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Demography and natural history of the damselfly *Mesamphiagrion gaudiimontanum* (Coenagrionidae), a Páramo endemic species in the Colombian Andes

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All relevant data are within the paper and its Supporting Information files.

Abstract. The páramos are high mountain ecosystems in the tropical regions of the New World, and they are particularly threatened by climate change. The Belmira páramo complex in Colombia is home to M*esamphiagrion gaudiimontanum*, an endemic and endangered damselfly species. This study presents the first demographic assessment of *M. gaudiimontanum* using the capture-recapture method to estimate population size, survival, and detection probabilities, focusing on differences in age, sex, female color morphs, and parasite infestation. The population size was estimated to be 730 ± 186.59 individuals, with an average survival probability of 0.89 ± 0.04 and a life expectancy of 8.34 days, these data are like the reported for other populations in the same genus in harsh environmental conditions. Ectoparasitic mites were more common on juveniles than adults. After several hours of observing the species few copula events have been recorded, all of them involving juvenile adult females, which points to a monandrous reproduction syndrome for the species. Another phenomenon observed in the species was a change in coloration due to body temperature in individuals, in which bright coloration becomes grayish in cold weather. This study provides fundamental data for future monitoring and conservation efforts, highlighting the species' vulnerability to environmental changes and the need for specific conservation strategies.

Key words. Dragonfly, ectoparasitic mites, population ecology, physiological color change, sexual dimorphism

Resumen. Los páramos son ecosistemas de alta montaña en las regiones tropicales del Nuevo Mundo y están altamente amenazados por el cambio climático. El complejo de páramo de Belmira, en Colombia, alberga a *Mesamphiagrion gaudiimontanum*, una especie de damisela endémica y en peligro de extinción. Este estudio presenta la primera evaluación demográfica de *M. gaudiimontanum* utilizando el método de captura-recaptura para estimar el tamaño de la población, la supervivencia y las probabilidades de detección, enfocándose en las diferencias de edad, sexo, morfotipos femeninos e infestación por parásitos. Se estimó que el tamaño de la población es de 730 ± 186.59 individuos, con una probabilidad de supervivencia promedio de 0.89 ± 0.04 y una expectativa de vida de 8.34

días, estos datos son similares a los reportados para otras poblaciones del mismo género en condiciones ambientales estresantes. La infestación por ácaros fue mayor en juveniles que en adultos. Tras varias horas de observación de la especie se han registrado pocos eventos de cópula, todos ellos con hembras adultas inmaduras, lo que apunta a un síndrome de reproducción monándrica de la especie. Otro fenómeno observado en la especie fue un cambio de coloración debido a la temperatura corporal en los individuos, en el que la coloración brillante se vuelve grisácea en climas fríos. Este estudio proporciona datos fundamentales para futuros monitoreos y esfuerzos de conservación, destacando la vulnerabilidad de la especie a los cambios ambientales y la necesidad de estrategias de conservación.

Palabras clave. Ácaros ectoparásitos, caballitos del diablo, cambio de coloración fisiológica, dimorfismo sexual, ecología poblacional

Introduction

Páramos are the top mountain ecosystems in the tropical mountains from Venezuela north to Costa Rica and south to northern Peru (Luteyn et al., 1999; Parsons, 1982). These biologically rich and unique ecosystems are considered highly threatened by climate change (Mamantov et al., 2021; Sheldon et al., 2011). One of the predictions for tropical mountains is the upslope movement of ecosystems, tracking their optimal environmental conditions (Colwell et al., 2008), this option will not be available for top mountain ecosystems which do not have any higher place to move.

