TITLE: How do wildfires influence reproductive behavior and mating dynamics? A case study with dragonflies

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AUTHORS: Sarah E. Nalley, Michael P. Moore, Ph.D. (Principal Investigator)

AFFILIATION: Department of Integrative Biology, University of Colorado Denver

EMAIL: sarah.nalley@ucdenver.edu; michael.p.moore@ucdenver.edu

EXECUTIVE SUMMARY

Wildfires are reshaping the American West—devastating people's homes and transforming wildlife habitats. Although recent research has documented traits that animal species need to survive in the aftermath of a wildfire, little is known about how wildfires affect mating interactions or what traits are necessary for successful reproduction in burned habitats.

We are investigating how wildfires affect the mating dynamics of dragonflies, including at sites in BCPOS. Among wildfire's major impacts are altered trophic webs, and reduced food resources in burned areas could constrain dragonflies' energetically demanding mating behaviors. Additionally, post-fire habitats are left warmer and drier, conditions to which ectothermic dragonflies' mating behaviors are highly sensitive. Some species' reproductively advantageous melanin wing patches absorb solar radiation that exacerbates thermal stress.

Our 2023 research indicates that dragonfly mating behaviors are disrupted at burned sites. In 2024, we explored how wildfires alter dragonfly breeding habitat and their morphological and physiological traits. Our team collected thermal and phenotypic data at 5 burned and 4 unburned sites across 3 wildfire areas in Colorado and Wyoming. Data analysis is ongoing, but initial results show that burned habitats are warmer on average than unburned, yet dragonfly body condition does not differ between habitat types. These findings indicate that dragonfly mating dynamics are constrained by post-wildfire thermal environments rather than limited food resources. While in the early phases, our research highlights several implications:

- *Animal populations rely on both survival and mating, and thermal constraints in post-wildfire habitats may disrupt mating more than nutritional limitations.*
- *Some species' traits will make them especially prone to mating disruptions after a fire.*
- *Post-fire habitats should be managed for the thermohydric conditions where species breed.*

ABSTRACT

Wildfires are dramatically altering the habitats of the American West, defoliating the landscape and leaving warmer and drier environments in their wake. Extensive research has detailed animal survival in burned habitats, but far less is known about how post-wildfire conditions affect mating. Dragonflies are ideal for exploring this topic due to their energetically demanding and thermally sensitive mating behaviors, and the presence of melanin wing patches that are critical for mating but amplify thermal stress by absorbing solar radiation. Our 2023 research revealed that wildfire disrupts dragonfly mating behavior. To investigate the underlying causes and potential consequences of these disruptions, we addressed two questions: 1) How do wildfires alter dragonfly breeding habitats? We hypothesized that temperatures are higher on average in burned habitats. 2) How do wildfires alter dragonfly morphological and physiological traits? We hypothesized that food limitation results in poorer body condition in burned sites than unburned sites.

In 2024, we collected thermal data and measured dragonfly phenotypic traits at 5 burned and 4 unburned sites across Colorado and Wyoming, including 3 burned and 2 unburned sites in Boulder County Parks and Open Space (BCPOS). Preliminary analyses show that burned habitats are hotter than unburned habitats, but dragonfly body condition did not differ between the site types. These findings suggest that the thermal impacts, rather than nutritional deficits, alter dragonfly mating dynamics in burned habitats. To further understand wildfire impacts on animal populations, we will analyze 2024 wing ornamentation data to identify reproductive traits that increase species vulnerability in burned habitats, as well as explore how post-wildfire environments dictate the traits required for successful mating. Our continued and future research aims to inform the development of targeted post-wildfire management strategies.

Keywords: Global change; wildfire; evolutionary ecology; sexual selection; wildlife biology; Anisoptera; odonates

INTRODUCTION

Anthropogenic activity is reshaping our planet, driving global environmental shifts and expanding the occurrence, frequency, and intensity of extreme climate events. The increasingly common and intense wildfires across the American West and here in Colorado are a prime example of these changes (Westerling et al. 2006, Marlon et al. 2012, Balch et al. 2017)—devastating the homes and livelihoods of our state's citizens and transforming the habitats of our valued plants and animals. These wildfires drive complex ecological changes, including altered trophic dynamics (Harris et al. 2018, McLaughlin et al. 2022, Preston et al. 2023) and exposure to environmental extremes (Wolf et al. 2021, de Sousa et al. 2023, Shrestha et al. 2024). Research shows that post-wildfire habitat alterations can be so severe that only species with specialized traits can survive in the hotter and drier conditions left in their wake (Nimmo et al. 2021, Bieber et al. 2023). However, animals often also need specialized traits to be able to successfully attract mates and reproduce in hotter and drier habitats (Leith et al. 2022), raising the possibility that a species' ability to persist in the aftermath of wildfire might also require unique specialized reproductive characteristics (Moore et al. 2024). Nonetheless, we know almost nothing about whether or how a species' mating dynamics are altered by wildfire, nor how mating-related traits influence a species' ability to reproduce in those habitats. Since the health of animal populations depends on both survival and reproduction, conservation and management efforts need to know how reproductive traits affect a species' ability to live in habitats that have experienced a wildfire.

To study wildfire's impacts on animal mating dynamics, we are using dragonflies as a model organism. Dragonflies are a classic system in behavioral research for studying animal mating interactions, and their behaviors lend themselves well to this research. In dragonfly mating systems, males typically engage in complex behaviors like territorial guarding and aerial battles at ponds, fiercely competing for access to females and defending reproductive territories where mating and egg-laying occur (Corbet 1999). While females primarily spend their time foraging in less environmentally stressful environments, dragonfly males' daily energy budgets are largely spent on activities related to mating, including the extremely metabolically-taxing territorial battles, at the pond (Fried and May 1983, Corbet 1999). As ectotherms, these reproductive behaviors are highly sensitive to rising environmental temperature (Moore et al. 2019, Leith et al. 2021), like those that accompany a habitat ravaged by wildfire (Bollenbacher et al. 2014, Elmore et al. 2017). The heating of habitats beyond species' optimal performance temperatures leads to dramatic reductions in their ability to fly and perform these essential behaviors (Kingsolver et al. 2013, Moore et al. 2019). Moreover, the primary mating-related trait of many dragonfly species is melanin wing ornamentation, which enhances mating displays yet carries substantial thermal consequences (Moore 1990, Corbet 1999, Moore et al. 2019, 2021, Hersch and Moore 2023). Larger patches of melanin wing ornamentation are advantageous for attracting mates and intimidating rivals (Moore 1990, Moore and Martin 2016). However, because the solar radiation absorbed by dark pigmentation also can heat individuals, larger melanin ornaments exacerbate thermal stress and can lead to dangerous levels of overheating in warm habitats (Svensson and Waller 2013, Moore et al. 2019, Laakso et al. 2021). Despite the significant mating advantage that ornaments confer, males possess less ornamentation in warmer habitats, and ornamentation across North America is decreasing as our planet warms (Moore et al. 2021). Preliminary results from Boulder County and other field sites in 2023 show that, indeed, the mating dynamics of ornamented species have been particularly disrupted in areas affected by recent wildfires.

