



Is body condition of Mexican rubyspot (Odonata:Zygoptera) associated with urbanization?

Catalina M. Suárez-Tovar^{1,2} · Maya Rocha-Ortega² · Alex Córdoba-Aguilar²

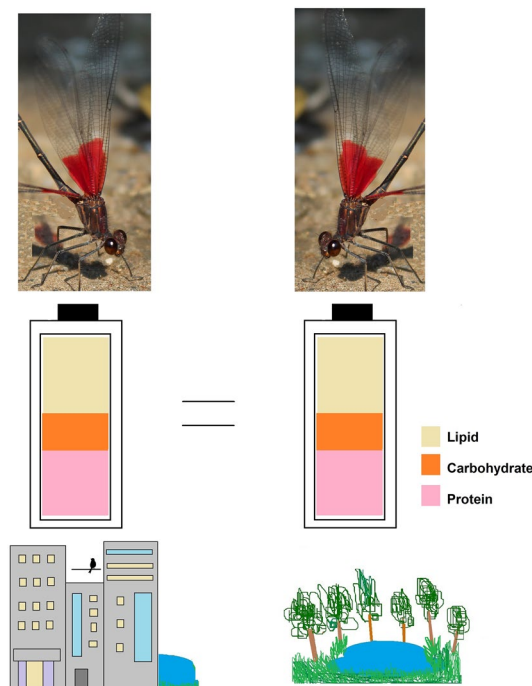
Received: 15 February 2023 / Accepted: 22 August 2023 / Published online: 2 September 2023
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Abstract

Urbanized areas can impose selective pressures on insects which can be identified at the individual level based on animal physiological condition. Physiological condition can be measured from variables such as body size, body mass or energetic budget of individuals. We examined whether body mass, wing spot size and energy reserves (proteins, lipids and carbohydrates) were reduced as urbanization increases, using adults of two damselflies, *Hetaerina americana* and *H. vulnerata*, in Central Mexico. We used a Habitat Integrity Index to assess the degree of urbanization in our sampled sites, considering biophysical attributes and the impact of anthropogenic activities. We did not find relation of above individual variables with urbanization degree. These results support possible resilience of rubyspot damselflies in the face of radical changes such as urbanization. Our finding echoes other results in damselflies research.

Implications for insect conservation Our results highlight the resilience of these damselflies species in the face of urban disturbances. Thus design cities considering not only requirements of humans is essential to promote the presence and conservation of these and other species of insects in cities.

Graphical abstract



Keywords Urban ecology · Habitat Integrity Index · Odonata · Resilience · Energy budget · *Hetaerina*

Extended author information available on the last page of the article

Introduction

Human concentration in urban areas and continuous modifications of native ecosystems for the construction of houses, roads, businesses, buildings and industries, have generated an irreversible impact on terrestrial and aquatic native environments worldwide (Grimm et al. 2008; Johnson and Munshi-South 2017). Even for species surviving in urban ecosystems, the modification of structural and environmental parameters as well as the alteration of the climate and microclimates, and the loss of the complexity of the available niches imply strong selective pressures (Alberti et al. 2017). These urban species can respond to new conditions at different levels: community, population or individual. Although, we have a good idea of community- (Blair & Launer 1997; Monteiro-Júnior et al. 2014; Kelly et al. 2019) and population-level effects (de Carvalho et al. 2017; da Conceição et al. 2020), we are still far from having a sound knowledge of individual-level effects of urbanization (e.g. Salomão et al. 2020).

The fact that many insect species can occur in both urban and non-urban habitats (Sattler et al. 2010), implies an opportunity to study the consequences of urbanization at the individual (i.e. morphological and/or physiological) level. For example, the physiological condition of individuals as reflected by traits such as body size or energy budget, could give an indication of how individuals do in altered environments (e.g. Salomão et al. 2020). Additionally, changes in the energy budget, can also modify behavior, resulting in the modulation or change of behavioral patterns when there is less energy available as a consequence of additional energy costs generated by new threats that take place in cities (Tynkkynen et al. 2008; Magura et al. 2021; Resende et al. 2021).

One insect genus with the ability to live in urbanized and non-urbanized areas, is that of *Hetaerina* Hagen, 1853 damselflies. Members of this taxon are also commonly known as rubyspot given the red wing spot adult males bear. *Hetaerina* species are good study subjects for answering how urbanization degree affects condition. For example, a recent study found that *H. americana* adults and larvae exposed to an increased level of wastewater inlets was related to a reduction in fat and muscle mass as well as egg hatching (Córdoba-Aguilar and Rocha-Ortega 2019). This study implied that a proxy of urbanization level negatively affected *Hetaerina* adult fitness in the long term.

