



## ARTICLE

# Rapid colonization of the post-burn environment improves egg survival in pyrophilic ground beetles

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## Abstract

Many insects are drawn to the heat, ash, and smoke produced by forest fires and arrive in large numbers at recent burns, often while the fire is still active. Some of these insects are pyrophilic and reproduce exclusively in the immediate aftermath of fire but are rarely, if ever, collected from unburnt habitats. Numerous observations made at active fires note an apparent preference among some pyrophilic insects to oviposit exclusively in the burnt portions of trees, raising broader questions about the adaptive benefits of reproduction in the post-burn environment. Here, we tested whether the reproductive output of pyrophilic ground beetles (i.e., *Sericoda* spp.) increased in heat-sterilized soils. In the first experiment, the eggs of *Sericoda quadripunctata* were reared in three types of soil collected from burnt forests: recently burnt soil (collected 1–2 weeks after the fire), soil collected 1 year after burn, and soil from an unburnt patch of forest adjacent to the fire. Daily monitoring through a dissecting microscope documented extensive predation of eggs by soil microarthropods (mites, springtails, and nematodes), especially in 1-year-old and unburnt soil treatments. This led to a second experiment that included the same three treatments and an additional fourth soil treatment: recently, burnt soil reheated to 100°C for 2 h (i.e., reheated soil). In this experiment, male and female pairs ( $n = 100$ ) of *Sericoda obsoleta* were reared for 14 days in jars containing 90 g of soil corresponding to each of the four soil treatments. Reproductive output, measured as the number of larvae produced by each breeding pair, was significantly higher in the reheated soil, suggesting that heat sterilization and removal of soil-dwelling predators improved egg survival. Our findings suggest that pyrophily in insects may have evolved as a means of increasing reproductive output in the post-burn environment through access to heat-sterilized ovipositing substrates. Furthermore, the abrupt disappearance of *Sericoda* and other pyrophilic insects following fire may be explained by suboptimal reproductive conditions as the burn is colonized by other organisms and by local emigration in favor of other recent burns on the landscape.

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**KEYWORDS**

egg laying, fire dependence, offspring survival, predation pressure, pyrophilic species, reproductive trade-off, *Sericoda*, wildfire

**INTRODUCTION**

Fire is an important disturbance agent in many ecosystems worldwide where it plays a crucial role in the generation of early-successional habitats. Pyrophilic insects are among the first organisms to colonize these habitats, and they possess a range of behavioral and physiological adaptations that allow them to fully exploit the post-burn environment. Detection of smoke and volatile cues from distant fires by these insects is facilitated by their exceptional olfactory senses that provide important information about the location and availability of prospective host trees (Eßinger et al., 2010; Paczkowski et al., 2011; Paczkowski et al., 2013; Schmitz et al., 2015; Schütz et al., 1999). Rapid colonization of the burnt environment is made possible by their exceptional dispersal capabilities (Paarmann, 1966; Schmitz & Bousack, 2012; Wikars, 1997) and extra-antennal infrared (IR) receptors that allow them to navigate the thermally complex environment of active fires (Hinz et al., 2018; Kreiss et al., 2007; Schmitz et al., 2016; Schmitz & Trenner, 2003). These IR receptors are known from at least 19 separate insect species, and they represent an extreme adaptation to fire that has likely evolved independently in at least four different genera of pyrophilic insects (Hoang, 2020; Schmitz et al., 2016). Although originally thought to be involved in the long-distance detection of distant forest fires (i.e., in line with the long-range orientation hypothesis; Evans, 1964, 1966), recent studies suggest that these IR receptors instead help protect the insects from hazardous conditions during reproduction at active fire sites (Evans, 2010; Kreiss et al., 2007; Schmitz et al., 2016).