The Belmira Páramo complex is located in the Central Andean Cordillera in northwestern Colombia, between 3100 and 3350 m a.s.l. (meters above sea level). These ecosystems are known as the most diverse paramos for dragonflies and damselflies, and among these species, three are endemic to this area (Bota-Sierra, 2014). One of them is *Mesamphiagrion gaudiimontanum* Bota-Sierra, 2013, which is the best known because of its abundance and beauty (Figure 1). This species inhabits ponds characterized by abundant *Sphagnum* moss (Bota-Sierra & Wolff, 2013), where individuals parasitized by immature stages of mites in the Arrenuridae family (Acari) are common (Figures 1d, 5). Females of this species exhibit two morphs in the same population (androchrome and gynochrome, Figure 1 b–c), while both sexes present ontogenic coloration changes (Bota-Sierra & Wolff, 2013) as in other Ischnurinae species (Sánchez-Guillén et al., 2020).

Mesamphiagrion gaudiimontanum is known from five locations in the Belmira Páramo Complex threatened by mining, agriculture expansion, and/or climate change (Bota-Sierra et al., 2016), and it is considered an endangered species according to IUCN Red List (Bota-Sierra et al., 2016). These five populations had been periodically and opportunistically visited in the past decade to monitor their status. One of them disappeared because of the introduction of an alien fish (*Cyprinius carpio*) in the small wetland it inhabited, showing how sensitive the species is (C. Bota-Sierra, personal observation).

Monitoring population trends in *M. gaudiimontanum* is a great opportunity to gather data that will help to understand the effects of climate change on the populations of high mountain ectotherms. This monitoring is also crucial for planning conservation actions for the species. Here we present the first demographic assessment for *M. gaudiimontanum* through mark-recapture methods. We estimate the population size for the larger known population of the species, and finally, we test if survival and detection probabilities change between sexes and parasitized individuals.

Methods

Mark recapture sampling

This study was done at "La Ciénaga" wetland, located at 3265 masl in the paramo "El Morro" (6.677602° N, 75.670953° W, Belmira municipality, Antioquia department, Colombia). This is the largest wetland in the Belmira paramo complex with a size of around 200.000 m². The wetland is a mosaic of thousands of small pools of around 1.5 m² surface area and 15 cm deep, with a lot of *Sphagnum* sp. moss in a matrix of grass and some scattered small shrubs. It harbors the largest known *M. gaudiimontanum* population (Figure 2). The map was done using QGIS v.3.12.3 (QGIS Development Team, 2024), it included a digital elevation model downloaded from http://srtm.csi.cgiar.org (Jarvis et al., 2008), a shape file of Colombian departmental political divisions, and a satellital image downloaded from Google Earth Pro v7.3.6.9796 (2024).

The daily activity of damselfly individuals is restricted to sunny warm hours, it was not possible to capture specimens in moments with rainy or cloudy weather, therefore free walks sampling through the wetland were carried out by two researchers between 9:00–16:00 h, getting a mean of nine hours person marking effort every day for 21 days, between July 10 and 31, 2022.

Captured specimens were marked with a number on their wings using a black ink Sharpie marker. Sex, age categories (according to body color, see Table 1), female color morphs, and number of parasitizing mites were recorded *in situ* (see Table 1). For more detail on ontogenic color changes see Bota-Sierra & Wolff (2013). In addition, observations and notes of copulation and oviposition activities of this species were made.

Data analysis

Data were analyzed using the Cormack-Jolly-Seber method (CJS) (Cormack, 1964; Jolly, 1965; Seber, 1965) in the package "Marked" (Laake et al., 2013) ran through R programmatic language (R Core Team, 2024) to estimate the survival (Φ) and detection (*p*) probabilities of the population. The time intervals among sam-

Figure 1. *Mesamphiagrion gaudiimontanum* in the field: (a) Mature male; (b) gynochrome juvenile female; (c) Androchrome juvenile female; (d) gynochrome mature female (marked with three points on its right hind wing); (e) androchrome mature female; (f) copula with gynochrome juvenile female, observe the clutches of ectoparasitic acari on the venter of the abdomen. Pictures a–c, e: Cornelio Bota; d: Sebastian Serna; f: Camilo Flórez.