To determine what consequences these mating disruptions may have for the ecological and/or evolutionary dynamics of ornamented dragonflies, we measured the physiology, behavior, and ecology of dragonflies at ponds following a wildfire in the Southern Rocky Mountain region of Colorado and Wyoming with 2024 permits from multiple local and federal agencies, including the Boulder County Parks and Open Space (BCPOS) system. Our work in 2024 had three objectives:

1) How do wildfires alter the characteristics of the breeding habitats of dragonflies?

After finding in 2023 that wildfires disrupt the mating dynamics of dragonflies, we aimed to characterize reproductively relevant habitat characteristics of the burned and unburned sites. Because warmer breeding habitats can cause dragonflies to overheat and impede their mating dynamics (May 1977; Marcellino et al. 2024), we tested if burned breeding habitats tend to be warmer than unburned breeding habitats.

2) How do wildfires alter the morphological and physiological traits of breeding dragonflies?

After finding in 2023 that wildfires disrupt dragonfly mating dynamics, we sought to test two hypotheses about the morphological and physiological traits of breeding dragonflies. First, because a lack of energy is one factor that disrupts dragonfly mating dynamics (Fried and May 1983), we hypothesized that reproductive dragonflies may be food-limited in post-fire habitats. Here, we tested if dragonflies breeding in burned habitats possess poorer “body condition”—a proxy of nutritional status in animals (Jakob et al. 1996, Stevenson and Woods 2006) whereby individuals that weigh less compared to their size are in “poor condition”. Second, because the mating dynamics of ornamented dragonflies seem to suffer more than those of non-ornamented dragonflies, we hypothesized that populations of ornamented species may be losing their ornamentation in burned habitats. Here, we tested if the populations of ornamented species in burned sites possess less ornamentation than their counterparts in unburned sites.

3) Do disruptions to mating in burned habitats alter dragonfly population dynamics?

Finally, because our 2023 results showed that ornamented dragonflies have disrupted mating dynamics in burned habitats, we aimed to determine if the populations of ornamented species are also being disrupted. Here, our goal was to test if fewer adults from ornamented species are recruiting into the population in burned sites compared to unburned sites. Due to time constraints, we were not able to accomplish this goal.

METHODS

Overview

At nine sites in Colorado and Wyoming that had been burned by wildfires that occurred since 2020 ("burned") or had not ("unburned), we measured several key morphological and physiological traits of dragonflies as well as the habitat characteristics of the sites. Sites were selected based on a combination of ecological factors, wildfire impact, and accessibility. Over 20 observation days in the summer of 2024, our approach focused on recording site temperatures and other habitat characteristics, as well as capturing, photographing, and releasing male and female dragonflies in their breeding habitats. This method allows for an analysis of the effects of wildfires on dragonfly reproductive habitat and physiology.

Field Sites

Field observations were conducted in the Rocky Mountain region of Colorado and Wyoming at ponds in unburned (n = 5) and burned sites (n = 6) within the perimeters of four recent wildfires (Fig. 1): the Calwood Fire (2020; Lat/Long: 40.14324, -105.30038; 4,092.56 ha burned; Fig. 2), Cameron Peak Fire (2020; Lat/Long: 40.58796, -105.84993; 84,544.09 ha burned), and Mullen Fire (2020; Lat/Long: 41.10152, -106.10349; 71,579.99 ha burned). All sites were required to be on permitted land and safely accessible. Since the Southern Rocky Mountain region has experienced many recent fires, we selected sites across different wildfires whose landscapes would have had similar recovery times. Burned sites within the wildfire perimeters were then chosen based on burn severity, with all levels of severity represented (MTBS Project [USDA Forest Service/U.S. Geological Survey] 2017). Unburned sites were chosen based on proximity and similar ecoregion to a paired burned site.

Boulder County Parks and Open Space Field Sites

In Boulder County Parks and Open Space, research was conducted at 5 sites from 10:00-16:00 MDT over 9 days (Table 1). Three burned sites were located within the Calwood Fire Perimeter on Heil Valley Ranch: 1) Frog Pond; 2) Ponderosa Loop Pond; and 3) the Quarry. The two unburned sites included: 1) the “Meadow” pond on Heil Valley Ranch; and 2) Mud Lake (Fig. 1).

Dragonfly research was conducted at all five BCPOS ponds in 2023, but in July and August of 2024, Frog Pond and Ponderosa Loop were completely dry, and the “Meadow” was nearly dry. No dragonflies were captured or measured at these sites as only a few individuals of one species were observed at some of the ponds on one day, but temperature loggers were deployed at these sites over multiple research days. Both thermal and dragonfly measurements were recorded at the burned Quarry site and unburned Mud Lake site.

Objective 1) How do wildfires alter the characteristics of the breeding habitats of dragonflies?

Field Methods: Each day, one of the nine sites was selected based on weather conditions and the number of prior visits. A site was excluded if there was a high chance of rain, temperatures below 20°C for most of the day, or any risk of flash flooding at burned sites (US Department of Commerce 2024). Upon arrival, the researcher deployed four to six HOBO thermal data loggers at distinct locations within dragonfly territory around the pond. Loggers were not deployed in or touching water to avoid contamination and were collected at the end of each research day.

Statistical Analyses: We compared the average temperatures between burned and unburned habitats using linear-mixed effects models. We included each temperature measurement from the data loggers as the response variable and site type (burned vs unburned) as a fixed effect. As random effects, we included: substrate type (e.g. rock, ground, log), to account for the different thermal properties of substrate on which the logger was placed; wildfire identity, to account for differences in other general conditions (e.g. overall climate) among the Calwood, Cameron Peak, and Mullen Fires; hour of the day, to control for temporal differences in temperature throughout the observation period; and date of observation, to control for non-independence of temperature measurements taken on the same day.

