviposition.

In the study population, breeding pairs used only vertical soft supports of three main plant species to lay eggs, namely *Nasturtium officinale*, *Lythrum junceum* and *Typha angustifolia*. Females used the part of the plant that was just above the water surface and often went underwater during oviposition. A total of 14 cases of underwater egg laying (only four of which were timed) were recorded including two cases in which both sexes totally submerged. Mean underwater oviposition duration was 7.7 ± 3.34 min (4–11.5 min, $n = 4$).

Reproductive site preferences

Eigenvalues, eigenvectors and percentage of variance explained by the two first principal components are presented in Table 2. The first two principal components described 74.87% of the cumulative variance with PC1 and PC2 accounting for 59.04% and 15.83%, respectively. PC1 was positively correlated to in-channel vegetation height and density, while PC2 was negatively related to stream width, but positively related to emergent stone density. Figure 1 illustrates a biplot of PCA based on nine environmental factors, male and reproductive pair density, and 12 sampling sections. It shows that single males and reproductive pairs had the same habitat preferences and they occurred mainly in areas where bank and in-channel vegetation height and density

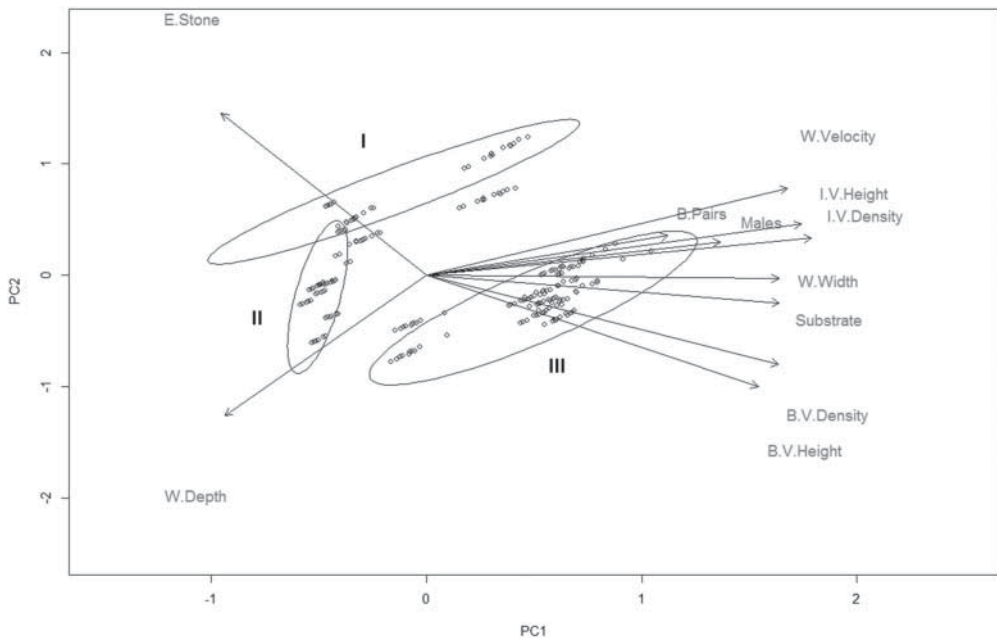


Figure 1. PCA biplot of habitat requirements of *C. mercuriale*. I, II, III refer to gravel-sand, sand-silt, and clay-silt substrates, respectively. Each point represents an observation in a single section. Ellipses were derived using the Bray–Curtis dissimilarity index and they represent 95% confidence areas enveloping each substrate type.

were high, there was a relatively large stream bed, and the substrate consisted of clay-silt. Areas where emergent stones density was high, on the other hand, were the least frequented by adults because they were characterized by low vegetation cover and a gravel-based substrate.

Discussion

The study presents new data on the reproductive behaviour and habitat preferences of the endangered *C. mercuriale* in its southern distribution range. A comparative analysis with British populations, which represent the northern extreme of the species geographic range, is presented and discussed hereafter.