plings due to rainy days were specified in the models. To test for changes in Φ and *p* among sexes, female color morphs, age categories, and intensity of acari infestation, four groups of models including all possibilities for each parameter were analyzed using multimodel selection under the statistic information theory. Akaike scores (AIC) were calculated for all the models, then the best models were chosen under the criteria of the minimum AIC or a difference in less than five (AIC < 5), and then the parsimony criterium was used. Parsimony criteria was used to indicate the model that best explains the resulting pattern using the minimum number of pa-

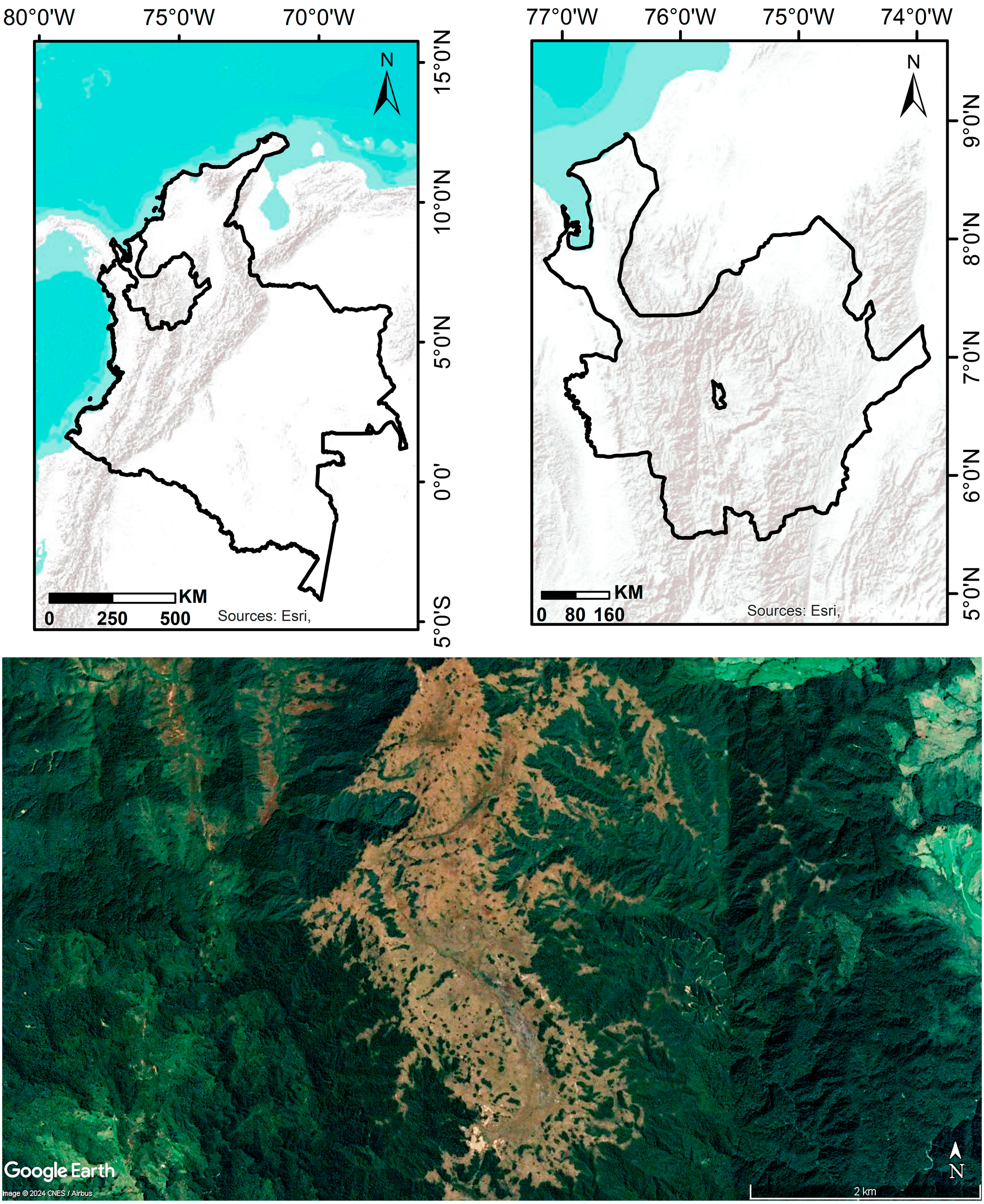

Figure 2. Map and satellite image of the study area in the Belmira Páramo Complex, (Antioquia), Colombia.