Objective 2) How do wildfires alter the morphological and physiological traits of breeding dragonflies?

Field Methods: Dragonfly collection and field measurements were conducted by one person (SEN) at each site from 10:00-16:00 MDT (Moore and Martin 2016). Dragonflies were captured using an aerial insect net, placed into individual Ziploc bags, and stored in a soft-sided cooler on ice for no more than one and a half hours (McCauley 2010, Moore and Martin 2016). These methods reduce dragonfly activity, allowing for safe handling during processing and release. After cooling, individuals were weighed (mg) using a Fisher™ portable scale. They were then placed in a lightbox on a white background (DGK Color Tools®) to standardize lighting conditions and photographed (Fig. 3) using a Canon Rebel T7 DSLR. A Fisher™ ruler was set on the white background for standardized body length measurements. After an individual was processed, it was released approximately 10 meters from the pond.

Species were identified using photographic field guides (Paulson 2009, Cooper 2014). We used ImageJ software to quantify body length and wing traits (Fig. 4). The ruler in each photograph was used to set the scale for measuring body length (mm) from the proximal point of the head to the cerci tips. For wing metrics, the width of the widest part of a dragonfly's head was used for scale as a relative measurement unit. The right wings were measured unless significantly damaged, in which case the left wings were used. We manually traced the forewing, hindwing, and melanin spots on each wing to measure area. Total wing area was calculated as the combined fore- and hindwing area and proportion melanized area was calculated as the combined melanized area of both wings divided by the total wing area (Moore and Martin 2016).

Statistical Analyses: We are still in the process of analyzing the large amount of morphological and physiological data that was collected.

One set of preliminary analyses that we have conducted examined the differences in body condition between burned and unburned sites. Body condition serves as a proxy for an animal's nutritional state, with individuals considered to be in "poor condition" when their weight is lower than expected for their size (Jakob et al. 1996, Stevenson and Woods 2006). In these analyses, we examined if males from burned sites were lighter relative to their body length compared to their counterparts in unburned sites (Jakob et al. 1996). Here, we conducted separate analyses for each species that had at least five measurements in both burned and unburned sites. In these statistical models, ln-transformed body mass was the response variable, ln-transformed body length was a continuous fixed effect, habitat type (burned vs unburned) was a categorical fixed effect, and their interaction was included as a third fixed effect. We included wildfire identify as a random effect to control for any other general environmental differences among the locations of the fires (e.g. climate, elevation).

We have not finished our male ornamentation measurements, and we therefore have not yet conducted any analyses on this trait.

RESULTS

Species Observed

Across all nine sites, 25 dragonfly species were observed in total (Fig. 5). No species occurred at every site, but the most commonly observed species were the variable darner (*Aeshna interrupta* - 5 sites), the four-spotted skimmer (*Libellula quadrimaculata* - 5 sites), and the cherry-faced meadowhawk (*Sympetrum internum* – 5 sites).

At the five sites in BCPOS, 21 dragonfly species were confirmed present. At the Mud Lake and Quarry sites, all species observed in 2023 were observed in 2024, along with an additional eight species at Mud Lake and 9 species at the Quarry. Other animal species present at each site were also documented by the researcher for BCPOS management (Table 1).

Objective 1) How do wildfires alter the characteristics of the breeding habitats of dragonflies?

In 2024, we logged 13,635 thermal measurements (Fig. 6). Our preliminary analyses indicate that the focal burned sites were 6.88 ± 0.38°C warmer than our focal unburned sites (95% CIs: 6.14 to 7.62°C; $t = 18.27$, $P < 0.001$).

Objective 2) How do wildfires alter the morphological and physiological traits of breeding dragonflies?

In 2024, we captured 338 dragonflies across all of our field sites, including 114 in BCPOS (Table 2). We are still in the process of making measurements and analyzing the data for both body condition and ornamentation. However, we have some early analyses we can report.

Our analyses indicate that the body condition of reproductively active dragonflies does not differ between the burned and unburned habitats. For three species that were abundant and captured in both the burned and unburned sites, adults from burned sites were not in poorer condition than those in unburned sites (Table 3; Fig. 7).

We next plan to analyze the total wing area between burned and unburned habitats for ornamented vs non-ornamented species, the proportion of melanized area for ornamented species between habitat types, and finalize our analyses of thermal and spectral site characteristics in 2023 and 2024.

DISCUSSION

As human-driven climate change and extreme events intensify under global change, understanding patterns of survival and reproduction is critical for forecasting animal responses and conserving their populations. Our 2023 field observations and statistical analyses indicated that male-male competition is stronger in burned habitats, and ornamented dragonflies are not able to defend their territories as vigorously in the warmer post-fire environments. These findings align with predictions that wildfire-altered microhabitats hinder mating activity and increase the thermal costs of secondary sexual traits (Leith et al. 2022).

Our preliminary 2024 analyses indicate that post-wildfire environments generally do not affect dragonflies' body condition. These findings reject our hypothesis that food resources are a limiting factor in burned habitats. Our results showing that reproductive habitat temperatures at burned sites are hotter on average than at unburned sites support that the post-wildfire thermal environment disrupts dragonflies' energetically demanding mating dynamics.

More analyses remain necessary, but these results suggest that wildfires disrupt animal mating dynamics by altering reproductive habitats. When faced with novel environmental conditions, sexual traits can play a critical role in determining a species' ability to adapt (Nalley and Moore 2024) and metabolically expensive sexual traits, like melanin ornamentation, can become a liability in these altered habitats (West and Packer 2002, Moore et al. 2019, Côte et al. 2019, Weiss and Brower 2021). Our wing ornamentation analyses will clarify how post-wildfire habitats influence the expression of sexual traits like melanin-based ornaments.

Collectively, this work bridges a major gap in global change research by illuminating how extreme events, like wildfires, reshape habitats across spatial scales to influence animals' mating dynamics and adaptive capacity in changing environments (Kearney et al. 2009, Kingsolver et al. 2013, Heerwaarden and Sgrò 2021, Parratt et al. 2021). These insights are critical for wildlife management strategies (Elmore et al. 2017, Buchholz et al. 2019, de Resende et al. 2021, Dolný et al. 2021, Harvey et al. 2023), particularly in adapting to the ecological consequences of climate change-induced wildfires, thereby aligning with the mission of BCPOS to conserve and manage natural habitats.

