



Female color polymorphism of *Ischnura capreolus* Hagen, 1861 (Odonata: Coenagrionidae) with notes on behavior and ontogenetic color changes

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Polymorphism in coenagrionids is widely known, mainly for *Ischnura*. Here, we present the case of *I. capreolus*, a Neotropical species of which, until now, little information concerning color polymorphism and ontogenetic color changes was known. We used a marking and recapture method to evidence ontogenetic coloration changes in females. We show that, in addition to the gynochrome morph, *I. capreolus* females also exhibit at least one additional morph: an androchrome color pattern. Gynochrome females (97.1% of marked females) are green-yellow when young and change to a brownish pattern with age, within a week. Androchrome females (2.9% of marked females) exhibit blue coloration, similarly to males. Our study provides the first evidence of ontogenetic color change in *I. capreolus*. Furthermore, field observations show that *I. capreolus* is similar to other *Ischnura* species regarding sexual harassment behavior.

Keywords: damselfly; Zygoptera; color change; morph; mark-recapture; dragonfly

Introduction

Color polymorphism can be defined as the occurrence of more than one color morph within a population at higher frequencies than expected by mutations alone (Ford, 1957; Huxley, 1955). The role that color polymorphism plays on animal communication, reproductive success and strategies to avoid predators (Bond, 2007; Huang, Chiou, Marshall, & Reinhard, 2014) comprises a wide range of studies that covers many taxa, from insects (e.g. damselflies, Cordero, 1990; Fincke, 1994) and crabs (Palma & Steneck, 2001), to mice (Hoekstra, Drumm, & Nachman, 2004) and red squirrels (Voipio & Hissa, 1970).

In Odonata, female polymorphism and ontogenetic color changes are also widely studied, mainly in Coenagrionidae (Cordero, 1990, 1992; Fincke, Jödicke, Paulson, & Schultz, 2005; Johnson, 1964, 1966; Robertson, 1985; Sánchez-Guillén, van Gossom, & Cordero-Rivera, 2005; Sanmartín-Villar & Cordero-Rivera, 2016; Sanmartín-Villar, Zhang, & Cordero-Rivera, 2016). In several coenagrionids, for instance in *Ischnura*, one female morph resembles male coloration

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pattern, while gynochrome morphs exhibit cryptic colors (Calvert, 1902; Fincke et al., 2005 for a review). Among the ischnurines, gynochrome females can be found in populations presenting from only one gynochrome morph, as in *I. fluviatilis* (McKee, Harvey, Thompson, & Sherratt, 2005), *I. ramburii* (Gering, 2017; Robertson, 1985) and *I. senegalensis* (Takahashi & Watanabe, 2011; Takahashi, Yoshimura, Morita, & Watanabe, 2011) to several morph types, as in *I. genei* (Sanmartín-Villar & Cordero-Rivera, 2016) and *I. elegans* (Cordero-Rivera, Santolamazza-Carbone, & Utzeri, 1998; Le Rouzic, Hansen, Gosden, & Svensson, 2015; Svensson, Abbott, & Härdling, 2005; Takahashi, Kagawa, Svensson, & Kawata, 2014).

In Brazil, three *Ischnura* species are known to occur: *I. capreolus*, *I. fluviatilis* and *I. ramburii*. Restricted to South America (Heckman, 2008; Lencioni, 2006), *I. fluviatilis* has an androchrome and a gynochrome female morph (McKee et al., 2005). In this species, young females are orange and change to brown as they age, while andromorphs are bright blue, similar to males (McKee et al., 2005). Studies with *I. fluviatilis* are often related to its taxonomy (Fonseca & Pujol-Luz, 1999; Muzón, Pessacq, & Lozano, 2014; von Ellenrieder & Muzón, 2003) or distribution (Muzón, 1997; Muzón, Lozano, Del Palacio, Ramos, & Lutz, 2015; von Ellenrieder, 2000). Thus, with the exception of McKee et al. (2005), no further data on ontogenetic color changes are available in the literature. Perhaps the species studied in most detail of the three is *I. ramburii*, which occurs from North to South America (Heckman, 2008) and, similarly to *I. fluviatilis*, has an androchrome and a gynochrome female morph (Robertson, 1985). Like *I. fluviatilis*, young gynochrome *I. ramburii* females are orange, and become brown/green within a few days, darkening as females age (Robertson, 1985).