Reproductive behavior, including swarming, mate selection, and ovipositing has been extensively documented for pyrophilic insects at active fire sites (Chandler, 2001; Schmitz et al., 2015; Snoddy & Tippins, 1968; Wickman, 1964, 1967). For example, smoke flies (*Microsania* spp.) are strongly attracted to smoke and assemble in mating swarms above plumes given off by fire (Chandler, 2001). These small flies are rarely collected outside of burnt areas, despite significant efforts to find them (e.g., Kessel, 1947), and it has been suggested that smoke provides an important attractant and meeting place for sexes (Chandler, 2001; Kessel, 1960; Klocke et al., 2011). Despite their strong association with smoke and the fact that more than 22 species have been described, the larval stage and habitat of these

flies are still unknown (Chandler, 2001; Klocke et al., 2011; Sinclair & Cumming, 2006). Reports of other rare Diptera in the ashes of cold fires are suggestive of a possible association of these larvae with burnt substrates (Chandler, 1978, 1992; Klocke et al., 2011). Furthermore, reports of other pyrophilic species preferentially ovipositing in ash or the burnt portions of trees have also indicated an apparent preference for burnt substrates (Schmitz et al., 2015; Wickman, 1967), raising broader questions about the adaptive benefits of reproduction in the post-burn environment. Although some authors have speculated that pyrophilic wood-boring insects (e.g., Buprestidae) seek out burnt areas because fire-scorched trees are less likely to kill invading larvae (Poulton, 1915), this explanation does not account for other pyrophilic insects, such as ground beetles (i.e., *Sericoda* spp.), that oviposit in soil (Burakowski, 1986) or other substrates.

A complementary hypothesis to the one suggested by Poulton (1915) is that the extreme heat from fire sterilizes prospective ovipositing substrates and provides a reproductive benefit through the removal of predators, pathogens, and parasites that kill eggs or developing larvae. In this context, rapid colonization of the post-burn environment increases the reproductive output of pyrophilic insects by providing access to sterilized oviposition substrates that have not yet been recolonized by other organisms. These reproductive advantages, in turn, help explain the extensive adaptations and pyrophilic behavior observed in these insects. Here, we test this hypothesis in two pyrophilic ground beetles, *Sericoda quadripunctata* (DeGeer, 1774) and *Sericoda obsoleta* (Say, 1823), by comparing reproductive output in burnt and unburnt soils collected from fire sites in central Canada. Specifically, we tested the prediction that reproductive output, measured as the number of larvae produced by captive mating pairs, is higher in soils more recently impacted (i.e., sterilized) by fire. By addressing this question, we aim to shed light on the evolution of pyrophily in insects and the advantages associated with rapid colonization of the post-burn environment.