Next, we will analyze summer 2024 measurements of total and melanized wing area to assess how burned environments affect species morphology and the expression of ornamented dragonflies' sexual traits. These analyses will further our exploration of the prediction that the exposed, warmer, drier conditions in burned habitats impact dragonfly mating dynamics by pushing them beyond their optimal thermal performance limits, with a stronger negative impact on ornamented species. Our future research will assess the relationship between fire-induced habitat changes and dragonfly species' reproductive phenotypes. These studies are aimed at understanding the broader implications of global change and post-wildfire ecosystems on animal mating dynamics and sexual selection.

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TABLES.

Table 1. Geography of the five research sites in Boulder County Parks and Open Space, the date(s) research was conducted in 2024, and other animal species observed at each site.

Site name	Lat/long coordinates	Pond area (m2)	Elevation (m asl)	Month/day				Other species[1]
Frog Pond	40.14324, -105.30038	42	1,781	07/02*	07/14*			*Zenaida macroura*
Meadow	40.18248, -105.29702	3,918	2,034	07/08*	07/14*			Genus *Corvus*; *Cathartes aura*; *Meleagris gallopavo*
Mud Lake	39.97801, -105.50952	14,440	2,560	07/03	07/11	07/25	08/31	*Alces alces*†; *Anas platyrhynchos*; Family Culicidae; *Neotamias minimus*; *Thamnophis elegans* ssp. *vagrans*; suborder Zygoptera
Ponderosa Loop	40.17899, -105.29725	373	2,062	07/08*	07/14*			Genus *Corvus*; *Cathartes aura*; *Meleagris gallopavo*
Quarry	40.17639, -105.30493	626	2,079	07/08	07/14	08/06	09/02	*Ambystoma mavortium*‡; *Cathartes aura*; *Cervus canadensis*†; Genus *Corvus*; *Pseudacris maculata*†; *Spinus psaltria*; *Thamnophis elegans* ssp. *vagrans*; *Ursus americanus*†; *Zenaida macroura*; suborder Zygoptera

*Pond nearly or completely dry; [1]Orders Diptera, Hymenoptera, Lepidoptera, and Orthoptera present at all sites; †Evidence of presence; ‡Juvenile life stage.

Table 2. Total mature adult dragonfly species captured, measured, and released for summer 2024 research, categorized by sex and habitat type.

	Female		Male		
Species	**Burned**	**Unburned**	**Burned**	**Unburned**	**Species Total**
Aeshna interrupta	1	1	5	3	10
Aeshna juncea	1		13	1	15
Aeshna palmata		1	2	13	16
Celithemis eponina	1				1
Cordulia shurtleffii				8	8
Leucorrhinia intacta			2		2
Leucorrhinia proxima			5	18	23
Libellula forensis			3		3
Libellula pulchella			6	3	9
Libellula quadrimaculata			7	41	48
Rhionaeschna multicolor			1	1	2
Somatochlora hudsonica			1	1	2
Somatochlora semicircularis		1	16		17
Sympetrum corruptum			2		2
Sympetrum danae	1	2	3	7	13
Sympetrum internum	17	3	105	20	145
Sympetrum pallipes	3		10	4	17
Sympetrum vicinum	1		2		3
Tramea lacerata	1		1		2
Site Total	26	8	184	120	338

Table 3. Pairwise comparison of slopes between burned and unburned habitats for the relationship between dragonfly species' body length and weight. The estimate (*β*) shows the slope difference ± standard error, with degrees of freedom, t-ratio, and p-value for each test.

Comparison	Species	β ± SE	DF	t	p
Burned-Unburned	*Leucorrhinia proxima*	-1.44 ± 1.40	18.10	-1.02	0.32
	Libellula quadrimaculata	0.69 ± 1.29	42.60	0.53	0.60
	Sympetrum internum	-0.20 ± 0.28	78.80	-0.70	0.48