Table 1. Criteria for age and acari infestation categories.

	Category	Characteristics
Age	Teneral	Red coloration on the first four abdominal segments; wing veins whitish and shiny; soft exoskeleton.
	Juvenile	Red to brown coloration on the first four abdominal segments; wing veins black; pterostigma red; hard exoskeleton.
	Adult	Black coloration on the first four abdominal segments on males and androchrome females, brown on gynochrome females; pterostigma blue on males or brown on females.
Acari	None or low	0–5 acari
	Medium	6–20 acari
	High	More than 21 acari

rameters. To check the assumptions of equal recapture and survival probabilities, an overall goodness of fit test was performed using the package "R2ucare" (Gimenez et al., 2017). Finally, as an indirect test of the effect of acari infestation on survival a non-parametric Kruskal-Wallis test was performed to compare the number of acari in each age category expecting that individuals that make it through maturity tend to have less acari.

Other demographic parameters were estimated as follows. For population size, the package "RMark" which estimates the population size for each recapture event was used and 95% confidence intervals were calculated (Laake, 2013). For average life expectancy (l_e) the algorithm proposed by Cook et al. (1967) was used: $l_e = -1/\text{Log}_e\Phi$

Results

The páramo weather allowed sampling for 16 out of the 21 days, and a total of 362 individuals were marked including all age classes. The average survival for the individuals in the population was 0.887 ± 0.040, the average recapture probability was 0.027 ± 0.007, and the average life expectancy was 8.34 days. The population size converged to 730 ± 186.59 individuals after 16 capture events (Supplementary Table 1).

Among the captured individuals, 278 (76.8%) were males and 84 (23.2%) were females (Figure 3a). The differences in survival and recapture probabilities between males and females showed no statistical support since the null model was among the best models according to the AIC scores (Table 2). Of the marked females, 20 (23.8%) were andromorphs and 64 (76.2%) were gynomorphs. (see Figure 3b). Differences in their survival and detectabilities did not show statistical support according to the morphotype since the null model was among the best models according to the AIC scores (Table 2).

Half of the captured individuals had ectoparasitic acari (182 individuals, 50%), 32 of them were females (18%), and 150 were males (82%) (Figure 4a). The average number of acari by male was 10.2 and by female was 9.1. The effect of the number of acari parasitizing the individuals on the survival and recapture probabilities of this population did not have statistical support