Ischnura capreolus is known to be polymorphic (Fincke et al., 2005) and androchrome females have been observed in populations from Central to South America (Dennis Paulson, personal communication). However, unlike the other New World ischnurine species, there is no information on possible female ontogenetic color changes in *I. capreolus*, despite Calvert's (1902) report of color variation in females (e.g. citron, orange and black), considering each ontogenetic stage as a different morph. Therefore, here we performed a mark-recapture study to unravel the possible coloration changes of this insufficiently studied species, of which little information regarding its biology is found in the literature, except for studies on species distribution and ecology (Loznik, 2012; Machado, 2012; Renner, Périco, & Sahlén, 2013; Renner, Sahlén, & Périco, 2016; Vilela, Guillermo-Ferreira, & Del-Claro, 2016; von Ellenrieder & Muzón, 2008).

Materials and methods

Study area and species

The study was carried out over 11 days between September and October 2016 in a small temporary pond in São Carlos (São Paulo state, Brazil; altitude 856 m, 21°59'S 47°54'W; Figure 1). The pond is surrounded by grassy vegetation in most of its margins. *Ischnura capreolus* is commonly found inhabiting lentic sites, such as the pond of our study site, occurring throughout the year (Renner et al., 2013; Vilela et al., 2016).

Marking and recapture

Every two days, females were collected and marked with an individual number on the right forewing using an indelible black pen. After marking, females were released. At the moment of capturing, we noted the following traits for each female: (i) body coloration; (ii) coloration of post-ocular spots; and (iii) color of the abdominal segments S9–S10. To follow up any possible color changes, we checked all these traits for every recaptured female.



Figure 1. Study area: a shallow pond inhabited by a large population of *I. capreolus*.

We checked for coloration of post-ocular spots because we noticed different post-ocular colorations on gynochrome (white spots) and androchrome (blue spots) females in previous observations. The coloration of S9–S10 was noted because female abdominal coloration may have a role on intersexual communication (Gorb, 1999; Hammers, Sánchez-Guillén, & van Gossum, 2009; van Gossum, Stoks, & De Bruyn, 2001). Coloration was classified as follows: thorax mostly green, yellow, brown or blue; post-ocular spots white or blue; S9–S10 coloration blue, white or absent (showing only dark abdominal coloration).

Data analyses

To estimate population size and probability of survival, the Jolly–Seber method was applied since it considers open populations (Jolly, 1965), similarly to the population of this study. We performed the Jolly–Seber analysis using an Excel[®] spreadsheet provided by the University of Missouri (see, <https://goo.gl/pSNf5F>). Results are represented as mean \pm SD.

To represent the ecological structure of the population, we built a diagram with the frequency of each ontogenetic color stage within our sampling period using Excel[®]. To verify if the number of young gynochrome females declined during the study period, we ran a simple linear regression with the number of marked females as dependent variable and the sampling days as the predictor variable. The simple linear regression test was made using the software Statistica 10.1 (StatSoft South America, statsoft.com.br).

Results

Marked and recaptured females

During the 11 marking sessions, we marked 316 *I. capreolus* females, and obtained 34 recaptures (11.1% of the marked females). Of all marked females, 69.3% ($n = 219$) showed green body coloration and blue S9–S10 coloration at the moment of marking. We also marked 31 (9.81%) yellow and 57 (18%) brown females. Gynochrome females represented 97.1% ($n = 307$) of the marked females on our study, whereas only 2.9% ($n = 9$) were androchromes.

The plot with the frequency of each color stage across time showed the ecological structure of the population within our sampling period (Figure 2a). According to our results, the number of young females decreased with time (simple linear regression, $\beta = -0.63$, $r^2 = 0.332$, $t = -2.44$, $p = 0.037$, Figure 2b), while the number of old females remained constant.