Maturation period was quite short and it was one day shorter in males (three days) than females (four days). Conversely, the maturation period in UK was longer (five to eight days) (Purse, 2001). This variability in the age at maturity could be the result of both genotypic and environmental differences between populations (Stearns & Koella, 1986). Similarly to the Algerian population of *C. mercuriale*, other coenagrionids showed a short pre-reproductive duration, e.g. *Ischnura graellsii* in which the male took 2–5 days while the female took 4–6 days (Cordero, 1987), and *I. verticalis*, in which the male completed its maturation after two days and females after five days (Fincke, 1987). Data on natal dispersal are very scarce in odonates (Buchwald, 1994; Dolný, Mižičová, & Harabiš, 2013) because it is less likely that a ‘fragile’ teneral will survive until maturation after handling and return to its emergence site (Cordero, Egado-Perez, & Andres, 2002). In our study, we reduced the likelihood of handling damage by keeping tenerals in cages until late afternoon before marking them so that their bodies were hard enough to resist handling. The fact that emergence took place mainly at the preferred reproductive sites also contributed to the observation of natal dispersal. In addition, the closest nearby population

is 8 km from the study site which may have reduced the dispersal probability. We found a shorter natal dispersal distance in males than females but the small sample size did not allow us to draw conclusive interpretation on sexual differences in philopatry to emergence sites.

Two main differences in the reproductive behaviour between the Algerian and British populations were found (Table 1). First, post-copulatory resting was significantly shorter in the Algerian population. One of the hypotheses that explain the importance of post-copulatory resting is that females require some time to handle sperm and fertilize their eggs (Miller & Miller, 1989). Therefore, we could assume that the shorter resting duration in the southern limit of the species range was probably due to the higher ambient temperature which accelerated female sperm handling. In fact, it is known in many insects that temperature affects sperm transfer in males (e.g. Katsuki & Miyatake, 2009). Second, oviposition duration was significantly longer in Algeria. Further studies should be carried out to determine whether this inter-population difference in oviposition duration is due to biological (e.g. clutch size) or behavioural (e.g. site selection) variations. Furthermore, we found a positive correlation between copulation duration and male body size. This relationship was already noted in the territorial damselfly *Paraphlebia zoe* (Wong-Munoz, Anderson, Mungua-Steyer, & Cordoba-Aguilar, 2013), and it is possible that a longer copulation leads to higher efficiency in sperm displacement (Waage, 1984) which can reach 100% in some coenagrionids and offer a fitness advantage (see Cordoba-Aguilar, Uhía, & Cordero Rivera, 2003). The positive correlation between resting time and copulation duration was probably due to the copulation energy cost, which induced reproductive pairs that had spent a longer time copulating to rest more before proceeding to the oviposition, as in other insects (Watson, Arnqvist, & Stallmann, 1998; Woods & Stevenson, 1996). According to our knowledge, underwater oviposition has never been reported in *C. mercuriale*, but it was documented in some other coenagrionids (Bick, 1972; Fincke, 1986; Miller, 1994; Sawchyn & Gillott, 1975). Laying eggs under the water surface decreases the risks of exposure and thus increases the hatching success (Fincke, 1986).

There was a concordance between habitat requirements of the adults found in our study and those presented by Rouquette & Thompson (2005). Both single and paired males showed similar habitat preferences, a finding that we expected since all mature single males perched in the bank vegetation near potential oviposition sites waiting for females. Bank and in-channel emergent vegetation and substrate played an important role in individual habitat choice. In fact, the highest densities of both males and breeding pairs were recorded in areas where bank and in-channel emergent vegetation was quite dense and substrate consisted of clay-silt. Bank vegetation provides shelter against predators and perching sites for males to intercept females. As in the present study, some authors have noted the importance of soft stems that are usually provided by in-channel emergent plants for female oviposition (Purse & Thompson, 2009; Rouquette & Thompson, 2005; Sternberg, Buchwald, & Röske, 1999). Vegetation composition of the study site and plants used in oviposition were not similar to the ones found with UK populations (Purse & Thompson, 2003a, 2009; Rouquette & Thompson, 2005). As part of another study on the life history of the species, water dip-netting revealed that larvae were associated exclusively with roots of emergent plants in areas where the substrate mainly consisted of clay-silt (Khelifa R., pers. obs.). These areas should provide suitable microhabitats where food and local abiotic conditions are optimal for larval growth.