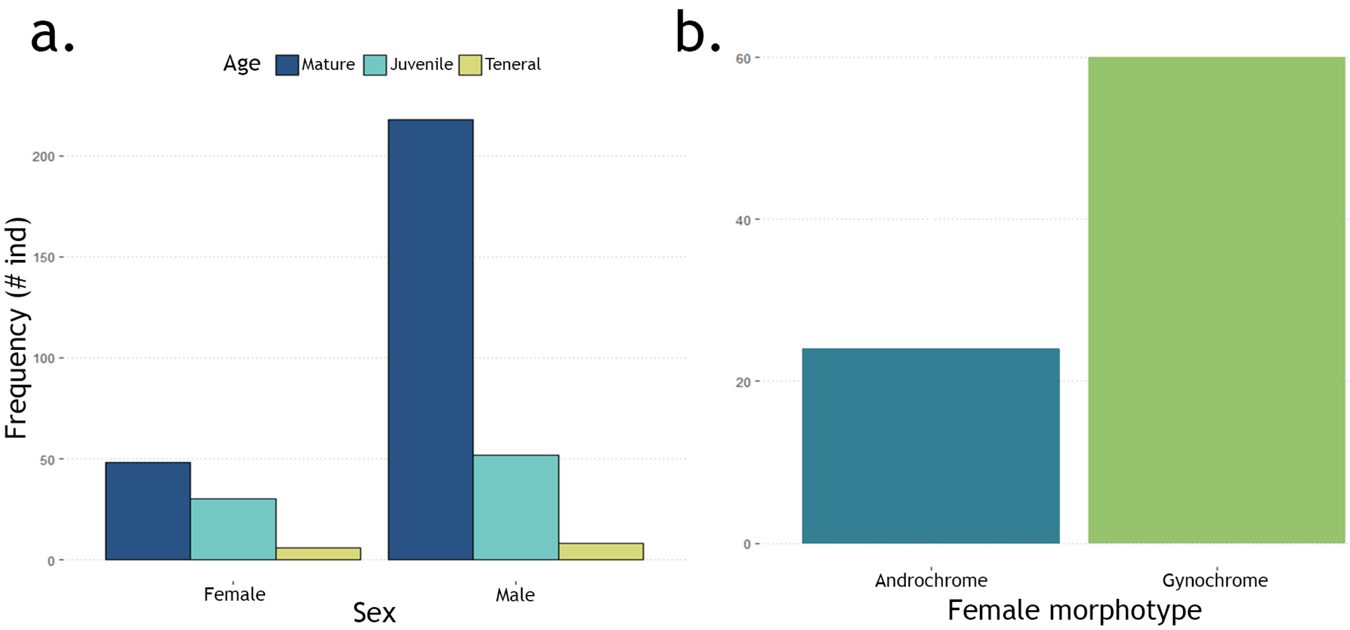

Figure 3. (a) Proportion of captured males and females by age class; (b) proportion of captured females by morphotype.

Table 2. Comark Jolly Seber multimodel analysis. This table shows the assessed models their AIC scores and the number of parameters in each model. Φ: Survival probability; *p*: recapture probability.

Factor	Model	AIC	ΔAIC	Parameters
Sex	Φ(.) *p*(.)	405.1622	0.0000000	2
	Φ(Sex) *p*(Sex)	405.6148	0.4525435	4
	Φ(.) *p*(Sex)	406.3969	1.2346411	3
	Φ(Sex) *p*(.)	407.0007	1.8384350	3
Female morphotype	Φ(.) *p*(.)	405.1622	0.0000000	2
	Φ(Morphotype) *p*(.)	405.8063	0.6440823	4
	Φ(Morphotype) *p*(Morphotype)	407.6311	2.4689176	6
	Φ(.) *p*(Morphotype)	408.1409	2.9786654	4
Acari number	Φ(.) *p*(.)	405.1622	0.000000	2
	Φ(.) *p*(Acari)	408.8231	3.660860	4
	Φ(Acari) *p*(.)	408.9503	3.788082	4
	Φ(Acari) *p*(Acari)	412.1980	7.035728	6

since among the group of best models according to their AIC scores the most parsimonious was the null model (Table 2). On the other hand, a Kruskal-Wallis test on the age of the individuals and acari infestation was performed, showing the age group was significantly related to the number of acari found (χ^2 = 22,50, p < 2,105e-06), with juvenile individuals as the most infested (Figures 4b–c).

The models including differences in survival and recapture probabilities among sexes, among female color morphs, and the ones that include the number of acari as a factor to explain survival or recapture probabilities of the individuals were included among the groups of best models. This indicates a tendency of these factors to affect both survival and recapture probabilities in the population, which could get statistical support with a larger sample size (Table 2).

Natural history notes

Only one pair composed of a mature male and a juvenile gynochrome female was observed in copula during the whole study (Figure 1d). The copula had started when noticed and it was followed for 17 minutes and 24 seconds, when the copula ended, but the pair kept the tandem, then they flew far, and it was lost.

Only one female was observed ovipositing during the whole study, it was an androchrome juvenile female. When first sighted, the male was releasing it from tandem position, the male remained nearby while the female started ovipositing on the base of the grass that was underwater about 1.5 cm below the surface.