FIGURES

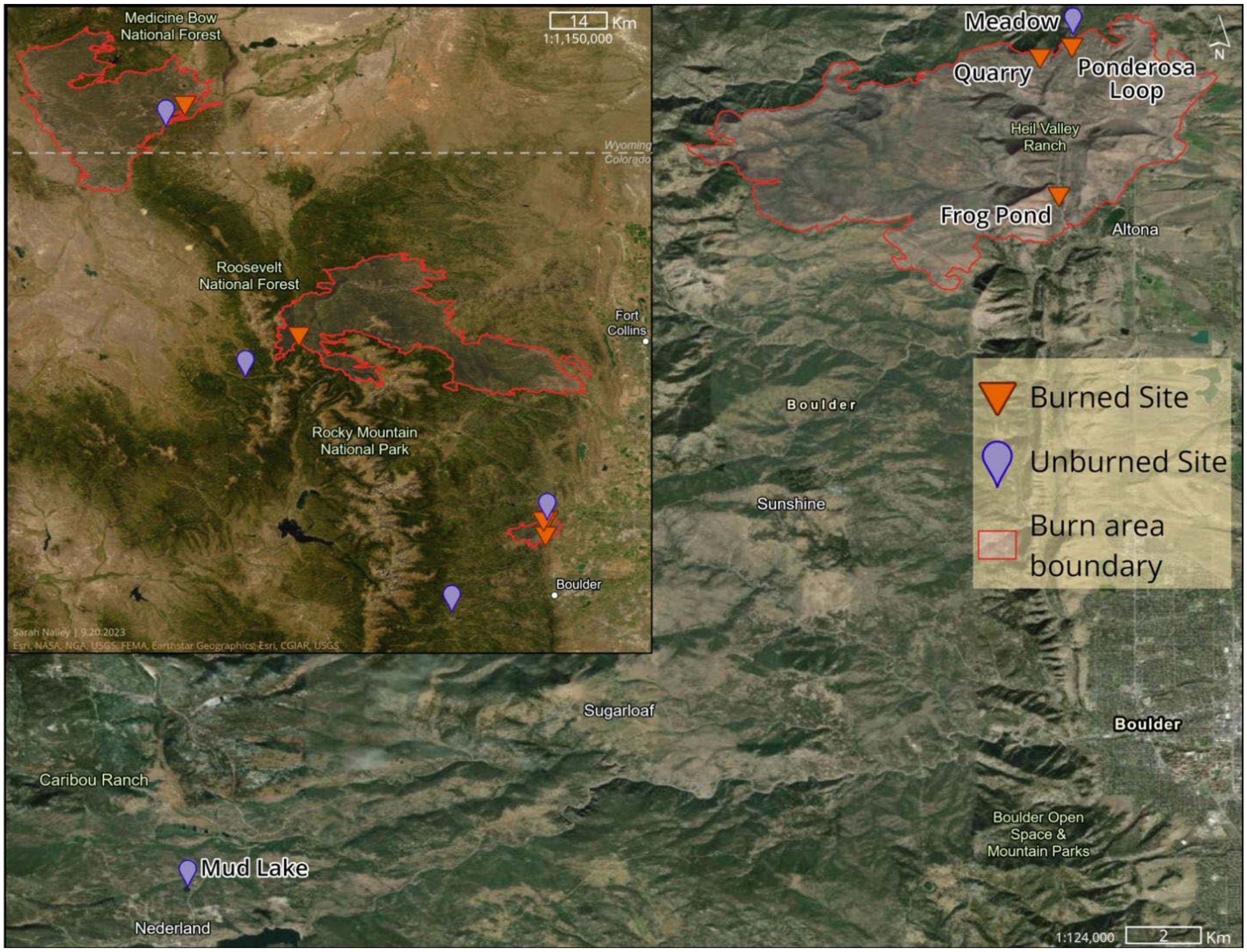

Figure 1. The Calwood Fire perimeter and five Boulder County Parks and Open Space research sites. Inset: all nine 2024 research sites across three wildfires in Colorado and Wyoming.

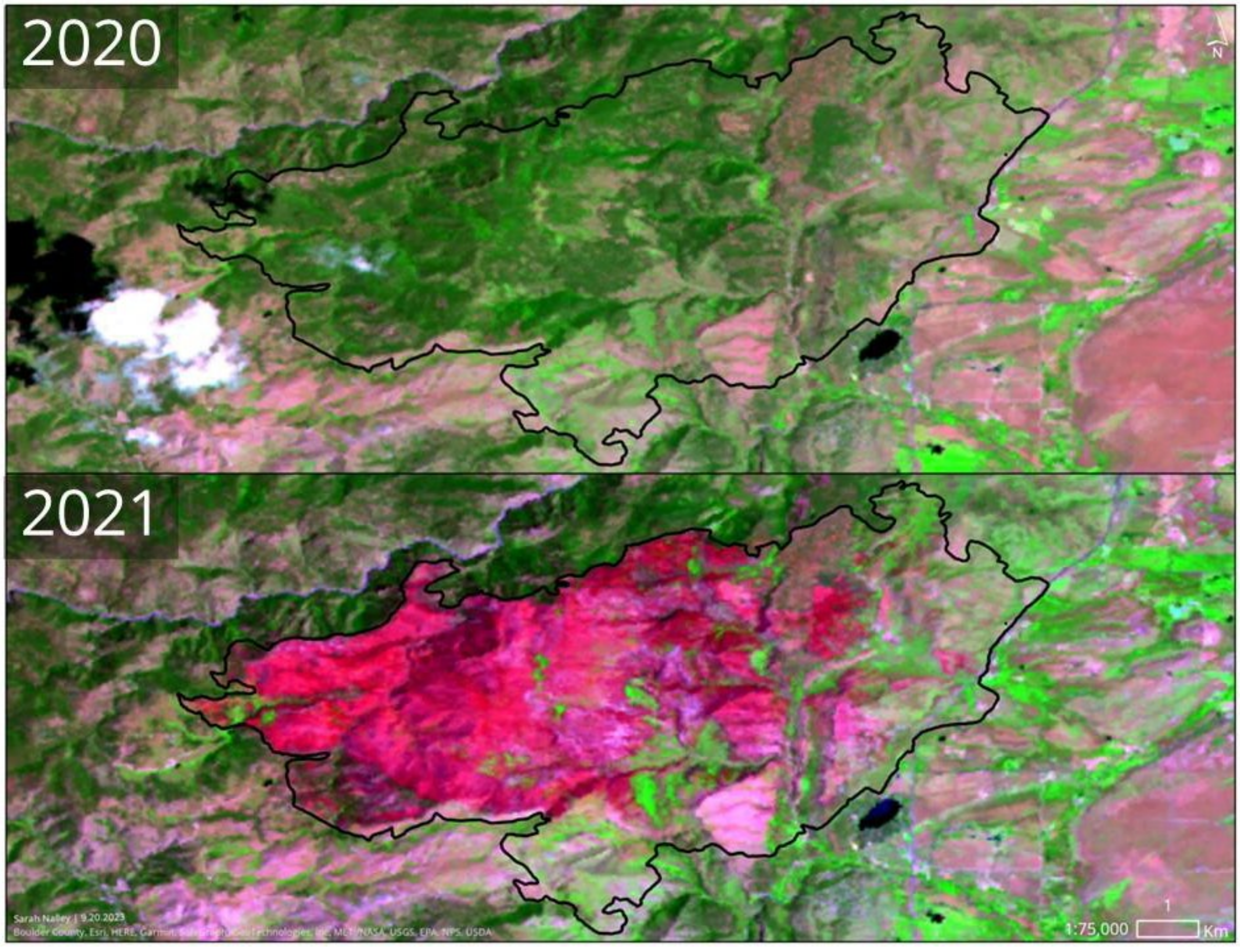

Figure 2. Landsat 8 Operational Land Imager (OLI) images from July 2020 and July 2021 show the landscape burn severity from the Calwood Fire (MTBS Project [USDA Forest Service/U.S. Geological Survey] 2017).

