Cooler and drier conditions increase parasitism in subtropical damselfly populations

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Abstract

Host-parasite interactions are impacted by climate, which may result variation of parasitism across landscapes and time. Understanding how parasitism varies across these spatio-temporal scales is crucial to predicting how organism will respond to and cope under a rapidly changing climate. Empirical work on how parasitism varies across climates is limited. Here, we examine the variation of parasitism across seasons and identify the likely climatic factors that explain this variation using *Agriocnemis femina* damselflies and *Arrenurus* water mite ectoparasites as host-parasite study system. We assessed parasitism in a natural population in a subtropical climate between 2021-2023 and calculated prevalence (percentage of infected individuals) and intensity (the number of parasites on an infected individual) of parasitism across different seasons. Parasite prevalence and intensity were greater during cooler seasons (autumn and winter) compared to hotter seasons (spring and summer). Mean temperature and precipitation were negatively correlated with parasite prevalence whereas only mean precipitation was negatively correlated with parasite intensity. Tropical, Subtropical and Mediterranean countries are predicted to experience extreme climatic events (extreme temperature, less precipitation and frequent drought) as a consequence of anthropogenic climate change, and our finding suggests that this could increase parasitism in aquatic insects.

Introduction

Host-pathogen interactions are impacted by the environment in which they occur (1,2). Local climate such as temperature, precipitation, as well as resource availability, predator-prey interactions impact hosts immunity as well as pathogen virulence (3–5). Consequently, the outcome of host-pathogen interactions, i.e., infections, varies across different climatic conditions. For example, in *Eulamprus quoyii* lizard, parasite intensity was greater in tropical climate compared to temperate climate (6). Similar to latitudinal variation, parasitism also varies across seasons mostly driven by the variation of temperature (4,7). For example, in fire ant (*Solenopsis invicta*) parasite infections were greater in in summer (8). Seasonal changes in rainfall, on the other hand, is the strongest predictor of parasite infection in aquatic and semi-aquatic organism (9,10). For example, in freshwater snails (e.g. *Elimia proxima*), and fish (e.g. *Hoplias malabaricus* and *Cirrhinus mrigala*) parasitism was negatively related to precipitation (9–11). How parasitism varies across season and what climatic factors drive parasitism in aquatic and semi-aquatic insects, is however less understood primarily because studies focus on northern hemisphere temperate populations where insects are active only for a shorter period.

Damselflies (Odonata: Insecta) are semi-aquatic insects with an aquatic larval stage and a terrestrial adult stage. They are frequently parasitised by *Arrenurus* water mites that externally attach to their body and wings (12,13). The extent of parasitism varies between sexes, developmental stages, and in different climates (5,12). For instance, ectoparasite prevalence and intensity in odonates were greater in temperate climates compared to boreal climates of the Northern Hemisphere (5). Studies on parasitism in damselflies across season are limited, with one of the few studies reporting that the extent of ectoparasitism in *Coenagrion puella* was greater at the start of the season (May) compared to the end (August) with temperature not associated with this variation (4). It is noteworthy that there is a significant knowledge gap about damselfly parasitism in tropical regions (14). Until now, most of the studies on parasitism in damselflies have been focused on temperate populations where the flight season is very short and variations of climatic factors are limited (14). Moreover, tropical insects (e.g. damselfly) are more vulnerable to climate change than temperate insects, therefore, understanding the influence of tropical seasons and identifying the climatic drivers in damselflies parasitism is of high priority to predict how climate change will affect damselfly-parasite interaction (15).

Our study aims to understand the pattern and driver of the seasonal variation of parasitism *Agriocnemis femina* damselflies. We studied the ectoparasite water mite infection in natural population in north-eastern Bangladesh, where these damselflies are active throughout a year. Based on previous studies in the Northern Hemisphere, we predict that 1) parasitism will vary over the season, 2) parasitism will be greatest in summer when temperatures are higher, and 3) will also be lower when precipitation is high.