A coloration change was observed in the individuals when the weather was cold and the individuals were not active, the body areas which usually have a light blue coloration turned gray (Figure 5), after warming them by holding it in one's hands, they got the normal light blue coloration.

Discussion

High elevation tropical mountain ecosystems are predicted as one of the most vulnerable habitats to global warming. This is because they often have specialist species which have no option of moving to higher and cooler areas when the habitat in which they have evolved heats (Deutsch et al., 2008; Ghalambor et al., 2006; Shah et al., 2017; Sheldon et al., 2018). This is the first population assessment for an odonate specialized on top mountain ecosystems. The estimated survival probability, life span, and population size are fundamental measures for future monitoring toward understanding the effects of climate change on this population and a practical example of the insect response to climate warming in these specialized habitats.

The estimated survival probabilities for *M. gaudiimontanum* (Φ = 0.887 ± 0.04) are similar to the values reported for the family Coenagrionidae (Sanmartín-Villar & Cordero-Rivera, 2022). The closer species whose demography has been studied is *Mesamphiagrion laterale* Selys, 1876, in the Colombian Eastern Andes (Palacino-Rodríguez et al., 2020a). This species occurs through a variety of high mountain habitats, from forest to agriculture-dominated landscapes and the survival probabilities in this population were higher than what we found for *M. gaudiimontanum,* except for the lower survival probabilities found in agriculture landscapes during the dry season (Φ = 0.87) that were very similar to our findings. Probably, this result is related to the extreme environmental conditions present in the paramos, where extensive periods of rain can occur, but also high levels of solar radiation, abrupt changes in temperature, and strong winds, which can affect the survival of individuals (Carvalho et al., 2013; Chang et al., 2007; Mcpeek, 2008).

Infestation by ectoparasitic mites has shown different effects on damselfly populations that tend to negatively affect their fitness (Baker et al., 2008; Dugès, 1834). Flight capacity may decrease when infestation grows, increasing the probability of being detected and diminishing their ability to disperse (Reinhardt, 1996). Likewise, the presence of mites can affect the general condition of the individuals, parasitized males are less likely to accumulate fat affecting their reproductive success (Forbes & Baker, 1990; Gómez-Llano et al., 2020; McPeek, 2008; Siva-Jothy, 2000; Siva-Jothy & Plaistow, 1999), or their reproductive success is reported to diminish but not necessarily the same happens with their lifespans (Andrés & Cordero, 1998), and finally reduction of survivorship have been found in some populations (Åbro, 1982; Robinson, 1983). Our results show no statistical support for *M. gaudiimontanum* survival probability to be negatively affected, probably due to a low sample. On the other hand, we found that mature adults have a lower number of acari, which can indicate low survival in densely-infested juveniles, as reported in other populations (e.g., Åbro, 1982). An equally plausible explanation for this is that acari have drop off naturally, and therefore we did not find them on mature adults, as it was shown by Andrés & Cordero (1998) who did not find effect on recapture probabilities associated to acari infestation. This host–parasite interaction deserves further attention since it could be key to understand the survival probabilities of the *M. gaudiimontanum* population.

Physiological differences among sexes have shown effects on body mass, temperature tolerance, and behavior (Bota-Sierra et al., 2022; Serrano-Meneses et al., 2008). For *M. gaudiimontanum* males are also more colorful than females, therefore we expected differences in survival and recapture probabilities between sexes as found for other coenagrionids (Anholt et al., 2001). This study reports a statistical tendency towards this pattern, but it was not significant even though more than three times as many males were captured compared to females, which could indicate that greater sampling effort is probably required to obtain statistical significance.