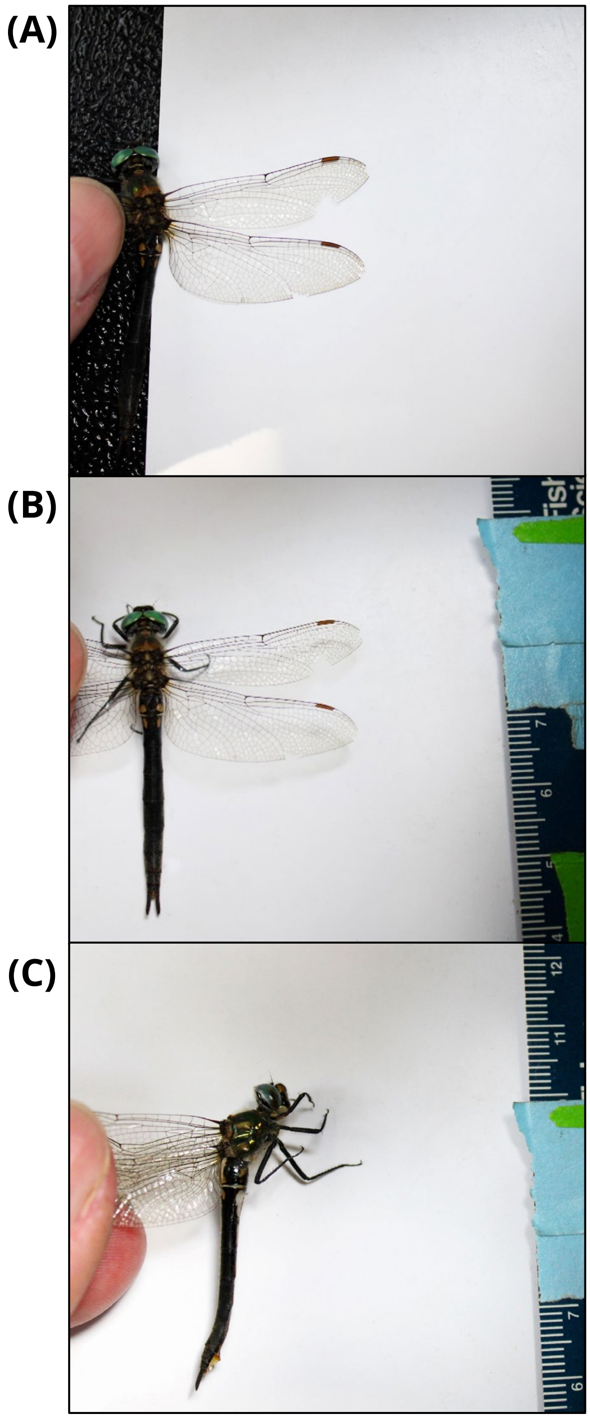

Figure 3. Standardized dragonfly imaging. Wings on one side (A), body length (B), and, when necessary for identification, a full-length side profile (C) were photographed under standardized conditions. Shown are images of a *S. semicircularis* female from Mud Lake on BCPOS.

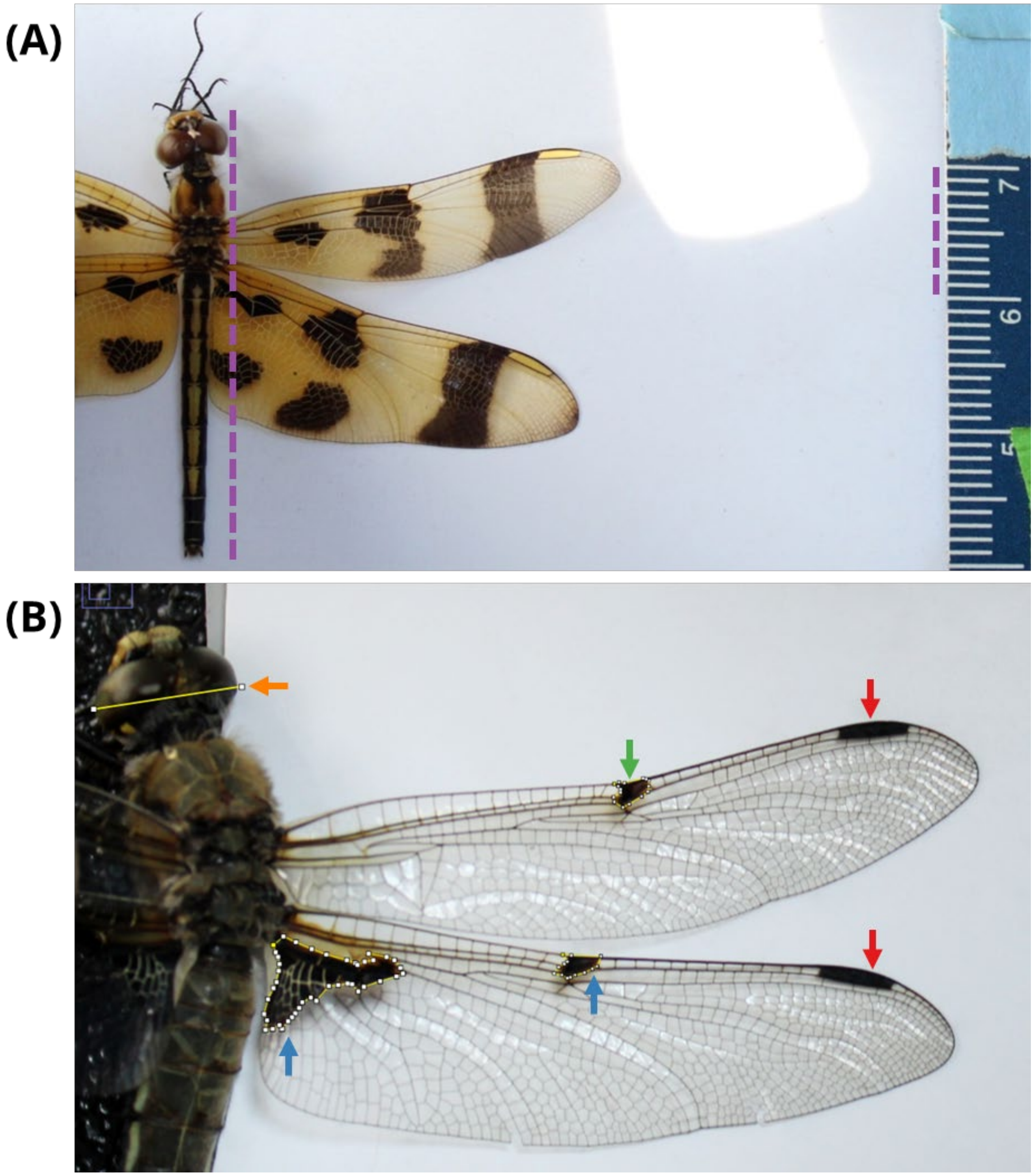

Figure 4. Post-processing in ImageJ. Body length (A) was measured using a ruler placed next to the dragonfly for scale. Wing traits (B) were measured using maximum head width for scale (orange arrow). Traits included melanized forewing (green arrow) and rearwing areas (blue arrows) excluding the pterostigma (red arrows), and total wing area. Shown are (A) a *C. eponina* female from the Quarry and (B) a male *L. quadrimaculata* from Mud Lake.