One other advantage of using *Hetaerina* damselflies is that we have a good knowledge of which traits could be used as proxies of condition. In this regard, wing spot size and aggressive behavior act as honest signals of physiological condition in these damselflies (Contreras-Garduño

et al. 2006; González-Santoyo et al. 2014). Within the genus *Hetaerina*, *H. americana* Fabricius, 1798 and *H. vulnerata* Hagen, 1853 are species widely distributed in Mexico. There, these two species can be found in sympatry, but it is more common to find them in allopatry due to their great similarity in both biology and sexual behavior (Álvarez et al. 2013). Both species are territorial species and from very early in their evolutionary history they are well adapted to open habitats (Córdoba-Aguilar and Cordero-Rivera 2005; Standing et al. 2022). Given these arguments, we provide here the results after asking whether adult *Hetaerina americana* and *H. vulnerata* show a reduced body condition with increasing urbanization in Central Mexico. We predicted that urbanization will negatively covary with the expression of body mass, wing spot size and energy reserves (proteins, lipids, and carbohydrates).

Materials and methods

Study area

We selected 18 lotic systems (small streams or small rivers) between 1200 and 1655 m.a.s.l. in the state of Morelos (Fig. 1) that shared similar physical conditions in terms of width and depth but that differed in urbanization levels ranging from highly modified to less modified streams with marginal vegetation that cover the stream bed. Morelos is located in Central Mexico where the concentration of most of the population in urban areas has generated a large transformation of the natural ecosystems, into industrialized, touristic and residential areas with high levels of pollution caused by the inadequate discharge of sewage and uncontrolled use of natural resources (INEGI 2020; Valladares-Cisneros et al. 2021).

At each study site, we registered the geographical coordinates, elevation, and water and air temperature. We conducted two visits at each site, in December 2019 and in November–December 2020. During each visit, we defined three 20-m transects in each site (corresponding to the transects where we conducted the biological sampling, as explained below). In each transect we measured habitat variables to describe three components of the environment that specifically affect odonates: (1) a green component, including both macrophytes and the vegetation adjacent to the lotic system, (2) a blue component, evaluating the physical and chemical properties of the water and the solid waste present in it, and (3) a gray component, assessing urban constructions and infrastructure, and indicators of human activity. How we determined such components are described below.

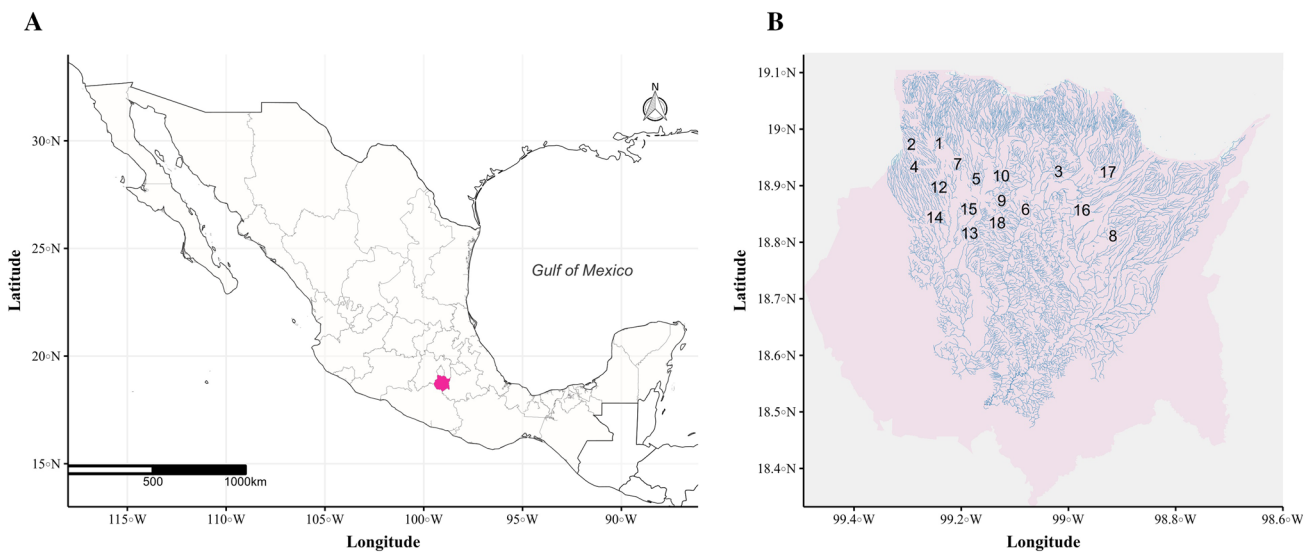


Fig. 1 **A** Location of Morelos in México. **B** Location of the 18 sampling sites in the State of Morelos

Green component

We determined the dominant vegetation stratum at each study site using the Canfield line-intercept method (Canfield 1941). For this, we considered three vegetation strata: herbaceous (0.3–1.5 m height), shrubby (1.5–5.0 m), or arboreal (> 5 m) following Rangel and Velásquez (1997). Then, we summed up the cover of each plant stratum in the three transects, divided by the 60 m length sampled (transect length occupied by each stratum/total length sampled), and multiplied by 100 to obtain the percentage of each plant stratum for each study site. Considering the predominant stratum of native vegetation, we calculate the state of preservation of the vegetation around each body of water. Additionally, we registered macrophytes using a 1-m² PVC square frame with 100 internal 10 × 10 cm squares. We placed the square randomly at three points in the water body and counted how many of the squares contained emerging, submerged, and/or floating macrophytes.