Ontogenetic color change

Our results indicate an ontogenetic coloration change in females and the existence of at least two morphs: gynochrome and androchrome. In the first days after emergence, *I. capreolus* females

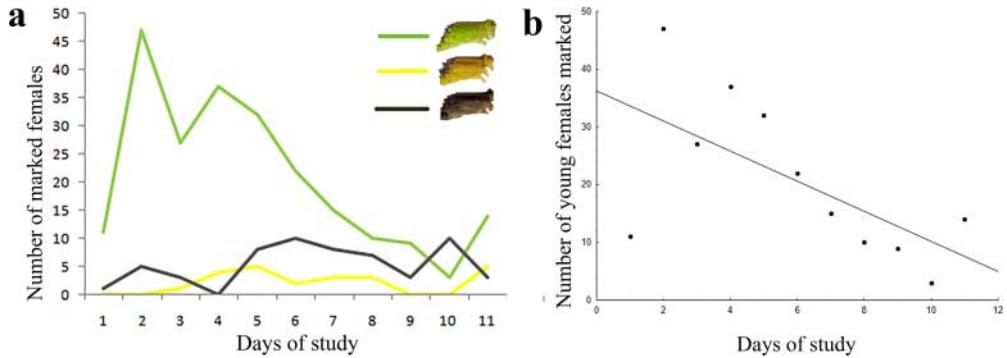


Figure 2. The frequency of female ontogenetic stages along the study period (a). The number of marked green young females decreased with time during the study (b).

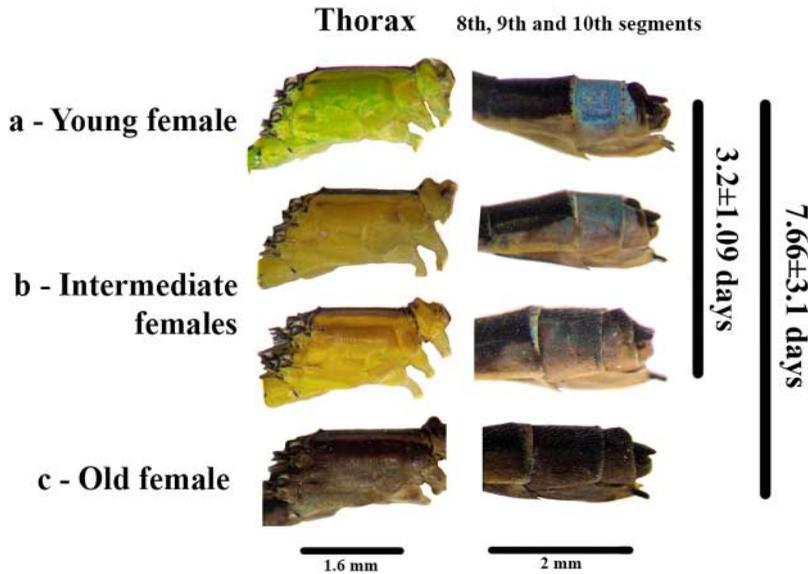


Figure 3. Ontogenetic color changes of gynochrome *I. capreolus* females. Young females exhibit green body coloration (a, left column) and conspicuous dorsolateral blue spots on S9 and most of S10 (a, right column). Females of Intermediate age exhibit a yellowish coloration (b, left column), and the blue dorsolateral spots start to vanish (b, right column). Old females are brown with dark lateral thoracic stripes (c, left column) and no dorsolateral spots on S9–S10 (c, right column).

exhibit a light-green coloration and a blue spot in most of S9–S10 segments, which fades out as the female reaches a certain age (Figure 3).

Of the 34 recaptured females, we found that 16 were marked and recaptured with no color changes, remaining with the same color pattern as at the moment of marking. The mean time of recapture of the females with no color changes was 2.61 ± 0.9 days. Five females which were green at the time of marking were recaptured with yellow body coloration, white S9–S10 coloration and white post ocular spots 3.20 ± 1.09 days after marking.

We recaptured 12 females that presented a remarkable coloration change. These females had green body coloration, white post-ocular spots and a blue abdominal spot at the moment of marking. After 7.66 ± 3.1 days from marking, the females presented brown body coloration, a darkening of the antehumeral stripes on the pterothorax, white post-ocular spots and no blue abdominal spot on S9–S10. Only one female was marked with yellow coloration and recaptured with brown coloration, eight days after marking.