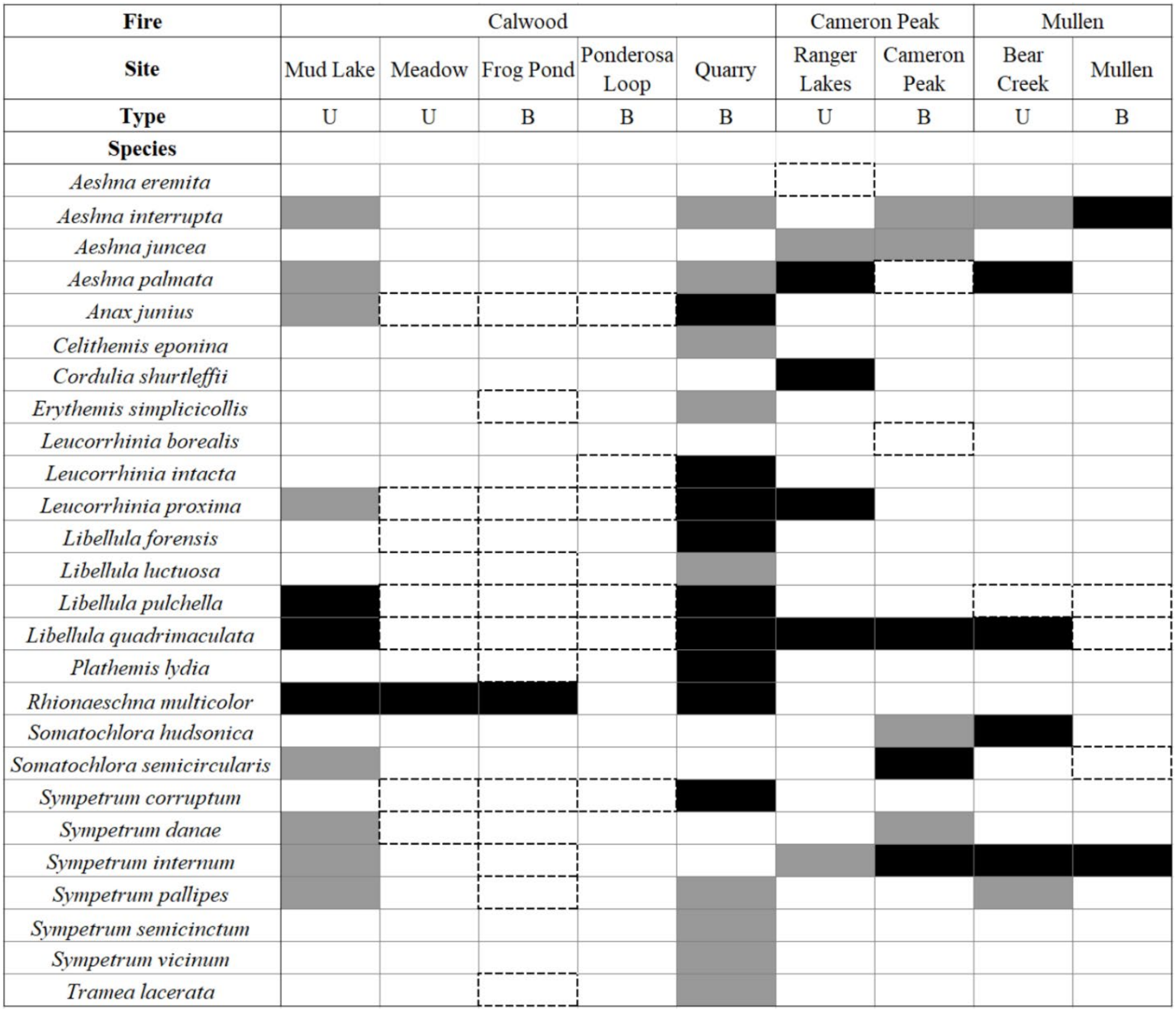

Figure 5. Site name, type (B, burned; U, unburned), associated fire, and incidence matrix of dragonfly species for all 2024 summer research sites. Black cells indicate species observed in both 2023 and 2024; gray represents species observed in 2024, but not 2023; dotted outline signifies a species was observed in 2023, but not 2024.