Blue component

We measured water temperature, pH, percentage of both dissolved solids and dissolved oxygen using a Hanna HI9829 multiparametric probe. We measured the mean maximum width of the water body with a 50 m flexometer and the mean maximum depth with a rope marked every 5 cm and tied to a plummet that was thrown to the bottom of each water body. We registered channel type (concrete walls, natural, or mixed), the presence or absence of sewage discharges and the amount of anthropic waste in the water using the same method used to quantify macrophytes. We placed the square randomly at points of each transect in the water

body and counted how many of the internal squares contained anthropic waste. Sewage discharges was defined as any liquid flow of at least 15 cm in width from any building into the river. We did not record the volume of these outlets nor the type of water contents. However, we observed that wastewaters included mainly laundry chemicals.

Gray component

We recorded the constructions and urban infrastructure in and around 300 m the sampling sites: roads, shops, households, or nearby buildings. This record was made by direct observation before beginning the collection of variables and the sampling of individuals in each site. Additionally, a count was made of the number of people and vehicles (cars, bicycles motorcycles) passing through each sampling site. For this, 3-min replications of observations were made at 10:00, 12:00 and 14:00 (UTC-6).

Measurements in each site were made on the same day of biological sampling, before starting the registration and collection of specimens. Each sampling site was visited for a full day from 9:00 to 16:00 h (UTC-6) each of the sampling years.

Habitat Integrity index (HII) calculation

The HII (modified from Petersen 1992), was calculated to assess the degree of disturbance of aquatic habitats, considering biophysical attributes of each site (green and blue components) and the impact of anthropogenic activities (gray component) for each sampling site. We included two variables from the green component, five from the blue component, and three from the gray component. Each

Table 1 Characteristics considered for the calculation of the Habitat Integrity Index, and the scores assigned to each of the identified conditions

Characteristic	Condition	Score
1. Preservation of the riparian forest	Grass with some shrubs	0
	Grass mixed with some pioneer trees and shrubs	1
	Regenerating habitat, with a predominance of pioneer species, secondary forest, and dense undergrowth	2
	More than 90% of the vegetation constituted by native or non-pioneer trees	3
2. Macrophyte coverage (%)	0	0
	1–15	1
	16–30	2
	31–45	3
	> 45	4
3. Anthropogenic waste (%)	> 20	0
	10.1–20	1
	5–10	2
	0–4.9	3
4. Channel structure	Width/depth ratio 25–50	0
	Width/depth ratio 15–25	1
	Width/depth ratio 8–15	2
	Width/depth ratio < 7	3
5. pH	Basic (8.56–11) * urban streams with high levels of impermeability are associated with neutral to slightly alkaline pH (Tippler et al. 2018)	0
	Neutral (6.55–8.55)	1
	Acid (< 6.55) * Non-urban streams with low impermeability are associated with generally acidic pH (Tippler et al. 2018)	2
6. Channel type	Concrete	0
	Mix	1
	Natural	2
7. Sewage discharge	Direct residual discharges (from homes or industries)	0
	Occasional discharges near or into the water body (soap, pesticides, etc.)	1
	No obvious discharges	2
8. Mean of persons walking	11–15	0
	6–10	1
	0–5	2
9. Mean of vehicles passing by	> 30	0
	16–30	1
	11–15	2
	6–10	3
	0–5	4
10. Type of constructions around (within 300 m)	Shops, schools and / or wide roads	0
	Households	1
	No construction	2

variable had three to five alternatives, with scores that increase with habitat integrity (Table. 1). To weigh (p) the different i variables equally, the scores for each variable (ao) were divided by its maximum (am) possible score ($p_i = ao / am$). The final HII score (Eq. 1) for each site was obtained from the mean value of these scores for the ten variables analyzed.

$$HII = \frac{\sum_{i=1}^n P_i}{n} \quad (1)$$

Our HII generates values that go from zero to one, where values close to zero correspond to sites with high urbanization, and values close to one correspond to sites with low urbanization.

Odonata collection and determination of individual variables

In each of the sampling sites, we used an entomological net, and collected at least ten adult males of *H. americana* or *H. vulnerata* (ten individuals of each species). This is due to the fact that males were more abundant compared to females in the sampled sites. In each of the sites we observed exuviae of the collected species, so we could infer that the collected adults have spent their entire life cycle in the sampled sites. Next, body mass (g), proportion of the wing spot to wing size, and the content of protein, lipid, and carbohydrate ($\mu\text{g}/\text{mg}$) of each individual were calculated. All these variables were considered as proxies of energetic condition (see Meillère et al. 2015).