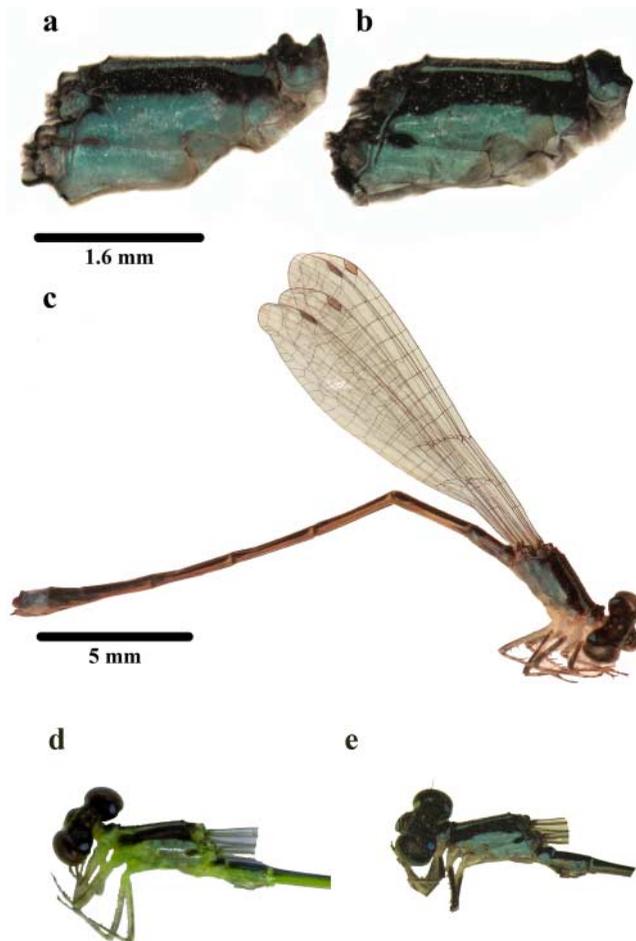


Figure 4. Androchrome female (a and c) and male (b, d and e) of *I. capreolus*. Males have a green coloration when teneral (d), differing from the blue coloration of the mature male (e). Scale bar is the same for (c), (d) and (e).

There were no color changes on post-ocular spots of gynochrome females, which remained white in spite of thoracic color changes. With the information on the sequential coloration changes, here we treated green females as “young females”, yellow females as “intermediate females” and brown females as “old females” (Figure 3).

We marked nine androchrome females that remarkably resemble male coloration. Androchrome females have a narrower antehumeral stripe, compared to males, and blue post-ocular spots (Figure 4a, c). Although we did not recapture any androchrome female, we noticed a slightly coloration change based on observation of a photograph of a mating androchrome (Figure 5a). The mating androchrome female has a light-green thoracic coloration and blue post-ocular spots (only observed in males and androchrome females). Although males were not marked in our study, we observed some teneral (Figure 4d) individuals which had green coloration (Figure 4b, d, e). Additionally, there are records of another female type (Figure 5d) that resembled that of the androchrome; however, the post-ocular spots are not blue (Dennis Paulson, personal communication). We did not mark or capture any female similar to that one, although it resembles an old gynochrome female before it gets brown (Dennis Paulson, personal communication).

Mating pairs

We observed 33 mating pairs. We emphasize that we did not follow the copulations from the beginning, and we only took notes on traits of mating females. Of the mating pairs, only one had an androchrome female (Figure 4a) and 32 were gynochrome females (Figure 4b, c). Of the gynochrome mating females, 19 had a yellowish coloration, similar to those we classified as intermediate females (Figure 4b), whereas 13 females had a brown coloration (Figure 4c), similar to those classified as old females. Therefore, males mated with both older gynochrome stages (yellow 59.38%, brown 40.61%) even though the population frequency of brown females was double that of the yellow ones.

Behavioral notes

During our marking procedures, we noted some behavioral aspects of *I. capreolus* females. Young (green) and intermediate (yellow) females were found mainly on the sunny areas of the pond, patrolling and hunting at the marginal vegetation, where males were also observed. The observations showed that the reproductive behavior of *I. capreolus* might be similar to other *Ischnura* (Cordero, 1989, 1990), with males rushing at and grasping females, and females ovipositing alone. Additionally, androchrome and old reproductive females (brown) were found mostly on the shaded areas of the pond, perched on the dirt road vegetation.

Population estimators

The Jolly–Seber analyses estimated that the studied female population of *I. capreolus* comprised 1117 ± 116 individuals. The probability of female survival between the days of marking was 39.4%.