Methods and materials

Study system

Agriocnemis femina (Coenagrionidae) is the one of the smallest damselflies (wing length: 10.5-11.00 mm) and is distributed in South Asia, South-East Asia, and Australia (16–18) (Fig S1). This species is commonly found in water body (ponds, lakes, rivers) associated grasslands. Female *Agriocnemis femina* exhibit ontogenetic colour change from red to green which signals sexual maturity (19). *Agriocnemis femina* is one of the most common species in the north-eastern region of Bangladesh and can be seen in flight all year round (17). In the natural population, this species is parasitised by *Arrenurus* water mites (12) that initially colonise the aquatic larvae and then shift to the adult during damselfly metamorphosis where they commence the parasitic phase (20), imposing considerable fitness costs on the host (13,21).

Study site

We surveyed parasitism in *Agriocnemis femina* damselflies in the north-eastern region of Bangladesh in a natural population located on the campus of Shahjalal University of Science and Technology, Bangladesh. Spring and summers are hot (average spring and summer temperature: 25.8°C, and 28.25°C respectively) with high rainfall (average spring and summer rainfall: 328.6 mm, and 695.3 mm respectively) (22). Autumn and winter are comparatively colder (average autumn and winter temperature: 25.8°C, and 18.5°C respectively) and experience less rainfall (average autumn and winter rainfall: 244.3 mm, and 21.5 mm) (22).

We surveyed the study site every month from March 2021 to February 2023 (except in July 2021, because of national lockdown, from February-June, and September-October 2022 due to temporary road closure to access the study area). No permits were required as *Agriocnemis femina* is not a protected species and the field site is protected.

Parasite prevalence and intensity

We captured damselflies with insect catching nets (dimensions: 1260mm handle, 456mm diameter hoop, 81cm long net bag) while walking along the edge of water and grasslands. For every captured individual, we recorded their sex (male and female), and the developmental stage of females (immature females are red and mature females are green) while male developmental status cannot be determined precisely under field conditions (12,19). We examined the damselfly's dorsal and ventral thorax, and abdomen for parasites and if present, counted the number of parasites. To prevent recapture, we marked their wings with a permanent marker and released them back into the population. We conducted the fieldwork between 08:00 and 10:00 hours when the species are mostly active, and condition are favorable for field work (MKK and SP personal observations).

Bioclimatic factors

We collected monthly data for temperature and precipitation for 2021-2023 from Bangladesh Meteorological Department (BMD) and calculated monthly average temperature (°C) and precipitation (mm) for each month that we surveyed the population (23).

Statistical analyses

We calculated parasite prevalence and intensity in damselflies and applied DurgaDiff function of Durga package to determine difference of parasite prevalence and parasite intensity between seasons (24). We applied a generalized linear mixed models (GLMMs) to identify the effect of temperature and precipitation on parasite prevalence and intensity. We fitted GLMM model with parasite prevalence as response variable, temperature and precipitation as fixed effects, and sampling year as random factor. We further applied generalized linear model (GLM) with a quasipoisson distribution with parasite intensity as response variable and temperature and precipitation as response variables. We analysed all data in R version 4.0.3 (25) using packages “lme 4” (26), “MuMIn” (27), “performance (28)” and “Durga” (24).

Results

A total of 2846 individuals of *Agriocnemis femina* were observed of which 10.6% were parasitised (Table S1, Supplementary file). Parasite prevalence was highest in winter (17.3%) and lowest in summer (4.5%). On average a parasitised individual had three parasites (range: 1-19). Parasite intensity was greatest in autumn (3.10 parasites/damselfly) and lowest in spring (1.92 parasites/damselfly).