To measure the size of the wing spot, each individual's right forewing was removed and photographed. We measured the area occupied by the red spot in the right forewing and the total area of the wing using ImageJ 1.53e (Schneider et al. 2012). Then, we calculated the spot ratio relative to the total wing area. To minimize possible errors of measurement, each metric was determined three times to obtain a mean that was used for the analysis. Finally, the content of energy reserves was performed following the protocol of Foray et al. (2012). According to this protocol, we used the thorax which was weighed on a Velab VE-210 analytical balance, with a sensitivity of 0.1 mg and a maximum capacity of 210 g. Then, we placed the thorax in a 2 ml centrifuge tube and crushed it with 180 μL of saline phosphate buffer to a hyaline solution using a TissueLyser II bead mill (Qiagen, Valencia, CA, U.S.A.). Once the thoracic tissue was homogenized, we calculated the amount of protein present in the tissue by centrifuging at 180 g relative centrifugal force (RCF) for 5 min at 4 °C. Next, we took 2.5 μL of the supernatant in duplicate and placed it into a 96-well microplate. Finally, we added 250 μL of Bradford reagent, incubated for 20 min, and read spectrophotometrically at 595 nm using an EPOCH spectrophotometer 200-900 nm (BioTek, Winooski, VT, U.S.A.). To calculate the amount of protein in the tissue from the absorbance values given by the spectrophotometer, we made a calibration curve using bovine serum albumin dilution series.

For lipid and carbohydrate determination we used 180 μL of original homogenized tissue and added 20 μL of Na_2SO_4 , 5 μL of PBS and 1500 μL of methanol:chloroform solution (2:1). We shook the vial for 2 min. The samples were then centrifuged twice for 15 min at 180 g RCF. After centrifugation, and for lipid quantification, we transferred 100 μL of supernatant to a U-bottom plate and heated at 90 °C until complete evaporation in a water bath. After total evaporation, we placed 10 μL of 98% sulfuric acid in each well and incubated for 2 min at 90 °C. We then cooled the reaction, added 190 μL vanillin reagent, incubated for 15 min and

read absorbance at 525 nm with a glyceryl trioleate lipid dilution series as standard for calibration. For carbohydrate calculation, we placed 150 μL of supernatant obtained after centrifugation in duplicate in a 96-well microplate until we get approximately 10 μL in a water bath. After obtaining 10 μL of sample, we placed 240 μL of anthrone reagent in each well and incubated the plate for 15 min at room temperature. We covered the microplate and incubated it at 90 °C for 15 min in a water bath. Finally, we read the absorbance at 625 nm with a standard curve of glucose dilution series as standard for calibration.

Statistical analysis

We used independent generalized linear mixed-effects using *lme4* (Bates et al. 2015) and *car* (Fox and Weisberg 2019) libraries in R, with the HII as an explanatory variable and body mass, proportion of the wing spot and the amount of energy content (proteins, lipids, and carbohydrates) as response variables. Additionally, the species were included in the model as a random effect to control their effect on the response variables. In order to know if any of variables used to calculate the HII affected independently response variables, we also repeated each model using each variable as an explanatory variable. We assessed the assumptions of normality and homoscedasticity in models residuals using *performance* library (Lüdecke et al. 2021) and finally we used *ggplot2* (Wickham 2016) to perform graphics. All these analyzes and graphs were performed in RStudio v. 1.1.456 (R Core Team 2018).

Results

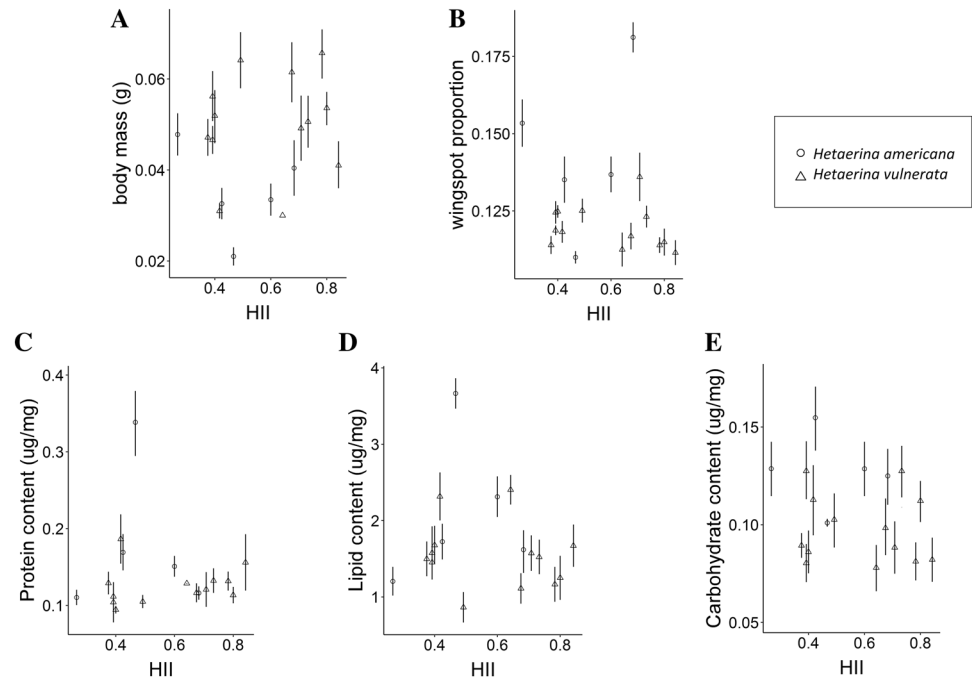
The HII calculated for the study sites ranged from 0.27 to 0.84 (Table. 2). The different environmental variables varied between the sampling sites (Table. S1). *H. americana* and *H. vulnerata* were abundant in the study area, but rarely occurred in sympatry: out of the 18 sampled sites, *H. americana* was present at 5 sites while *H. vulnerata* was present at 13 sites. We thus collected data for 61 individuals of *H. americana* and 143 of *H. vulnerata*. Body mass and wing spot were not related to HII ($R^2=0.9$, $F=0.12$, $p=0.76$ and $R^2=0.26$, $F=0.03$, $p=0.85$ respectively), as well as the content of protein ($R^2=0.29$, $F=0.0004$, $p=0.98$), lipid ($R^2=0.026$, $F=0.07$, $p=0.79$) and carbohydrates ($R^2=0.39$, $F=0.26$, $p=0.6$) (Fig. 2). However, when we evaluated each variable individually we found a negative relation between the amount of lipids and proteins with the pH ($F=12.98$, $p=0.0002$ and $F=12.14$, $p=0.0005$, respectively). That is,