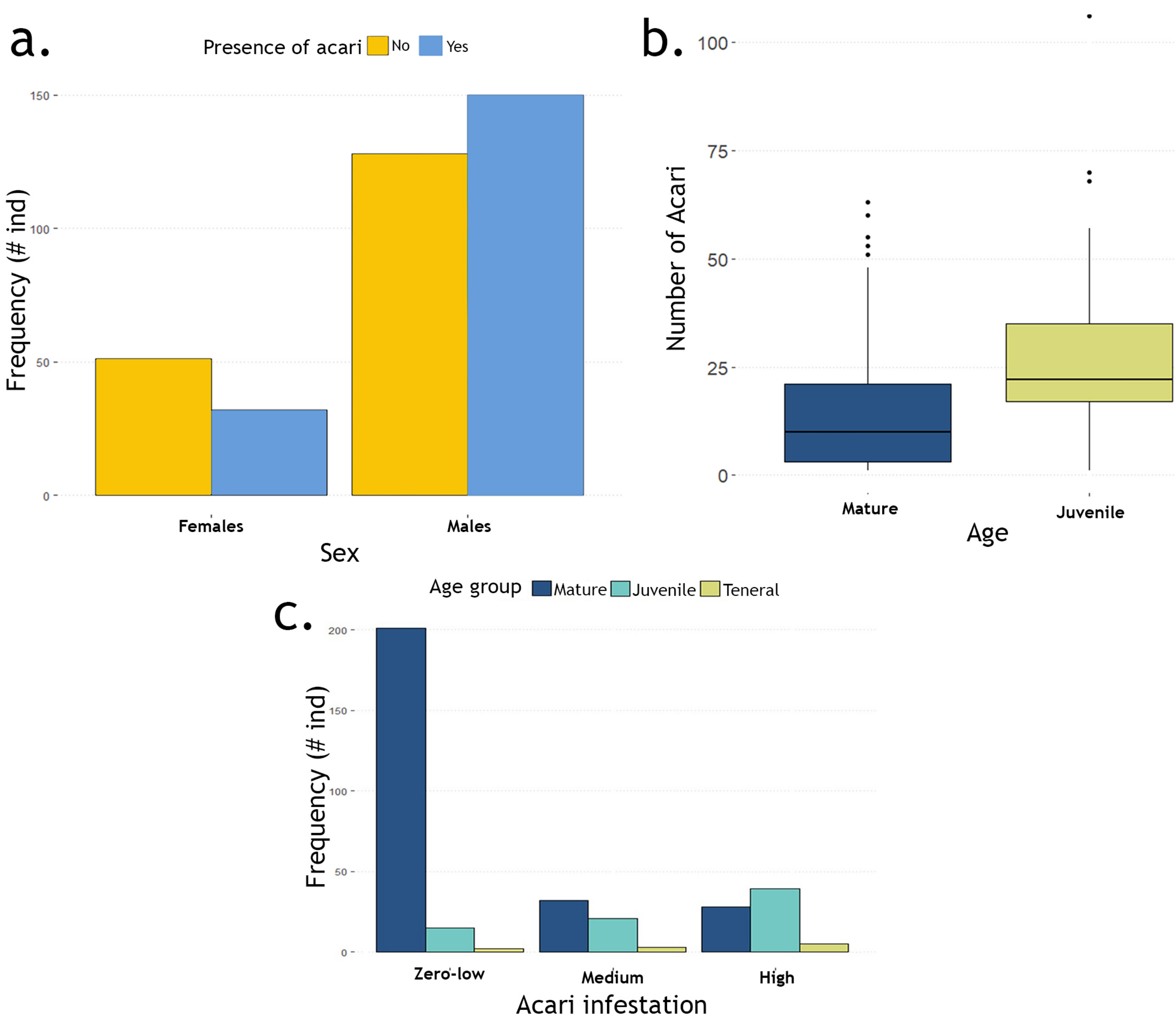

Figure 4. (a) Proportion of captured individuals with ectoparasitic acarii by sex; (b) number of ectoparasitic acari on individuals of different age groups; (c) number of individuals in each age group according to the number of acari on them.