Discussion

Our results indicate that *I. capreolus* exhibit female limited polymorphism with at least two different female morphs: gynochrome and androchrome. Gynochrome young females are green and go through an ontogenetic color change. Gynochrome intermediate females are yellow and become brown within a few days. Androchrome females are almost identical to males, and we did not notice any coloration change, since no androchrome female was recaptured. However, despite no androchrome recaptures, we noticed a slightly coloration change based on observation of a photograph of a mating androchrome (Figure 5a) which resembles the ontogenetic changes of European ischnurines (Hammers et al., 2016). The mating androchrome female has a light-green thoracic coloration and blue post-ocular spots (only observed in males and androchrome females). We found that, as gynochrome females aged, they changed body coloration, so that old females do not resemble the young females in terms of body coloration. Indeed, there are many cases where this body color change occurs in the genus *Ischnura* (Cordero-Rivera & Andrés, 1996; Hammers et al., 2009; Sanmartín-Villar et al., 2016).

We also noticed some behavioral aspects of *I. capreolus* females: (i) young and intermediate females were found mainly on the sunny areas of the pond, patrolling and hunting at the marginal vegetation, where males were also observed; (ii) in addition, we found more yellow mating females in comparison to brown females, even though we marked twice as much brown females than yellow females. These results may suggest that: (i) intermediate females have a higher probability of being virgins and coloration may signal age and reproductive status to



Figure 5. Mating females observed during the study. An androchrome female (a), an intermediate gynochrome female (b) and an old gynochrome female (c). A female with green coloration, resembling the androchrome morph, however with pale post-ocular spots (d, courtesy of Dennis Paulson).

males (Takahashi & Watanabi, 2011), which may prefer virgin females (e.g. Andrés & Cordero-Rivera 2000); and (ii) there is a high chance that older brown females have already mated, and may avoid multiple matings (Fincke, 2015). A possible alternative explanation for this difference relies on the background coloration. As color polymorphism may be an evolutionary response to male harassment (Fincke, 1997; Fincke et al., 2005), females may evolve some strategies to avoid males when not ready to mate (Fincke et al., 2005). In *I. capreolus*, besides the blue spot on S9–S10, green young females are more cryptic in the pond vegetation, mainly composed of grass sticks, whereas brown females may be more cryptic in the shaded areas of the pond, where we found them. Thus, males may benefit from female yellow color pattern that contrasts with the green background, facilitating mate recognition and detection (e.g. Huang et al., 2014; Schultz & Fincke, 2013).

A diverse array of visual abilities exists within and across Odonata species, the group with the largest eyes among insects (Bybee, Johnson, & Gering, 2012). Odonates rely on their vision for their basic needs, such as feeding and reproduction. Since dragonflies and damselflies exhibit a wide arsenal of opsins that allow a wide range and plasticity of visible spectra (Bybee et al., 2012; Huang et al., 2014), color patterns can be visually recognized and, thus, play significant roles in inter and intraspecific communication, sexual selection and mate recognition (Gorb, 1998; Guillermo-Ferreira, Bispo, Appel, Kovalev, & Gorb, 2015; Harris, Forman, Battell, 2011; Huang et al., 2014).

In other words, photoreceptors and color perception are species-specific, creating an intraspecific private communication channel that allows selection of signaller coloration and receiver sensorial bias to promote mate recognition and attraction (Bybee et al., 2012; Huang et al., 2014). For polymorphic species, these physiological traits are particularly under selective pressures as they play a role in male mate recognition/choice and female reproductive success (Huang et al., 2014). Considering the sensorial traits involved in intra and interspecific recognition, one might suggest that variations in male perception and female coloration may explain how female polymorphisms occur and are maintained (e.g. Schultz, Anderson, & Symes, 2008). For instance, in the case of ontogenetic coloration changes, as shown here for *I. capreolus* females, color patterns can be interpreted as a signal of sexual maturity, as shown for other ischnurines (Huang & Reinhard, 2012). Thus, we suggest that ontogenetic color changes in polymorphic species may act as visual cues used by males to recognize (or learn to recognize) female sexual maturity and willingness to mate (Takahashi & Watanabi, 2011; van Gossum et al., 2011).

In relation to the population results, the estimator test suggests a large number of *I. capreolus* females. Our marking-recapture procedures showed that the frequency of the color stages varied

throughout the days of sampling. As we advanced in the sampling days, the number of green young females decreased, while the number of marked mature females remained constant. This result may indicate that, as we found a high number of young females in the first days of the study, our studied population may be at the beginning of the flight period, where a larger number of young individuals are expected to be found (Corbet, 1999).