Table 2 Geographical coordinates, elevation and Habitat Integrity Index values calculated for each sampled site

Site	HII	Latitude	Longitude	Elevation (masl)
1	0.60	18° 53' 11.0" N	99° 11' 11.6" W	1374
2	0.39	18° 53' 12.0" N	99° 11' 44.3" W	1397
3	0.68	18° 56' 37.8" N	99° 15' 39.3" W	1655
4	0.68	18° 54' 26.9" N	99° 02' 26.4" W	1232
5	0.42	18° 56' 09.8" N	99° 14' 50.9" W	1593
6	0.38	18° 54' 16.7" N	99° 12' 15.9" W	1420
7	0.27	18° 52' 58.9" N	99° 03' 44.5" W	1206
8	0.73	18° 54' 57.0" N	99° 12' 29.3" W	1458
9	0.71	18° 49' 54.2" N	98° 56' 18.5" W	1341
10	0.80	18° 53' 45.4" N	99° 08' 59.9" W	1387
11	0.49	18° 56' 25.9" N	99° 13' 46.9" W	1590
12	0.64	18° 55' 45.2" N	99° 13' 53.4" W	1544
13	0.43	18° 50' 18.4" N	99° 12' 16.9" W	1209
14	0.40	18° 51' 59.9" N	99° 13' 34" W	1277
15	0.39	18° 52' 30.5" N	99° 13' 15.8" W	1322
16	0.47	18° 50' 10.9" N	98° 57' 04.8" W	1338
17	0.84	18° 54' 09.6" N	98° 57' 08.6" W	1369
18	0.78	18° 52' 36.4" N	99° 09' 56.4" W	1341

masl meters above sea level

Fig. 2 Observed data included in linear mixed-effects models for how urbanization relates to **A** Body mass, **B** Wingspot proportion, **C** Protein content, **D** Lipid content and **E** Carbohydrate content. Error bars indicate standard deviation (SD)



at higher (i. e. basic) values of pH the amount of lipids and proteins decreases (Fig S1).

Discussion

Unlike previous works (Salomão et al. 2020; Córdoba-Aguilar and Rocha-Ortega 2019; Iserhard et al. 2019), we did not find a significant relation between insect's body condition and urbanization measure as HII. However, and despite the values recorded in our sampling sites were neutral to basic (7.9–10.5), it is possible to appreciate a negative relationship of lipids and proteins with pH values, similar to what was found by Córdoba-Aguilar and Rocha-Ortega (2019). Basic pH values have previously been associated with urbanized environments (Tippler et al. 2018). If we consider that the lipid and protein reserves, being long-term reserves (Arrese and Soulages 2010), are stored from the larval stage, we could infer that the way in which the pH affects the larvae's muscle construction and fat reserves generation, also affects the constitution of the adult, as previously reported Tüzün and Stoks (2018) in *Coenagrion puella* populations reared in water with different physicochemical conditions.

Although we do not have a reference point from which we can ensure that the energetic condition that we find in the individuals is good or bad, we can infer from our results that the energetic condition of the individuals, measured from different proxies, is maintained in high urbanized and less urbanized sites included in our study. These results support possible resilience of rubyspot damselflies in the face of radical changes such as urbanization. There are several possible explanations for the absence of a relation between energy condition indicators and habitat integrity related to urbanization.