Although the Algerian population is located in the opposite latitudinal extreme of the distribution range compared to the British population, there were only some behavioural but no conspicuous ecological (habitat requirements) variations in the adult stage. It is possible that variations occur mainly in the larval stage and especially in life history traits related to the species seasonal regulation. Finally, our data may contribute to better conserving the species locally and to establishing management plans in Algeria and in North Africa generally.

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References

- Allan, J. D. (1995). *Stream ecology: structure and function of running waters*. New York: Chapman & Hall.
- Atkinson, D., & Sibly, R. M. (1997). Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends in Ecology & Evolution*, *12*, 235–239. doi:10.1016/S0169-5347(97)01058-6
- Beals, E. W. (1984). Bray Curtis ordination: an effective strategy for analysis of multivariate ecological data. *Advances in Ecological Research*, *14*, 1–55. doi:10.1016/S0065-2504(08)60168-3
- Bergmann, C. (1847). Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien*, *1*, 595–708.
- Bick, G. H. (1972). A review of territorial and reproductive behavior in Zygoptera. *Contactbrief Nederlandse Libellenonderzoekers*, *10*, 1–15.
- Boudot, J.-P. (2006). *Coenagrion mercuriale*. In: IUCN 2014. IUCN Red List of threatened species. Version 2014.1. Retrieved June 14, 2014 from www.iucnredlist.org
- Bridle, J. R., & Vines, T. H. (2007). Limits to evolution at range margins: when and why does adaptation fail? *Trends in Ecology & Evolution*, *22*, 140–147. doi:10.1016/j.tree.2006.11.002
- Buchwald, R. (1994). Experimentelle Untersuchungen zu Habitatselektion und Biotopbindung bei *Ceriatagrion tenellum* De Villiers, 1789 (Coenagrionidae, Odonata). *Zoologische Jahrbücher Abteilung für Systematik, Ökologie und Geographie der Tiere*, *121*, 71–98.
- Conover, D. O. (1992). Seasonality and the scheduling of life history at different latitudes. *Journal of Fish Biology*, *41*, 161–178. doi:10.1111/j.1095-8649.1992.tb03876.x
- Corbet, P. S., Suhling, F., & Soendgerath, D. (2006). Voltinism of Odonata: a review. *International Journal of Odonatology*, *9*, 1–44. doi:10.1080/13887890.2006.9748261
- Cordero, A. (1987). Estructura de población en *Ischnura graellsii* Rambur, 1842 (Zygop. Coenagrionidae). *Boletín Asociación española de Entomología*, *11*, 269–286.
- Cordero-Rivera, A., Egidio-Perez, F. J., & Andres, J. A. (2002). The effect of handling damage, mobility, body size, and fluctuating asymmetry on lifetime mating success of *Ischnura graellsii* (Rambur) (Zygoptera: Coenagrionidae). *Odonatologica*, *31*, 117–128.
- Cordoba-Aguilar, A., Uhiá, E., & Cordero Rivera, A. (2003). Sperm competition in Odonata (Insecta): the evolution of female sperm storage and rivals' sperm displacement. *Journal of Zoology*, *261*, 381–398. doi:10.1017/S0952836903004357