In conclusion, our study provides new information on female polymorphism in *Ischnura*, a Coenagrionidae genus where the female polymorphism and inheritance system is well studied (Cordero, 1989, 1990, 1991, 1992; Cordero-Rivera & Andrés, 1996; Sanmartín-Villar & Cordero-Rivera, 2016; Sanmartín-Villar et al., 2016). Compared with other American species (e.g. *I. fluviatilis* and *I. ramburii*), *I. capreolus* is similar in having a simple color polymorphism with only one gynochrome morph, but it presents a unique young coloration. Further studies should focus on a complete investigation of the roles of coloration changes on male choices (e.g. blue abdominal spots and thoracic coloration), which will contribute to a better understanding regarding visual communication and reproductive success of ischnurine damselflies.

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References

- Andrés, J. A., & Cordero-Rivera, A. (2000). Copulation duration and fertilization success in a damselfly: an example of cryptic female choice? *Animal Behaviour*, *59*, 695–703.
- Bond, A. B. (2007). The evolution of color polymorphism: crypticity, searching images, and apostatic selection. *Annual Review of Ecology and Systematics*, *38*, 489–514.
- Bybee, S. M., Johnson, K. K., & Gering, E. J. (2012). All the better to see you with: A review of odonate color vision with transcriptomic insight into the odonate eye. *Organisms Diversity & Evolution*, *12*, 241–250. doi:10.1007/s13127-012-0090-6
- Calvert, P. P. (1902). Odonata. In: Godman, F. D., & Salvin, O. (Eds.), *Biologia Centrali Americana – Insecta Neuroptera*. R.H. Porter and Dulau, London.
- Corbet, P. S. (1999). *Dragonflies: Behaviour and ecology of Odonata*. Cornell University Press, Ithaca, New York.
- Cordero, A. (1989). Reproductive behaviour of *Ischnura graellsii* (Rambur) (Zygoptera: Coenagrionidae). *Odonatologica*, *18*, 237–244.
- Cordero, A. (1990). The adaptive significance of the prolonged copulations of the damselfly, *Ischnura graellsii* (Odonata: Coenagrionidae). *Animal Behaviour*, *40*, 43–48.
- Cordero, A. (1991). Fecundity of *Ischnura graellsii* (Rambur) in the laboratory (Zygoptera: Coenagrionidae). *Odonatologica*, *20*, 37–44.
- Cordero, A. (1992). Density-dependent mating success and colour polymorphism in females of the damselfly *Ischnura graellsii* (Odonata: Coenagrionidae). *Journal of Animal Ecology*, 769–780.
- Cordero-Rivera, A., & Andrés, J. A. (1996). Colour polymorphism in odonates: females that mimic males? *Journal of the British Dragonfly Society*, *12*, 50–60.
- Cordero-Rivera, A., Santolamazza-Carbone, S., & Utzeri, C. (1998). Mating opportunities and mating costs are reduced in androchrome female damselflies, *Ischnura elegans* (Odonata). *Animal Behaviour*, *55*, 185–197.
- Fincke, O. M. (1994). Female colour polymorphism in damselflies: failure to reject the null hypothesis. *Animal Behaviour*, *47*, 1249–1266.
- Fincke, O. M. (1997). Conflict resolution in the Odonata: implications for understanding female mating patterns and female choice. *Biological Journal of the Linnean Society*, *60*, 201–220.
- Fincke, O. M. (2015). Trade-offs in female signal apparency to males offer alternative anti-harassment strategies for colour polymorphic females. *Journal of evolutionary biology*, *28*, 931–943.