First, it is important to consider that rubyspot damselflies are abundant and widely distributed species in the American continent (Garrison 1990; Standing et al. 2022). These two characteristics may be a reflection of the fact that they are highly variable species in their traits, which allows them to adapt more easily to stressful environments like cities without presenting radical changes in its morphology or energetic condition. This has been recorded in other common damselflies species (e.g. *Ischnura elegans*) that face urban environments in Europe (Goertzen and Suhling 2013; Villalobos-Jiménez and Hassall 2019). Continuing to study the responses at the individual level, not only of abundant and widely distributed species, but also of more sensitive species with restricted distribution, will allow us to clarify the scenario of changes in the individual condition of organisms that face changes in their environment derived from urbanization.

A second reason could be that animals have already responded to habitat changes. Urbanization processes in the study area began around 70 years ago (INEGI 2020) which can be enough time for current individuals to be already adapted to environmental disturbance. This considering, for example, that in previous studies *Hetaerina* species have responded (modifying aspects such as habitat use and interspecific fights frequency) after three-year observations in populations that face changes in their environment associated with the density of competing species (Anderson and Grether 2011). In this sense, the impact of urbanization on common and tolerant species (as *Hetaerina* species) could only be detected by sampling in the same place over time. This explanation is not at all surprising considering that insects respond quickly to stressors related to changes in their environment (Halsch et al. 2021).

A third possible explanation is about food resources. Although wing spot size in *Hetaerina* males is determined by the amount of resources that individuals obtain from their diet during their larval stage, energy reserves depend almost exclusively on the feeding of individuals during their adult stage (Contreras-Garduño et al. 2008; Córdoba-Aguilar and González-Tokman 2014). Our results, together with recent

findings where the availability of food resources of *H. vulnerata* were assessed daily (Córdoba-Aguilar et al. 2021), indicate that despite the alteration caused by urban habitats, food resources may remain stable which could explain why individual body condition did not vary.

Finally, another explanation could be associated with the fact that individuals are modifying their behavior in urbanized places to reduce energy expenditure facing up new stressors. Some studies have recorded changes in the diversity of behaviors in the face of environmental impacts (Resende et al. 2021) and others have registered that changes in behavior patterns are the fastest response of some animals to relatively quick environmental changes (Tynkkynen et al. 2008; Magura et al. 2021). In this sense, rubyspot damselflies and other Odonata or insect species could be responding with changes in their behavior in urbanized or novel environments. Thus, further studies should be carried out to unravel a possible relation between fitness, behavior, and urbanization.

Although cities can drastically affect native ecosystems worldwide, urban areas can also be a suitable habitat for different groups of animals that can maintain viable populations and individuals with a good energetic condition (e.g. Pacheco-Muñoz et al. 2022). These animals have a set of morphological and physiological traits that allow them to survive the environmental filters imposed by cities (Iserhard et al. 2019; Villalobos-Jiménez and Hassall 2019; Salomão et al. 2020). However, it is important to highlight that not all species can survive in the face of environmental changes related to urbanization. It is enough to compare communities associated with lotic or lentic environments (e.g. Prescott and Eason 2018) to realize that there are different responses of the species depending on the initial conditions of the environments they inhabit. For this reason and being aware of the multiple species and their different requirements, we must generate cities designed not only for the human species, but for all the others that fly over the urban jungle and its surroundings.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10841-023-00512-9>.

Acknowledgements To the anonymous reviewers, many thanks for the valuable comments that helped improve the final version of this manuscript. Authors thank the Posgrado en Ciencias Biológicas at Universidad Nacional Autónoma de México (UNAM) as well as Consejo Nacional de Humanidades, Ciencias y Tecnologías (CONAHCYT) for postgraduate scholarship to CMS-T. To Marco Tulio Solano, David Schneider, Erik Aguilar, Michelle Maldonado and Angela Suárez for their help in the laboratory tests. To Javier Pérez-López for his help with the map. Jorge Schondube and Zenón Cano-Santana provided guidance. Financial support was gathered from a PAPIIT-UNAM project IN204921 to AC-A.

Author contributions Author contributions: CMST project design, data collection, writing original draft and analysis, MRO analysis, ACA project design, corrections of final versions, and funding acquisition. All authors commented on original draft of the manuscript. All authors read and approved the final manuscript.

Declarations

Competing interests The authors declare no competing interests.