**METHODS****Study site and initial observations of *Sericoda* in the post-burn environment**

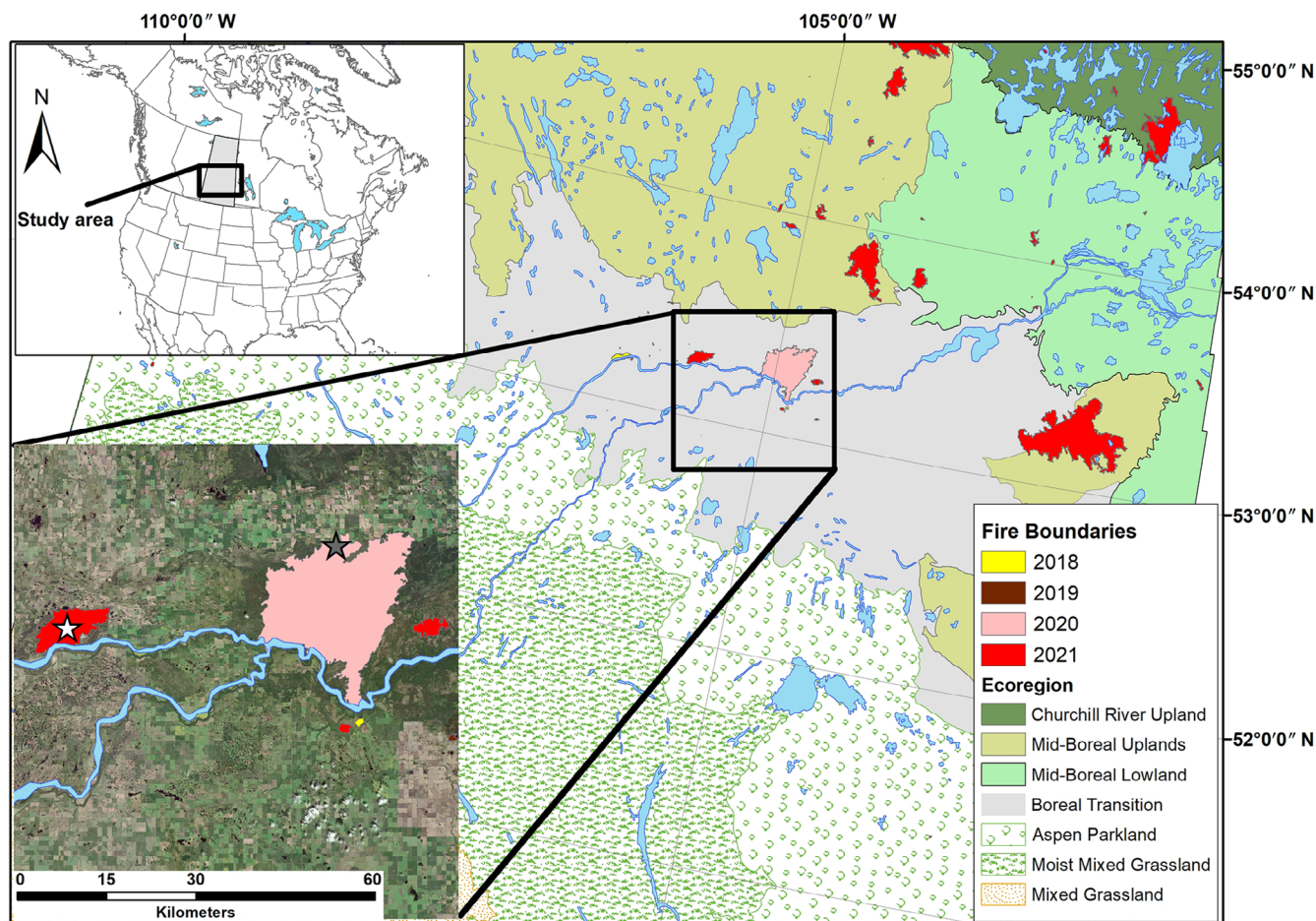
Materials for this study were collected from two burnt forest sites located east of Prince Albert, Saskatchewan,

in central Canada. This area is within the Boreal Transition ecoregion and is comprised of a mixture of forests, urban development, and farmland. Overstory vegetation in the area is characterized by a mix of trembling aspen (*Populus tremuloides*) and jack pine (*Pinus banksiana*), and white spruce (*Picea glauca*) and black spruce (*Picea mariana*) in well and poorly drained areas, respectively. Wildfires have been an important post-glacial disturbance in the area, but changes in land use, fire suppression, and human development in the area have resulted in fewer naturally occurring fires throughout the region (Parisien et al., 2004). As a result, the current fire interval is approximately 292–423 years, with the vast majority (>80%) of fires occurring because of human-caused ignitions (Parisien et al., 2004).