Parasite prevalence was greater in winter compared to spring (mean difference = 0.166, 95% CI [0.053, 0.304]; Fig 1a) and summer (mean difference = 0.167, 95% CI [0.050, 0.295]; Fig 1a). But parasitism did not differ between winter and autumn (mean difference = 0.010, 95% CI [-0.144, 0.193]; Fig 1a). Parasite intensity was higher in autumn compared to spring (mean difference = 1.180, 95% CI [0.634, 1.839]; Fig 1b) and summer (mean difference = 0.970, 95% CI [-0.532, 1.745]; Fig 1b), but there was no difference in parasite intensity between autumn and winter (mean difference = 0.392, 95% CI [-0.187, 1.071]; Fig 1b).

Parasite prevalence was negatively related to monthly temperature (GLMM: estimate = -0.391 ± 0.089, z = -4.375, $P < 0.00001$; $R^2 = 0.098$; Fig 2a) and mean monthly precipitation (GLMM: estimate = -0.475 ± 0.110, z = -4.320, $P < 0.00001$; $R^2 = 0.098$; Fig 2b). Parasite intensity was negatively correlated only with precipitation, (GLM: estimate = -0.303 ± 0.126, t = -2.398, P =

0.017; $R^2 = 0.050$; Fig 2d) but not with temperature (GLM: estimate = 0.051 ± 0.074, t = 0.692, P = 0.489; $R^2 = 0.050$; Fig 2c).

Discussion

Climatic variables, such as temperature or precipitation influence insect physiology, and host-pathogen interactions which might result in differential level of parasitism across seasons (29–33). In this study, we provided strong evidence that water mite prevalence and intensity in damselflies vary across seasons, with higher rates of infection occurring during cooler months (winter and autumn) compared to hotter months (spring and summer). We further showed that, mean temperature and rainfall were negatively related with parasite prevalence, whereas mean precipitation was negatively related with parasite intensity.

The higher prevalence and intensity of parasitism in autumn and winter months compared to spring and summer could stem from increased susceptibility of damselflies to parasitic infections (34,35). Larval growth rate (36) and development time are longer in colder months compared to warmer months (37–39). Furthermore, both larvae and adult damselflies are less active when temperature is low (36). The longer larval period and reduced mobility might increase exposure of damselflies to parasites (40,41). Consequently, water mites might have more time to find a host and engorge (42) thereby increasing parasitism in colder months (41,42).

On the other hand, hotter seasons (summer and spring) with high temperature provides an ideal habitat condition for the development of invertebrates including damselflies and water mites (43). However, we observed water mite parasitism is lower at higher temperature. Damselflies mount a greater immune response (encapsulation rate) to infection at higher temperatures which could further reduce parasitism in summer and spring (34). Accordingly, parasitism in *Coenagrion puella* damselflies was lower in warmer seasons compared to the cooler seasons (4).

The lower rate of parasitism in spring and summer compared to winter could arise because of the impact of the subtropical monsoon in the northeast region of Bangladesh which brings heavy rainfall (on average 695.33 mm during wet and hot summer months) (22). Additionally, our low altitude study area (altitude = 10m), receives water from the adjacent Meghalaya Hills (altitude = 1961m), which often experience one of the highest average rainfalls around the world (44–46). As a consequence the study area frequently floods (46). We argue that the flash flooding probably diluted the density of water mites in the small ponds similar to a previous study that observed water mite abundance in the tropical river Ganga was greater in winter months compared to monsoon months (47). Similarly, lower parasitism during high rainfall was also recorded in other aquatic and semi-aquatic organisms such as in fish (*Cirrhinus mrigala*) and in snail (*Elimia proxima*) (9,10). Conversely, reduced precipitation probably increases parasitism by increasing damselflies susceptibility and also by increasing the concentration of water mites in ponds (48,49).

Our study provide evidence that parasitism in subtropical climate increases during cooler and drier seasons. Our subtropical study has relatively less fluctuation of climatic factors across seasons. Under ongoing anthropogenic climate change, Tropical, Subtropical, and Mediterranean regions are expected to experience climatic extremes, and seasonal instability which could stress insects such as damselflies, making them vulnerable, which may further be advantageous for their parasites (50–52). Therefore, we predict that parasitism might increase in aquatic and semi-aquatic insects especially in Tropical, Subtropical, and Mediterranean regions. Odonates with lentic habitats are more threatened than odonates with lotic habitat because climate change induced varying temperature and rainfall patterns e.g. arid conditions may cause habitat loss in lentic odonates more quickly (53). Our study highlights that, in addition to habitat loss, climate change induced increase in parasitism might further exacerbate odonates fitness and contribute to local extinctions– a research avenue in need of further attention.