- Fincke, O. M., Jödicke, R., Paulson, D. R., & Schultz, T. D. (2005). The evolution and frequency of female color morphs in Holarctic Odonata: why are male-like females typically the minority? *International Journal of Odonatology*, *8*, 183–212.
- Fonseca, R., & Pujol-Luz, J. R. (1999). Notas sobre a larva de *Ischnura fluviatilis* Selys, 1876 (Odonata, Coenagrionidae). *Contribuições Avulsas sobre a História Natural do Brasil, Série Zoologia*, *1*, 1–4.
- Ford, E. B. (1957). Polymorphism in plants, animals and man. *Nature*, *180*, 1315–1319. doi:10.1038/1801315a0
- Gering, E. J. (2017). Male-mimicking females increase male–male interactions, and decrease male survival and condition in a female-polymorphic damselfly. *Evolution*, *71*, 1390–1396.
- Gorb, S. N. (1998). Visual cues in mate recognition by males of the damselfly, *Coenagrion puella* (Odonata: Coenagrionidae). *Journal of Insect Behavior*, *11*, 73–92.
- Gorb, S. N. (1999). Visual cues in mate recognition in the damselfly *Ischnura elegans* Vander Linden (Zygoptera: Coenagrionidae). *International Journal of Odonatology*, *2*, 83–93.
- Guillermo-Ferreira, R., Bispo, P. C., Appel, E., Kovalev, A., & Gorb, S. N. (2015). Mechanism of the wing colouration in the dragonfly *Zenithoptera lanei* (Odonata: Libellulidae) and its role in intraspecific communication. *Journal of Insect Physiology*, *81*, 129–136.
- Hammers, M., Sánchez-Guillén, R. A., & van Gossum, H. (2009). Differences in mating propensity between immature female color morphs in the damselfly *Ischnura elegans* (Insecta: Odonata). *Journal of Insect Behavior*, *22*, 324–337.
- Harris, W. E., Forman, D. W., Battell, R. D. (2011). Odonata colour: more than meets the eye? *International Journal of Odonatology*, *14*, 281–289.
- Heckman, C. W. (2008). *Encyclopedia of South American aquatic insects: Odonata-Zygoptera: Illustrated keys to known families, genera, and species in South America*. Olympia Washington, USA: Springer Science & Business Media.
- Hoekstra, H. E., Drumm, K. E., & Nachman, M. W. (2004). Ecological genetics of adaptive color polymorphism in pocket mice: geographic variation in selected and neutral genes. *Evolution*, *58*, 1329–1341.
- Huang, S. C., Chiou, T. H., Marshall, J., & Reinhard, J. (2014). Spectral sensitivities and color signals in a polymorphic damselfly. *PLoS One*, *9*, e87972.
- Huang, S. C., & Reinhard, J. (2012). Color change from male-mimic to gynomorphic: a new aspect of signaling sexual status in damselflies (Odonata, Zygoptera). *Behavioral Ecology*, *23*, 1269–1275.
- Huxley, J. (1955). Morphism and evolution. *Heredity*, *9*, 1–52. doi:10.1038/hdy.1955.1
- Johnson, C. (1964). The inheritance of female dimorphism in the damselfly, *Ischnura damula*. *Genetics*, *49*, 513–519.
- Johnson, C. (1966). Genetics of female dimorphism in *Ischnura demorsa*. *Heredity*, *21*, 453–459. doi:10.1038/hdy.1966.44
- Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika*, *52*, 225–248.
- Lencioni, F. A. A. (2006). *Damselflies of Brazil: An illustrated identification guide*. São Paulo, All Print Editora.
- Le Rouzic, A., Hansen, T. F., Gosden, T. P., & Svensson, E. I. (2015). Evolutionary time-series analysis reveals the signature of frequency-dependent selection on a female mating polymorphism. *The American Naturalist*, *185*, E182–E196.
- Loznik, B. (2012). Odonata of the Osa Peninsula: A species Checklist. *Frontier Costa Rica*. Retrieved from <https://go.gl/92sh3l>
- Machado, A. B. M. (2012). A new species of *Ischnura* (Odonata: Coenagrionidae) from high altitude eastern Andes, of Colombia. *Zoologia*, *29*, 598–600.
- McKee, D., Harvey, I. F., Thompson, D. J., & Sherratt, T. N. (2005). Frequency of female colour morphs in populations of four coenagrionid damselfies (Zygoptera: Coenagrionidae). *Odonatologica*, *34*, 37–49.
- Muzón, J. (1997). Odonata (Insecta) from Patagonia: species richness and distributional patterns. *Biogeographica*, *73*, 123–134.
- Muzón, J., Lozano, F., Del Palacio, A., Ramos, L. S., & Lutz, A. (2015). Odonata from the Lower Delta of the Paraná River, Argentina. *Agrion*, *20*, 68–72.
- Muzón, J., Pessacq, P., & Lozano, F. (2014). The Odonata (Insecta) of Patagonia: A synopsis of their current status with illustrated keys for their identification. *Zootaxa*, *3784*, 346–388.
- Palma, A. T., & Steneck, R. S. (2001). Does variable coloration in juvenile marine crabs reduce risk of visual predation? *Ecology*, *82*, 2961–2967.
- Renner, S., Périco, E., & Sahlén, G. (2013). Libélulas (Odonata) em subtropicais fragmentos de Mata Atlântica no Rio Grande do Sul, Brasil: diversidade sazonal e composição. *Scientia Plena*, *9*, 1–8.
- Robertson, H. M. (1985). Female dimorphism and mating behaviour in a damselfly, *Ischnura ramburi*: females mimicking males. *Animal Behaviour*, *33*, 805–809.
- Sánchez-Guillén, R. A., van Gossum, H., & Cordero-Rivera, A. (2005). Hybridization and the inheritance of female colour polymorphism in two ischnurid damselfies (Odonata: Coenagrionidae). *Biological Journal of the Linnean Society*, *85*, 471–481.
- Sanmartín-Villar, I., & Cordero-Rivera, A. (2016). The inheritance of female colour polymorphism in *Ischnura genei* (Zygoptera: Coenagrionidae), with observations on melanism under laboratory conditions. *PeerJ*, *4*, p. e2380.
- Sanmartín-Villar, I., Zhang, H. M., & Cordero-Rivera, A. (2016). Colour polymorphism and ontogenetic colour changes in *Ischnura rufostigma* (Odonata: Coenagrionidae). *Odonatologica*, *45*, 77–86.
- Schultz, T. D., Anderson, C. N., & Symes, L. B. (2008). The conspicuousness of colour cues in male pond damselfies depends on ambient light and visual system. *Animal Behaviour*, *76*, 1357–1364.