The English fire (53°23'35" N, –104°56'53" W) started on 8 May 2020 approximately 45 km east of the city of Prince Albert and was reported as contained on 26 May 2020 at a size of more than 41,000 ha (Figure 1; Appendix S1: Figure S1). The fire burned through our study site at the English fire on 16 May 2020 with an

estimated head fire intensity of 18,300 kW/m based on temperature, humidity, foliar moisture content, and fuel type. This area was visited for the first time on 9 May 2021, approximately 1 year after fire, to search for pyrophilic insects and record general observations of insect activity in the post-burn environment. Observations made then and on subsequent visits revealed that densities of *S. quadripunctata* (Figure 2) were highest in the litter of severely burnt areas. Abundance generally declined over the 3 weeks following our initial visit as individuals became increasingly harder to find. Although copulation was not observed naturally, captured beetles readily engaged in copulatory behavior within collecting jars. In contrast to the high abundance of *S. quadripunctata* at this site, only a single male individual of *S. obsoleta* (Figure 2) was collected from this burn, on 11 May 2021.

The Cloverdale fire (53°16'12" N, –105°36'29" W) started on 17 May 2021 and was reported as contained on 20 May 2021 at a size of approximately 5500 ha (Figure 1; Appendix S1: Figure S2). The intensity at the fire head was estimated to be 54,800 kW/m on 18 May



**FIGURE 1** Map of our study site within the Boreal Transition ecoregion including the boundaries of all fires in the area dating back to 2018. The bottom left panel shows the boundaries and location of our study site for the Cloverdale (white star) and English (gray star) fires.



**FIGURE 2** Photographs of the two pyrophilic ground beetles in our study, *Sericoda obsoleta* (left) and *Sericoda quadripunctata* (right).

2021, when the head of the fire burned through our study site. The first visit to this burn site occurred on 23 May 2021, approximately 5 days after peak fire intensity in the area, although there were several hotspots still smoldering and emitting smoke. At this time, we observed many *S. obsoleta* flying over the burnt area, copulating, and running along the ground, which was covered in a thick (ca. 10 cm) layer of ash. Several individuals were seen walking along burning logs and copulating near active hotspots. However, while we observed and collected many specimens of *S. obsoleta* in this initial visit, no individuals of *S. quadripunctata* were seen or collected.

These occurrence patterns, including the apparent short residency time of *S. obsoleta* in the older burn (English fire) and the absence of *S. quadripunctata* in the immediate aftermath of the more recent burn (Cloverdale fire), prompted us to document the order of arrival, residency time, and relative abundance of these two species in the aftermath of the Cloverdale fire. To do this, we conducted time-standardized searches (minimum 1 h per visit) at the Cloverdale fire in the same 30 × 30 m area during repeated visits 5, 13, 18, 36, and 113 days after fire. During each of these visits to the burn, we conducted visual searches for beetles on the burnt ground and among fallen logs and scorched deadwood of the burnt area. Captured beetles were placed in a vial and kept in a cooler until they could be identified, counted, and sexed. Beetles were then transported back to the laboratory or released after the survey was complete. Surveys were only conducted under ideal conditions (warm and sunny) and by the same observers to improve the consistency of capture probabilities between repeated visits to the area.

## Sampling protocol and experimental design

We conducted breeding experiments using soil and beetles collected from the English and Cloverdale fires in the summer of 2021. Using a shovel, we collected soil and litter from the uppermost 10 cm of the forest floor in the two burnt areas (in the Cloverdale and English burn areas) and an adjacent unburnt area near the English fire. To help ensure that the soil used in rearing chambers was fresh, we collected bulk soil samples from the English fire on 11 May 2021 and from both the English and Cloverdale fires on 23 May and 31 May 2021. The soil was transferred to 60-L Rubbermaid containers and brought back to the laboratory where it was kept in the shade under natural conditions. Additional beetles (primarily *S. quadripunctata*) that were not collected during our standardized surveys at the Cloverdale fire (see above) were collected by hand and placed in 1-L glass Mason jars for transport to the laboratory. Once back at the laboratory, we isolated individual female beetles in 20-ml glass vials (10 × 1.3 cm) each stoppered with a cotton ball and provided with fresh food (pieces of larval *Tenebrio molitor*) and water (wetted filter paper cut into 1 × 3 cm rectangles) daily. Female *S. quadripunctata* readily laid eggs on filter paper, the cotton ball, and along the edges of the glass vial, provided they had adequate food and had recently mated.