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References

- Alberti M, Marzluff J, Hunt VM (2017) Urban driven phenotypic changes: empirical observations and theoretical implications for eco-evolutionary feedback. *Philos Trans R Soc B* 372:20160029
- Álvarez HA, Serrano-Meneses M, Reyes-Márquez I et al (2013) Allometry of a sexual trait in relation to diet experience and alternative mating tactics in two rubyspot damselflies (Calopterygidae: Hetaerina). *Biol J Linn Soc* 108:521–533. <https://doi.org/10.1111/j.1095-8312.2012.02031.x>
- Anderson C, Grether GF (2011) Multiple routes to reduced interspecific territorial fighting in Hetaerina damselflies. *Behav Ecol* 22:527–534. <https://doi.org/10.1093/beheco/arr013>
- Arrese EL, Soulages JL (2010) Insect fat body: energy, metabolism, and regulation. *Annu Rev Entomol* 55:207–225. <https://doi.org/10.1146/annurev-ento-112408-085356>
- Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48
- Blair RB, Launer AE (1997) Butterfly diversity and human land use: species assemblages along an urban gradient. *Biol Conserv* 80:113–125. [https://doi.org/10.1016/S0006-3207\(96\)00056-0](https://doi.org/10.1016/S0006-3207(96)00056-0)
- Canfield RH (1941) Application of the line interception method in sampling range vegetation. *J For* 39:388–394
- Contreras-Garduño, Alves Buzatto B, Serrano-Meneses MA et al (2008) The size of the red wing spot of the American rubyspot as a heightened condition-dependent ornament. *Behav Ecol* 19:724–732
- Contreras-Garduño J, Canales-Lazcano J, Córdoba-Aguilar A (2006) Wing pigmentation, immune ability, fat reserves and territorial status in males of the rubyspot damselfly Hetaerina americana. *J Ethol* 24:165–173
- Córdoba-Aguilar A, Cordero-Rivera A (2005) Evolution and ecology of Calopterygidae (Zygoptera: Odonata): status of knowledge and research perspectives. *Neotrop Entomol* 34:861–879
- Córdoba-Aguilar A, González-Tokman DM (2014) The behavioral and physiological ecology of adult rubyspot damselflies (Hetaerina, Calopterygidae, Odonata). In: Naguib M, Barrett L, Brockmann HJ et al (eds) *Advances in the study of behavior*. Academic Press, pp 311–341
- Córdoba-Aguilar A, Rocha-Ortega M (2019) Damselfly (Odonata: Calopterygidae) population decline in an urbanizing watershed. *J Insect Sci* 19(30):1–6. <https://doi.org/10.1093/jisesa/iez063>
- Córdoba-Aguilar A, San Miguel-Rodríguez M, Rocha-Ortega M et al (2021) Adult damselflies as possible regulators of mosquito populations in urban areas. *Pest Manag Sci* 77:4274–4287. <https://doi.org/10.1002/ps.6496>
- da Conceição AA, Albertoni EF, Milesi SV, Hepp LU (2020) Influence of Anthropogenic Impacts on the Functional Structure of Aquatic Invertebrates in Subtropical Wetlands. *Wetlands* 40:2287–2296. <https://doi.org/10.1007/s13157-020-01317-1>
- de Carvalho GP, Vendrami DP, Marrelli MT, Wilke ABB (2017) Wing variation in Culex nigripalpus (Diptera: Culicidae) in urban parks. *Parasit Vectors* 10:423. <https://doi.org/10.1186/s13071-017-2348-5>
- Foray V, Pelisson PP, Bel VM et al (2012) A handbook for uncovering the complete energetic budget in insects: the van Handel's method (1985) revisited. *Physiol Entomol* 37:297–302. <https://doi.org/10.1111/j.1365-3032.2012.00831.x>
- Fox J, Weisberg S (2019) *An R companion to applied regression*, 3rd edn. Sage, Thousand Oaks
- Garrison RW (1990) A synopsis of the genus Hetaerina with descriptions of 4 new species (Odonata: Calopterygidae). *Trans Am Entomol Soc* 116:175–259
- Goertzen D, Suhling F (2013) Promoting dragonfly diversity in cities: major determinants and implications for urban pond design. *J Insect Conserv* 17:399–409. <https://doi.org/10.1007/s10841-012-9522-z>
- González-Santoyo I, González-Tokman D, Munguía-Steyer R, Córdoba-Aguilar A (2014) A mismatch between the perceived fighting signal and fighting ability reveals survival and physiological costs for bearers. *PLOS ONE* 9:e84571. <https://doi.org/10.1371/journal.pone.0084571>
- Grimm NB, Faeth SH, Golubiewski NE et al (2008) Global change and the ecology of cities. *Science* 319:756–760
- Halsch CA, Shapiro AM, Fordyce JA et al (2021) Insects and recent climate change. *Proc Natl Acad Sci USA* 118:e200254317. <https://doi.org/10.1073/pnas.2002543117>
- INEGI (2020) Población total por Entidad federativa. Instituto Nacional de Estadística y Geografía.
- Iserhard CA, Duarte L, Seraphim N, Freitas AVL (2019) How urbanization affects multiple dimensions of biodiversity in tropical butterfly assemblages. *Biodivers Conserv* 28:621–638. <https://doi.org/10.1007/s10531-018-1678-8>
- Johnson MTJ, Munshi-South J (2017) Evolution of life in urban environments. *Science* 358:6363
- Kelly P, Cuevas E, Ramírez A (2019) Urbanization increases the proportion of aquatic insects in the diets of riparian spiders. *Freshw Sci* 38:379–390. <https://doi.org/10.1086/703442>
- Lüdecke D, Ben-Shachar M, Patil I, Waggoner P, Makowski D (2021) Performance: an R package for assessment, comparison and testing of statistical models. *J Open Source Softw* 6(60):3139. <https://doi.org/10.21105/joss.03139>
- Magura T, Mizser S, Horváth R et al (2021) Are there personality differences between rural vs. urban-living individuals of a specialist ground beetle, *Carabus convexus*? *Insects* 12:646. <https://doi.org/10.3390/insects12070646>
- Meillère A, Brischox F, Parenteau C, Angelier F (2015) Influence of urbanization on body size, condition, and physiology in an urban exploiter: a multi-component approach. *PLoS ONE*. <https://doi.org/10.1371/journal.pone.0135685>
- Monteiro-Júnior CS, Juen L, Hamada N (2014) Effects of urbanization on stream habitats and associated adult dragonfly and damselfly communities in central Brazilian Amazonia. *Landsc Urban Plan* 127:28–40. <https://doi.org/10.1016/j.landurbplan.2014.03.006>
- Moore MP (2021) Larval habitats impose trait-dependent limits on the direction and rate of adult evolution in dragonflies. *Biol Lett* 17:20210023. <https://doi.org/10.1098/rsbl.2021.0023>
- Pacheco-Muñoz R, Ceja-Madriral A, Pérez-Negrón E et al (2022) Wintering town: individual quality of migratory warblers using green urban areas in a neotropical city. *Front Ecol Evol*. <https://doi.org/10.3389/fevo.2021.779507>