- Dolný, A., Mižičová, H., & Harabiš, F. (2013). Natal philopatry in four European species of dragonflies (Odonata: Symptetrinae) and possible implications for conservation management. *Journal of Insect Conservation*, *17*, 821–829. doi:10.1007/s10841-013-9564-x
- Fincke, O. M. (1986). Underwater oviposition in a damselfly (Odonata: Coenagrionidae) favors male vigilance, and multiple mating by females. *Behavioural Ecology and Sociobiology*, *18*, 405–412. doi:10.1007/BF00300514
- Fincke, O. M. (1987). Female monogamy in the damselfly *Ischnura verticalis* Say (Zygoptera: Coenagrionidae). *Odonatologica*, *16*, 129–143.
- Grand, D. (1996). *Coenagrion mercuriale* (Charpentier, 1840). In: P. J. van Helsdingen, L. Willems & M. C. D. Speight (Eds.), *Background information on invertebrates of the Habitats Directive and the Bern Convention. Part II – Mantodea, Odonata, Orthoptera and Arachnida* (pp. 245–253). Strasbourg: Council of Europe Publishing.
- Hassall, C., Keat, S., Thompson, D. J., & Watts, P. C. (2014). Bergman's rule is maintained during range expansion in a damselfly. *Global Change Biology*, *20*, 475–482. doi:10.1111/gcb.12340
- Hassall, C., Thompson, D. J., & Harvey, I. F. (2009). Variation in morphology between core and marginal populations of three British damselflies. *Aquatic Insects*, *31*, 187–197. doi:10.1080/01650420902776708
- Katsuki, M., & Miyatake, T. (2009). Effects of temperature on mating duration, sperm transfer and remating frequency in *Callosobruchus chinensis*. *Journal of Insect Physiology*, *55*, 112–115. doi:10.1016/j.jinsphys.2008.10.012
- Kerry, L. (2001). Habitat management for the southern damselfly *Coenagrion mercuriale* (Charpentier) on Aylesbeare Common, Devon. *Journal of the British Dragonfly Society*, *17*, 45–48.
- Khelifa, R., Youcefi, A., Kahlerras, A., Alfarhan, A., Al-Rasheid, K. A. S., & Samraoui, B. (2011). L'odonatofaune (Insecta : Odonata) du bassin de la Seybouse en Algérie : intérêt pour la biodiversité du Maghreb. *Revue d'écologie (Terre et Vie)*, *66*, 55–66.
- Miller, P. L. (1994). Submerged oviposition and responses to oxygen lack in *Enallagma cyathigerum* (Charpentier) (Zygoptera: Coenagrionidae). *Advances in Odonatology*, *6*, 79–88.
- Miller, P. L., & Miller, A. K. (1989). Post-copulatory 'resting' in *Orthetrum coerulescens* (Fabricius) and some other Libellulidae: time for 'sperm handling'? (Anisoptera). *Odonatologica*, *18*, 33–41.
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Henry, M., Stevens, H., & Wagner, H. (2013). Vegan Community Ecology Package. R package version 2.0-10. Retrieved from <http://CRAN.R-project.org/package=vegan>
- Purse, B. V. (2001). *The ecology and conservation of the southern damselfly (Coenagrion mercuriale)* (PhD thesis). University of Liverpool, Liverpool, UK.