Statement of diversity and inclusion

We believe and support equity, diversity, and inclusion in science and everywhere. The authors come from different nationalities and cultural backgrounds (Bangladesh, Austria, and Australia) They represent different career stages (Masters student, Early career researcher, and Professor). One or more of the authors self-identifies as a member of the LGBTQI+ community and represents ethnic as well as religious minority in science. We actively maintained gender balance while citing scientific articles.

Acknowledgment

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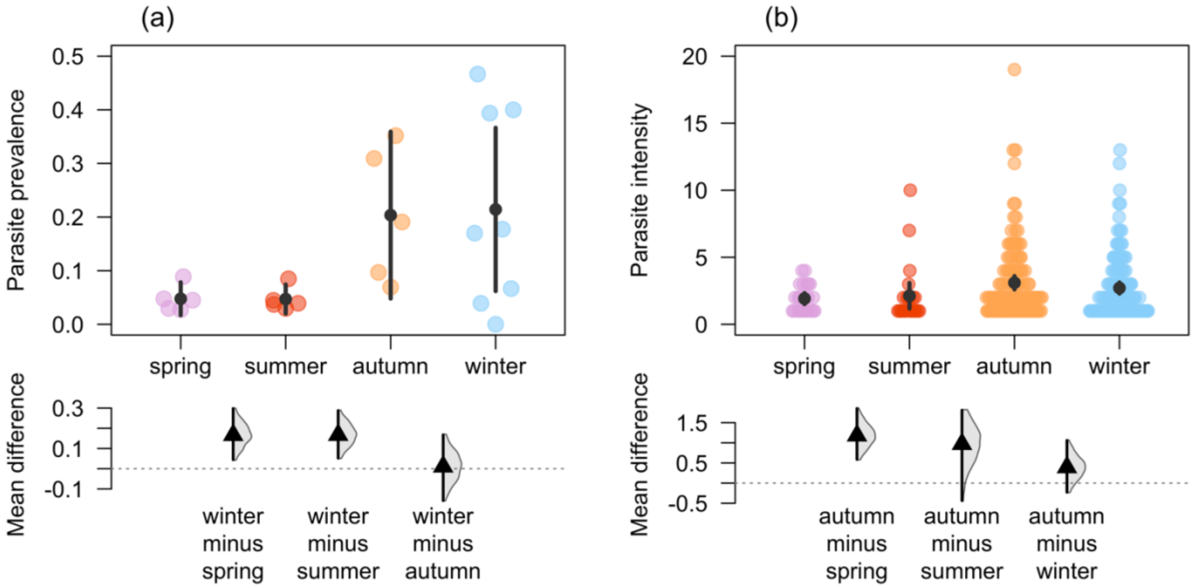

Fig 1. Seasonal variation of parasite prevalence and intensity in *Agriocnemis femina* damselflies. (a) Parasite prevalence and (b) parasite intensity across four seasons. Each circle in (a) represents a sampling event and in (b) represents a parasitised damselfly. The effect size (mean differences) in parasite prevalence and in parasite intensity between seasons are shown in the lower panel.