In the first experiment, individual eggs of mated female *S. quadripunctata* were randomly assigned to one of three soil treatments ( $n = 18$  per treatment) and transferred using fine forceps to 500-ml plastic containers with approximately 90 g of soil. The soil in each rearing container varied in the elapsed time since fire, hereafter referred to as the following treatments:

1. “New-burn”—soil collected from the more recent Cloverdale fire (5 and 13 days after peak fire intensity);
2. “Old-burn”—soil collected approximately 1 year after the burn at the English fire; and
3. “Unburnt”—unburnt soil collected from the adjacent unburnt area at the English fire.

A single egg, transferred within 12 h of laying, was placed in a small depression made at the center of each rearing container and monitored at least once per day by visual inspection through a dissecting scope. Upon inspection, the overall condition of the egg was recorded and the presence (if any) of active soil microarthropods in the vicinity of the egg was noted. The elapsed time between when the egg was added to the soil treatment and when its condition changed (i.e., egg death or hatching) was also recorded and is hereafter referred to as “time to outcome.” Indicators of egg mortality included substantial changes in the overall shape of the egg (e.g., deflation; Rosenheim, 2001) or the presence of mold or fungi growing on eggs. Comparisons with previous observations (i.e., when the egg was intact) helped establish whether egg mortality occurred and the approximate time that the condition of the egg changed. For eggs that became deflated or failed to hatch, we attempted to discern the cause of death using information recorded during visual inspections. In instances where we observed predators actively feeding on an intact egg, we attributed death to “predation” and recorded the identity of the egg predator. We also attributed death to “predation” in instances where developing eggs were lost or removed and could not be relocated within the container, although in these cases, the identity of the predator could not be determined. In instances where the egg became deflated and predation was suspected but could not be visually confirmed, we assigned the cause of death to be “uncertain.” For eggs that developed mold or fungi, were not predated, and failed to hatch after 72 h (see Burakowski, 1986), we assigned the cause of death to be “fungi” with the understanding that other pathogenic agents (i.e., bacteria) may have also contributed to egg death in these cases.

In the second rearing experiment, we placed 100 male and female pairs of *S. obsoleta* in 500-ml jars (i.e., 25 replicate jars for each of the four treatments), each containing approximately 90 g of soil. Three of these contained the same soil as used in the three treatments set up in the first experiment (see above), while a fourth treatment (hereafter referred to as “Heated”) consisted of recently burnt soil from the Cloverdale fire that we reheated to 100°C for 2 h. Soil for each rearing jar was first passed through a 5 × 5 mm mesh sieve. Like in the first experiment, adult and developing larvae were fed and watered daily with

fresh larvae of *T. molitor*. Although Burakowski (1986) reported instances of cannibalism in *Sericoda* larvae when they were reared together and food was restricted, we did not observe any instances of cannibalism in our study, likely because adequate food was provided. Adults were removed from the jars after 10 days, allowing 4 days for any recently laid eggs to hatch, and the total number of larvae produced by each adult pair was counted after 14 days. Larvae were counted by carefully sifting through the soil of each jar in a large white sorting tray and extracting them by hand. Identification of *Sericoda* larvae and determination of larval instar (i.e., development stage) were made using the width of the larval head capsule (Bousquet, 2010).