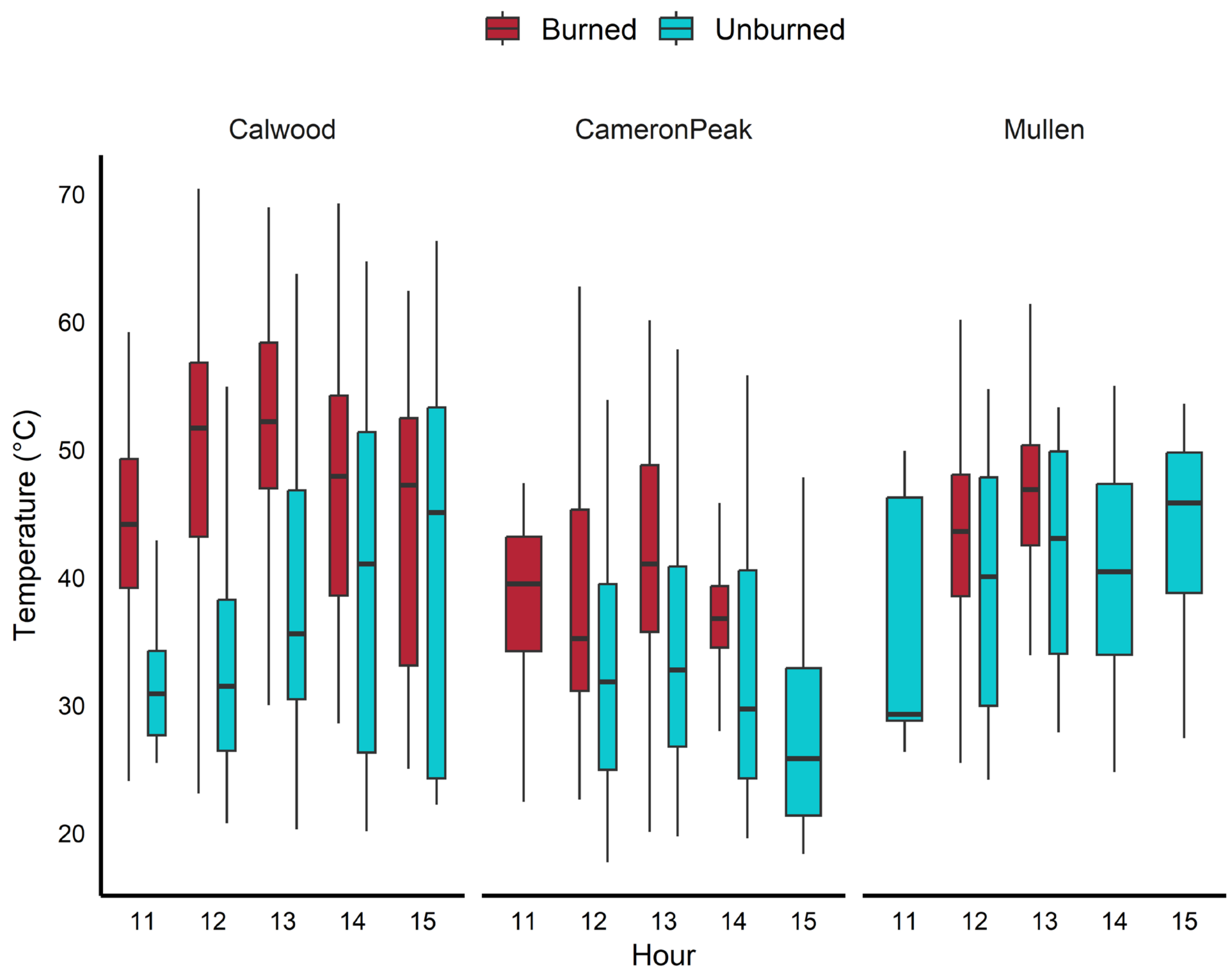

Figure 6. Hourly temperature distribution for burned and unburned sites across three wildfire areas. Burned sites consistently exhibit higher median temperatures compared to unburned sites.

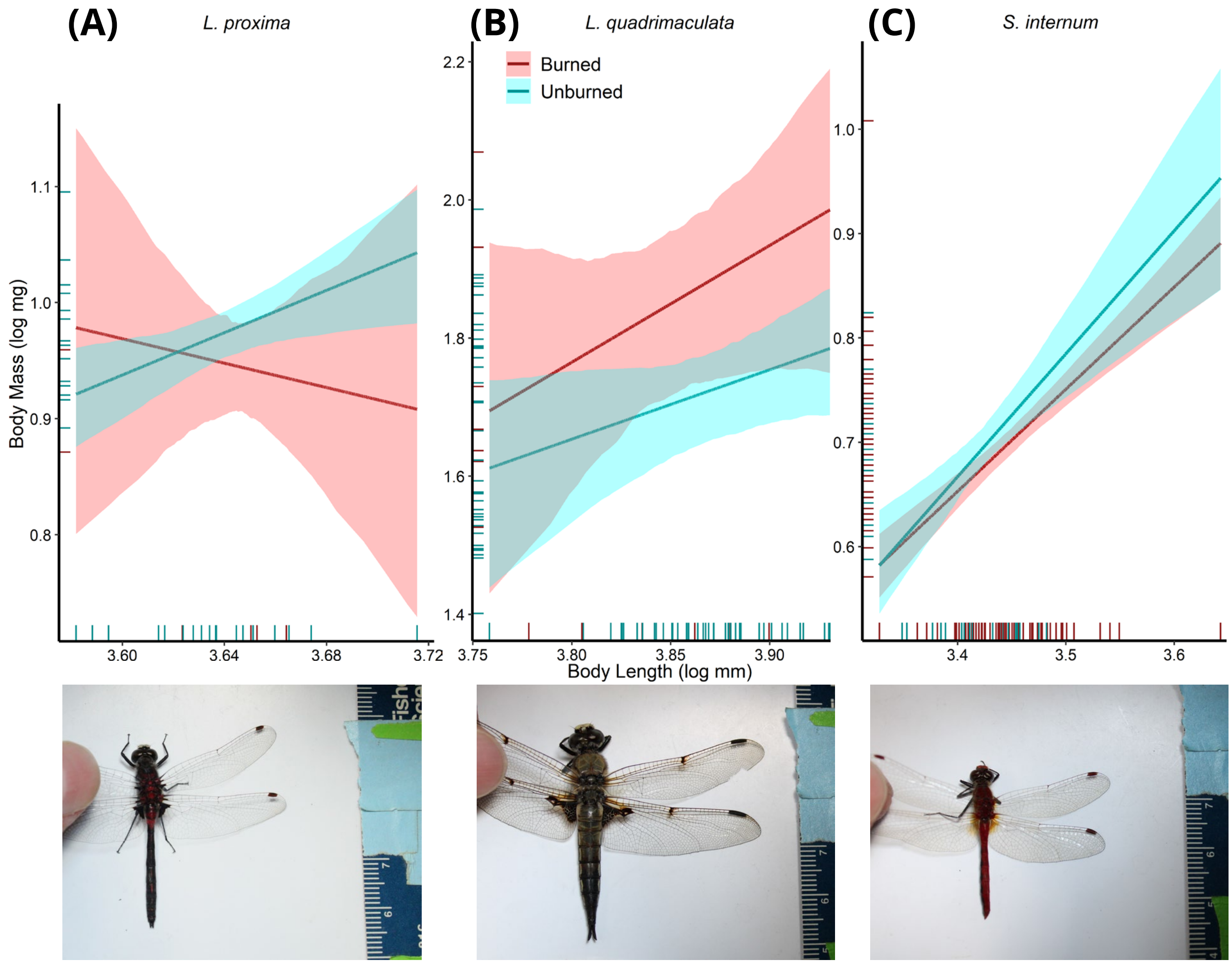

Figure 7. Body condition in burned vs unburned habitats for *Leucorrhinia proxima* (A), *Libellula quadrimaculata* (B), and *Sympetrum internum* (C). Pairwise comparisons indicated no significant difference in body condition between habitat types for any species. Least squares regression lines show the predicted values of body mass based on fixed effects of linear mixed effects models, and 95% confidence intervals are from 1,000 bootstrap replicates. Representative photos of a male from each species are below the corresponding panel for reference.