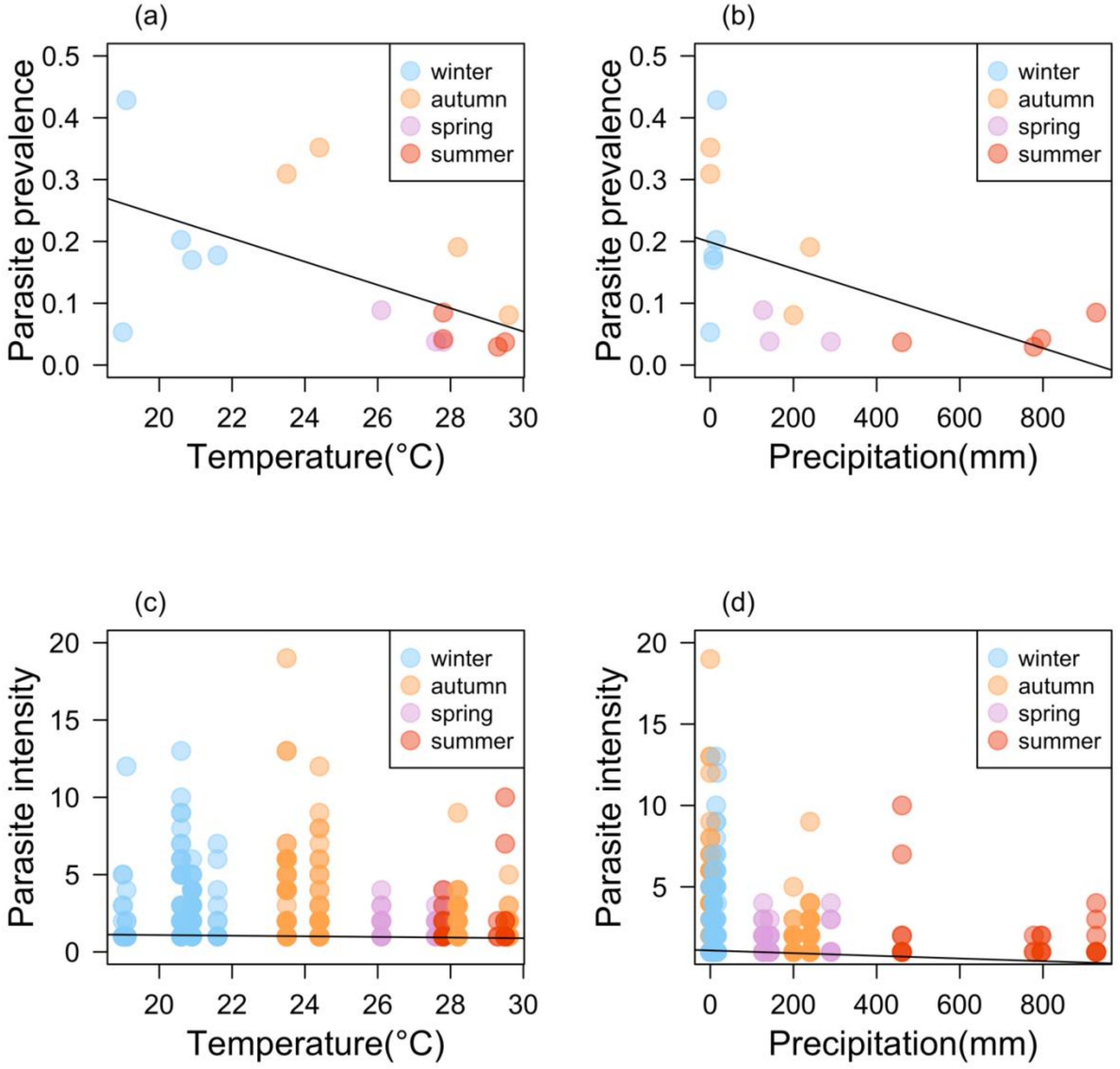

Fig 2. Correlation of parasite prevalence and intensity with temperature and precipitation in *Agriocnemis femina* damselflies. Correlation of parasite prevalence with mean monthly temperature (a) and mean monthly precipitation (b) Correlation of parasite intensity with mean monthly temperature (c) and mean monthly precipitation (d) Each circle in (a) and (b) represents a sampling event and in (c) and (d) represents a parasitised damselfly. The fitted lines in each figure represent overall trend of data points.