The additional Heated treatment was incorporated in the second experiment because of the delay (up to 13 days) between peak fire intensity in our sampling area and when the soil was collected for our experiment, which may have been sufficient for at least some egg predators to recolonize the burnt area (Wikars & Schimmel, 2001). A temperature of 100°C was chosen because it is sufficient to cause microbial and soil faunal mortality (Granström & Schimmel, 1993; Grasso et al., 1996; Heessen, 1981) while not significantly impacting soil structure, water repellency, or the amount of soil organic matter, which tends to occur at temperatures above 175°C (Certini, 2005; DeBano, 1981; García-Corona et al., 2004; Stoof et al., 2010). In addition, we used *S. obsoleta* in this second experiment because it became increasingly challenging to find *S. quadripunctata* at the location of the English fire for use in our study. Lastly, this experimental approach also allowed females to choose oviposition sites within the rearing chamber, thereby removing the risk of incidental damage to eggs that may have occurred during their transfer to treatment containers in the first experiment.

Soil samples were also collected from the same location as rearing substrates (see above) to characterize the abundance of soil microarthropods in the different soil treatments. Samples ( $n = 4$  per treatment) were collected on 27 May 2021 from the English and Cloverdale fire areas using a 10 × 10 cm square quadrat dug to a depth of 5 cm. The samples were carefully removed and transported back to the laboratory in plastic bags that were placed in a cooler to prevent exposure to direct sunlight. The soil was then passed through a 5 × 5 mm sieve, and 500 ml of soil was placed in a Berlese funnel for 96 h. This method was also used to extract and quantify invertebrates leftover from rearing jars at the end of the second experiment. Leftover soil was gathered in bulk samples for each treatment, mixed thoroughly, and divided into four 500-ml subsamples before passing them through a Berlese funnel for 96 h. Invertebrates were sorted under 20× magnification and identified to subclass (mites and springtails).

## Statistical analysis

For the first experiment, data for assessing time to outcome in hours between the three treatments were analyzed using Welch's ANOVA because the residuals of the model failed to meet assumptions of equal variance. Post hoc comparisons were conducted using pairwise *t* tests with non-pooled SD and Holm-adjusted *p* values for multiple inferences. Abundance data of soil-dwelling predators extracted from field plots and the number of larvae in our rearing chambers in the second experiment were analyzed using a negative binomial error distribution to control for overdispersion in our count data (O'Hara & Kotze, 2010). Effects of our experimental treatment were evaluated using the likelihood-ratio  $\chi^2$  tests comparing a model that included soil treatment with a null model that did not (i.e., intercept only). Post hoc tests exploring differences between treatment means were conducted using pairwise comparisons with Tukey-adjusted *p* values. All statistical analyses for this study were carried out in R 4.1.1 (R Core Team, 2021) using the car (Fox & Weisberg, 2019), emmeans (Lenth, 2021), dplyr (Wickham et al., 2021), and FSA (Ogle, 2016) packages.