- Purse, B. V., & Thompson, D. J. (2002). Voltinism and larval growth pattern in *Coenagrion mercuriale* (Odonata: Coenagrionidae) at its northern range margin. *European Journal of Entomology*, 99, 11–18. doi:10.14411/eje.2002.004
- Purse, B. V., & Thompson, D. J. (2003a). Reproductive morphology and behaviour in *Coenagrion mercuriale* (Charpentier) (Zygoptera: Coenagrionidae). *Odonatologica*, 32, 29–37.
- Purse, B. V., & Thompson, D. J. (2003b). Emergence of the damselflies, *Coenagrion mercuriale* and *Ceriagrion tenellum* (Odonata: Coenagrionidae) at their northern range margins, in Britain. *European Journal of Entomology*, 100, 93–99. doi:10.14411/eje.2003.018
- Purse, B. V., & Thompson, D. J. (2005). Lifetime mating success in a marginal population of a damselfly, *Coenagrion mercuriale*. *Animal Behaviour*, 69, 1303–1315. doi:10.1016/j.anbehav.2004.10.009
- Purse, B. V., & Thompson, D. J. (2009). Oviposition site selection by *Coenagrion mercuriale* (Odonata: Coenagrionidae). *International Journal of Odonatology*, 12, 257–273. doi:10.1080/13887890.2009.9748344
- R Project. The R Project for Statistical Computing (Version 3.0.1). Retrieved from <http://www.r-project.org/>
- Rouquette, J. R., & Thompson, D. J. (2005). Habitat associations of the endangered damselfly, *Coenagrion mercuriale*, in a water meadow ditch system in southern England. *Biological Conservation*, 123, 225–235. doi:10.1016/j.biocon.2004.11.011
- Rouquette, J. R., & Thompson, D. J. (2007). Patterns of movement and dispersal in an endangered damselfly with implications for its management. *Journal of Applied Ecology*, 44, 692–701. doi:10.1111/j.1365-2664.2007.01284.x
- Samraoui, B., Boudot, J. P., Ferreira, S., Riservato, E., Jović, M., Kalkman, V. J., & Schneider, W. (2010). The status and distribution of dragonflies. In N. Garcia, A. Cuttelod, & D. Abdul Malak (Eds.), *The status and distribution of freshwater biodiversity in Northern Africa* (pp. 51–70). Gland, Switzerland: IUCN.
- Sawchyn, W. W., & Gillott, C. (1975). The biology of two related species of coenagrionid dragonflies (Odonata: Zygoptera) in western Canada. *Canadian Entomologist*, 107, 119–128. doi:10.4039/Ent107119-2
- Scheiner, S. M. (2002). Selection experiments and the study of phenotypic plasticity. *Journal of Evolutionary Biology*, 15, 889–898. doi:10.1046/j.1420-9101.2002.00468.x
- Smith-Gill, S. J. (1983). Developmental plasticity: developmental conversion versus phenotypic modulation. *American Zoologist*, 23, 47–55. doi:10.1093/icb/23.1.47
- Śniegula, S., Nilsson-Örtman, V., & Johansson, F. (2012). Growth pattern responses to photoperiod across latitudes in a northern damselfly. *PLoS One*, 7(9), e46024. doi:10.1371/journal.pone.0046024
- Stearns, S. C. (1992). *The evolution of life histories*. Oxford: Oxford University Press.
- Stearns, S. C., & Koella, J. C. (1986). The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. *Evolution*, 40, 893–913.
- Sternberg, K., Buchwald, R., & Röske, W. (1999). *Coenagrion mercuriale*. In K. Sternberg, R. Buchwald (Eds.), *Die Libellen Baden-Württemberg* (pp. 255–270). Stuttgart: Eugen Ulmer Press.
- Stoks, R., Swillen, I., & De Block, M. (2012). Behaviour and physiology shape the growth accelerations associated with predation risk, high temperatures and southern latitudes in *Ischnura* damselfly larvae. *Journal of Animal Ecology*, 81, 1034–1040. doi:10.1111/j.1365-2656.2012.01987.x
- Tanaka, S. (2004). Environmental control of body-color polyphenism in the American grasshopper, *Schistocerca americana*. *Annals of the Entomological Society of America*, 97, 293–301. doi:10.1603/0013-8746(2004)097[0293:ECOBPI]2.0.CO;2
- Thompson, D. B. (1992). Consumption rates and the evolution of diet-induced plasticity in the head morphology of *Melanoplus femurrubrum* (Orthoptera: Acrididae). *Oecologia*, 89, 204–213. doi:10.1007/BF00317219
- Van Buskirk, J. (2002). A comparative test of the adaptive plasticity hypothesis: relationships between habitat and phenotype in anuran larvae. *The American Naturalist*, 160, 87–102. doi:10.1086/340599
- Van Buskirk, J., & Arioli, M. (2005). Habitat specialization and adaptive phenotypic divergence of anuran populations. *Journal of Evolutionary Biology*, 18, 596–608. doi:10.1111/j.1420-9101.2004.00869.x
- Waage, J. K. (1984). Sperm competition and the evolution of odonate mating systems. In R.L. Smith (Ed.), *Sperm competition and the evolution of animal mating systems* (pp. 251–290). Orlando: Academic Press.
- Watson, P. J., Arnqvist, G., & Stallmann, R. R. (1998). Sexual conflict and the energetic costs of mating and mate choice in water striders. *The American Naturalist*, 151, 46–58. doi:10.1086/286101
- Watts, P. C., Kemp, S. J., Saccheri, I. J., & Thompson, D. J. (2005). Conservation implications of genetic variation between spatially and temporally distinct colonies of the endangered damselfly *Coenagrion mercuriale*. *Ecological Entomology*, 30, 541–547. doi:10.1111/j.0307-6946.2005.00721.x
- Wong-Munoz, J., Anderson, C. N., Munguia-Steyer, R., & Cordoba-Aguilar, A. (2013). Body size and morph as drivers of copulation duration in a male dimorphic damselfly. *Ethology*, 119, 407–416. doi:10.1111/eth.12077
- Woods, W. A., & Stevenson, R. D. (1996). Time and energy costs of copulation for the Sphinx Moth, *Manduca sexta*. *Physiological Zoology*, 69, 682–700.