- Petersen RC (1992) The RCE: a riparian, channel, and environmental inventory for small streams in the agricultural landscape. *Freshw Biol* 27:295–306. <https://doi.org/10.1111/j.1365-2427.1992.tb00541.x>
- Prescott VA, Eason PK (2018) Lentic and lotic odonate communities and the factors that influence them in urban versus rural landscapes. *Urban Ecosyst* 21:737–750. <https://doi.org/10.1007/s11252-018-0752-z>
- R Core Team (2018) R: a language and environment for statistical computing. R Core Team, Austria
- Rangel JO, Velásquez A (1997) Métodos de estudio de la vegetación. In: Rangel JO (ed) Colombia diversidad biótica II: tipos de vegetación en Colombia. Instituto de Ciencias Naturales, Universidad Nacional de Colombia. Instituto de Hidrología, Meteorología y Estudios Ambientales IDEAM, Ministerio del Medio Ambiente, Colombia
- Resende BO, Ferreira VRS, Brasil LS et al (2021) Impact of environmental changes on the behavioral diversity of the Odonata (Insecta) in the Amazon. *Sci Rep* 11:9742. <https://doi.org/10.1038/s41598-021-88999-7>
- Salomão RP, Alvarado F, Baena-Díaz F et al (2020) Negative effects of urbanisation on the physical condition of an endemic dung beetle from a neotropical hotspot. *Ecol Entomol* 45:886–895. <https://doi.org/10.1111/een.12865>
- Sattler T, Duelli P, Obrist MK et al (2010) Response of arthropod species richness and functional groups to urban habitat structure and management. *Landsc Ecol* 25:941–954. <https://doi.org/10.1007/s10980-010-9473-2>
- Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. *Nat Methods* 9:671
- Standring S, Sánchez-Herrera M, Guillermo-Ferreira R et al (2022) Evolution and biogeographic history of Rubyspot damselflies (Hetaeriniinae: Calopterygidae: Odonata). *Diversity* 14:757. <https://doi.org/10.3390/d14090757>
- Tippler C, Wright IA, Davies PJ, Evans CR (2018) Are Odonata nymphs adversely affected by impaired water quality in urban streams. *Austral Ecol* 43:890–902. <https://doi.org/10.1111/aec.12630>
- Tüzün N, Stoks R (2018) Pathways to fitness: carry-over effects of late hatching and urbanisation on lifetime mating success. *Oikos* 127:949–959. <https://doi.org/10.1111/oik.05033>
- Tynkkynen K, Kotiaho J, Svensson EI (2008) Interspecific interactions and premating reproductive isolation. Dragonflies and damselflies: model organisms for ecological and evolutionary research. Oxford University Press, Oxford, pp 139–152
- Valladares-Cisneros M, Miranda ZL, González Z (2021) Índice de Calidad del Agua del río Yauatepec del estado de Morelos. *Inventio* 17:1–7. <https://doi.org/10.30973/inventio/2021.17.41/7>
- Villalobos-Jiménez G, Hassall C (2019) Wing shape patterns among urban, suburban, and rural populations of *Ischnura elegans* (Odonata: Coenagrionidae). *Int J Odonatol* 22:37–49. <https://doi.org/10.1080/13887890.2018.1564074>
- Wickham H (2016) ggplot2: elegant graphics for data analysis. Springer, New York

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Authors and Affiliations

Catalina M. Suárez-Tovar^{1,2}  · Maya Rocha-Ortega²  · Alex Córdoba-Aguilar² 

✉ Alex Córdoba-Aguilar
acordoba@ieciologia.unam.mx

² Instituto de Ecología, Universidad Nacional Autónoma de México, Apdo. Postal 70-275, Circuito Exterior, Ciudad Universitaria, Coyoacán, 04510 México City, México

¹ Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, Av. Universidad 3000, Ciudad Universitaria, Coyoacán, 04510 Mexico City, México