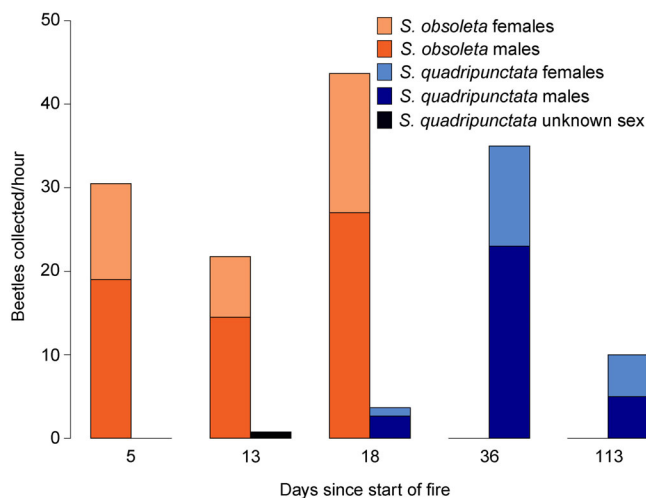
## RESULTS

### Relative abundance of *S. obsoleta* and *S. quadripunctata* following fire

Standardized searches at the Cloverdale fire showed that many *S. obsoleta* were already abundant in the area during our initial visit, approximately 5 days after peak fire intensity at the site (Figure 3). Interestingly, these initial searches did not detect *S. quadripunctata* at the site until Day 13. Peak abundance of *S. obsoleta* occurred approximately 18 days after fire, shortly after the arrival of *S. quadripunctata* at the site, whereas peak abundance of *S. quadripunctata* occurred approximately 36 days after fire, when adult *S. obsoleta* were no longer present at the site (Figure 3). Visual inspection of the protarsi of beetles collected during each visit confirmed the presence of both sexes at the site, although the sex ratio was slightly skewed in favor of males for both species (62%–67% in *S. obsoleta* and 50%–73% in *S. quadripunctata*; Figure 3).

### Experiment 1: Observations of egg mortality

Of the 54 *S. quadripunctata* eggs included in the first experiment, only one successfully hatched, while the remaining 53 eggs did not due to predation ( $n = 20$ ),

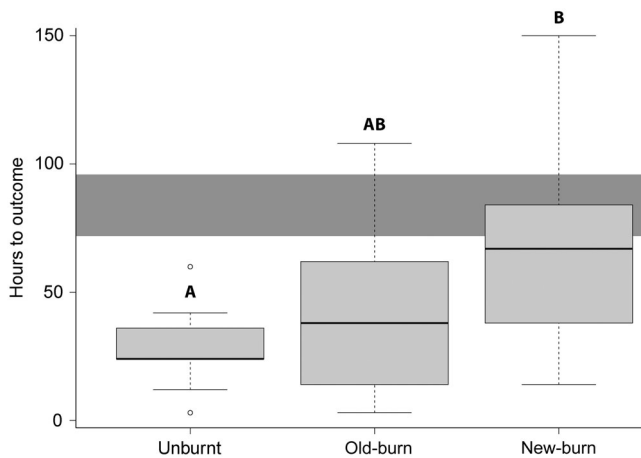


**FIGURE 3** Relative abundance of *Sericoda obsoleta* and *Sericoda quadripunctata* based on standardized searches at the same site within the Cloverdale fire 5–113 days after peak fire intensity. Note that sex was not recorded for the three *S. quadripunctata* individuals collected 13 days after fire.

uncertain causes ( $n = 20$ ), or fungal growth ( $n = 13$ ). Predation by soil-dwelling microarthropods including nematodes ( $n = 8$ ), mites ( $n = 3$ ), springtails ( $n = 2$ ), and a single juvenile spider (Linyphiidae) accounted for most of these events (Appendix S1: Figure S3), although egg mortality due to unknown predators was assumed in several instances ( $n = 6$ ) when eggs were lost and could not be relocated in the rearing container. Although the majority ( $n = 18$ ) of documented predation events occurred in Unburnt and Old-burn treatments, a post hoc  $\chi^2$  test of independence indicated that predation was unrelated to treatment ( $\chi^2$  [df = 4,  $n = 54$ ] = 8.26,  $p = 0.083$ ). In contrast, egg death that occurred due to excessive growth of fungi was related to treatment ( $\chi^2$  [df = 4,  $n = 54$ ] = 16.0,  $p = 0.003$ ) with most of these events ( $n = 10$ ) occurring in the New-burn treatment, possibly due to excess moisture in rearing chambers. This general pattern of higher predation rates within Unburnt and Old-burn treatments and egg death due to fungi in the New-burn treatment were also reflected in our analysis of time to outcome (Figure 4). Here, there was an overall effect of treatment on elapsed time to egg mortality ( $F_{2,27.0} = 10.7$ ,  $p \leq 0.001$ ), although this difference was only significant ( $p \leq 0.001$ ) between Unburnt ( $26.4 \text{ h} \pm 3.11$ ; mean  $\pm$  SE) and New-burn ( $64.6 \text{ h} \pm 8.1$ ) soils.