Female polymorphism is one of the most striking population phenomena for Odonata, most of the studies have concentrated on the fecundity differences or the mechanism maintaining the different color morphs (e.g., Fincke, 1994; Svensson et al., 2005). However, its effects on survival and recapture probabilities have been poorly studied due to the high sampling effort that this phenomenon requires (Sanmartín-Villar & Cordero-Rivera, 2022). Studies on *Enallagma* populations had shown no differences in life span between the different female color morphs (Fincke, 1994). We find the proportion of androchrome-gynochrome females is close to 1–3 as reported by Bota-Sierra & Wolff (2013), which is expected if the gene frequency is 50:50 for the genes controlling color morphs with androchrome being recessive (Van Gossum et al., 2008). One of the most accepted hypotheses explaining the evolution of female polymorphism is androchrome females survival will be favored since the mimetism with males will help them avoid sexual harassment while accessing oviposition sites which are usually high-resource habitats (Van Gossum et al., 2008). On the other hand, gynochrome females are more cryptic against vegetation (Schultz & Fincke, 2013). In some studies harassment rates were no different between female morphs (Fincke, 2015; Piersanti et al., 2021; Rebora et al., 2018), our findings support this pattern, nevertheless, there is a statistical tendency pointing to differences in survival and recapture probabilities between female morphs, but as stated by Sanmartín-Villar & Cordero-Rivera (2022) our sample was low to have statistically supported results.

Figure 5. Male individual showing the change in coloration from regular light blue to gray when the weather is cold, notice the ectoparasitic acari on the ventral base of the abdomen. Picture: Alejandro Hoyos.

It is important to note that copulation has only been documented on three occasions for this species, and juvenile females have been found in these events (Bota-Sierra, personal data). This difficulty in finding copulating individuals, reduced competition, and age of the females could resemble a monandrous reproduction syndrome scenario (Cordero & Andrés, 1996; Robinson & Allgeyer, 1996; Sánchez-Guillén et al., 2020), wherein a single copulation event, females can fertilize all their eggs during their life cycle and actively reject males after this. This phenomenon has been observed in some species of the Coenagrionidae family (Cordero, 1990; Cordero-Rivera et al., 2023; Fincke, 1987), although in *M. laterale,* the only congener whose reproductive behavior has been studied, the tandem pairs were frequently observed and both mature and juvenile females were part of copulating pairs (Palacino-Rodríguez et al., 2020b). The advantages and disadvantages of this model may be related to male harassment, especially in terms of survival, which can be diminished by very extensive copulations, increasing the time they can spend in foraging and egg maturation, but in contrast, there would be reduced genetic variability. Because only one copulation event was obtained during the entire sampling, it is impossible to resolve this question at present, but in future monitoring a more specialized experimental design could be considered, including the number of ovipositions per female, copulation duration, and longevity of females.

Reversible color change has been observed mainly in aeshnids (Sternberg, 1987), but also in some coenagrionids (May, 1976; Sanmartín-Villar et al., 2017). This is the first record of color change with temperature in the genus *Mesamphiagrion.* Color change in odonates is a mechanism that has been reported for several species, where at temperatures between 4 and 10° Celsius the bright colors in the body of the individuals become more opaque, taking on grayish and brown tones (May, 1976, 1998). These coloration changes are reversible when temperature increases, they are mediated by various mechanisms related to chromatophores, and their main function is probably related to thermoregulation since these pigments are useful for absorbing the greatest amount of energy in unfavorable climatic and lighting conditions (May, 1976; Okude & Futahashi, 2021). Another possible explanation for this coloration change is camouflage, during the rainy season in the páramo ecosystems cloudy weather can persist for weeks, so camouflage probably enhances individual survival during these long inactive times. Although we only observed coloration change in male specimens, it is expected both sexes will display this coloration change.

All these findings lay the foundation for population monitoring and conservation programs for this species whose survival is probably endangered by climate change and has several interesting population dynamics and adaptations to the harsh environmental conditions at the top of the tropical mountains. Hopefully, new studies will come with a bigger sampling effort at páramo ecosystems which will allow solving several of the questions that remain open after this study.

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Supplementary Material

Supplementary Material 1. Estimated population size values after each capture event.