- Schultz, T. D., & Fincke, O. M. (2013). Lost in the crowd or hidden in the grass: signal apparency of female polymorphic damselflies in alternative habitats. *Animal behaviour*, *86*, 923–931.
- Svensson, E. I., Abbott, J., & Härdling, R. (2005). Female polymorphism, frequency dependence, and rapid evolutionary dynamics in natural populations. *The American Naturalist*, *165*, 567–576.
- Takahashi, Y., Kagawa, K., Svensson, E. I., & Kawata, M. (2014). Evolution of increased phenotypic diversity enhances population performance by reducing sexual harassment in damselflies. *Nature Communications*, *5*, 4468. doi:10.1038/ncomms5468
- Takahashi, Y., & Watanabe, M. (2011). Male mate choice based on ontogenetic colour changes of females in the damselfly *Ischnura senegalensis*. *Journal of Ethology*, *29*, 293–299.
- Takahashi, Y., Yoshimura, J., Morita, S., & Watanabe, M. (2010). Negative frequency-dependent selection in female color polymorphism of a damselfly. *Evolution*, *64*, 3620–3628. doi:10.1111/j.1558-5646.2010.01083.x
- van Gossum, H., Bots, J., Van Heusden, J., Hammers, M., Huyghe, K., & Morehouse, N. I. (2011). Reflectance spectra and mating patterns support intraspecific mimicry in the colour polymorphic damselfly *Ischnura elegans*. *Evolutionary Ecology*, *25*, 139–154.
- van Gossum, H., Stoks, R., & De Bruyn, L. (2001). Discriminative mate choice in relation with female maturation in *Ischnura elegans* (Odonata: Coenagrionidae). *International Journal of Odonatology*, *4*, 83–91.
- Vilela, D. S., Guillermo-Ferreira, R., & Del-Claro, K. (2016). The odonata community of a brazilian vereda: seasonal patterns, species diversity and rarity in a palm swamp environment. *Bioscience Journal*, *32*, 486–495.
- Voipio, P., & Hissa, R. (1970). Correlation with fur density of color polymorphism in *Sciurus vulgaris*. *Journal of Mammalogy*, *51*, 185–187.
- von Ellenrieder, N. (2000). Species composition and temporal variation of odonate assemblages in the subtropical-pampasic ecotone, Buenos Aires, Argentina. *Odonatologica*, *29*, 17–30.
- von Ellenrieder, N., & Muzón, J. (2003). Description of the last larval instar of *Ischnura fluviatilis* Selys (Coenagrionidae). *Bulletin of American Odonatology*, *7*, 57–60.
- von Ellenrieder, N., & Muzón, J. (2008). An updated checklist of the Odonata from Argentina. *Odonatologica*, *37*, 55–68.