### Experiment 2: Number of larvae produced by *S. obsoleta* male/female pairs

In the second experiment, we found an overall effect of treatment ( $\chi^2 = 9.95$ ,  $p = 0.019$ ; Figure 5a) on the total

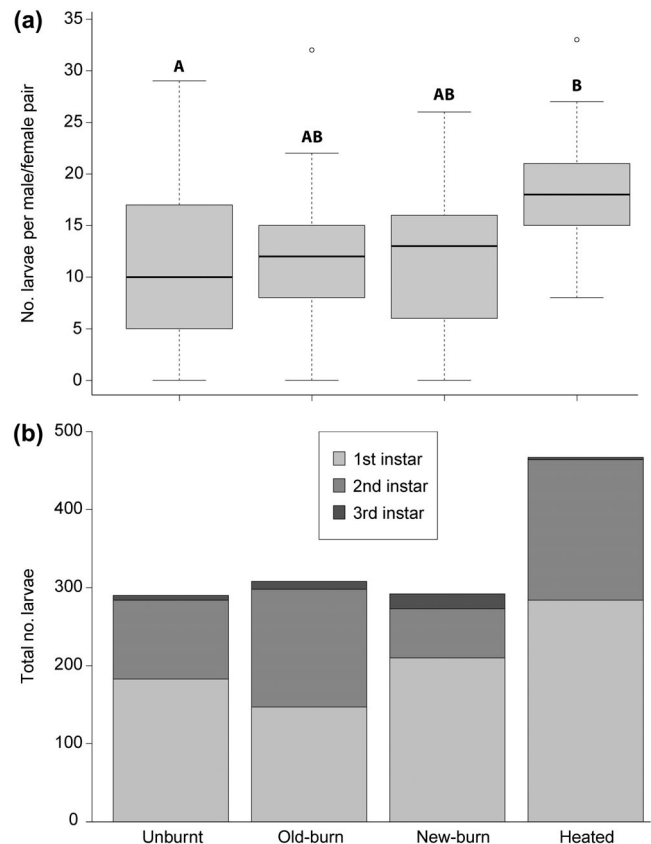


**FIGURE 4** Approximate time between when the egg was added to the soil treatment and when its condition changed (hours to outcome). Boxes represent 50% of values, whiskers represent 95% of values, and the thick line represents the median hours to outcome for each treatment. Treatments topped with the same capital letter do not differ ( $p = 0.05$ ) according to post hoc testing. The dark gray rectangle in the background depicts the 72- to 96-h period needed for embryonal development for *Sericoda quadripunctata* (Burakowski, 1986).

number of larvae produced by male and female pairs, although this difference was only significant ( $p = 0.047$ ) between Heated (median = 18 larvae, mean =  $18.7 \pm 1.3$ ) and Unburnt (median = 10 larvae, mean =  $11.6 \pm 1.7$ ) treatments. Whereas most larvae produced by male and female pairs were of the first instar, rearing chambers frequently contained a mix of larvae at varying development stages (Figure 5b), suggesting that egg laying was staggered over the 10-day period that adults were kept in rearing chambers.

### Soil predators in field plots and leftover soil from rearing chambers

We found no significant differences in the number of soil-dwelling predators (springtails and mites combined) extracted from burnt versus unburnt soils at the Cloverdale and English fires ( $\chi^2 = 4.08$ ,  $p = 0.130$ ; Figure 6a). In contrast, the number of soil-dwelling predators that were extracted from the soil at the end of our rearing experiment varied significantly between treatments ( $\chi^2 = 30.7$ ,  $p \leq 0.0001$ ; Figure 6b). The median number of soil-dwelling predators was significantly lower in the Heated treatment (2.5 individuals, mean =  $2.3 \pm 0.9$ ) than in all other treatments according to our post hoc test. Soil-dwelling predators in the New-burn treatment (median = 5, mean =  $24 \pm 19.3$ ) were also significantly lower than those in both Old-burn

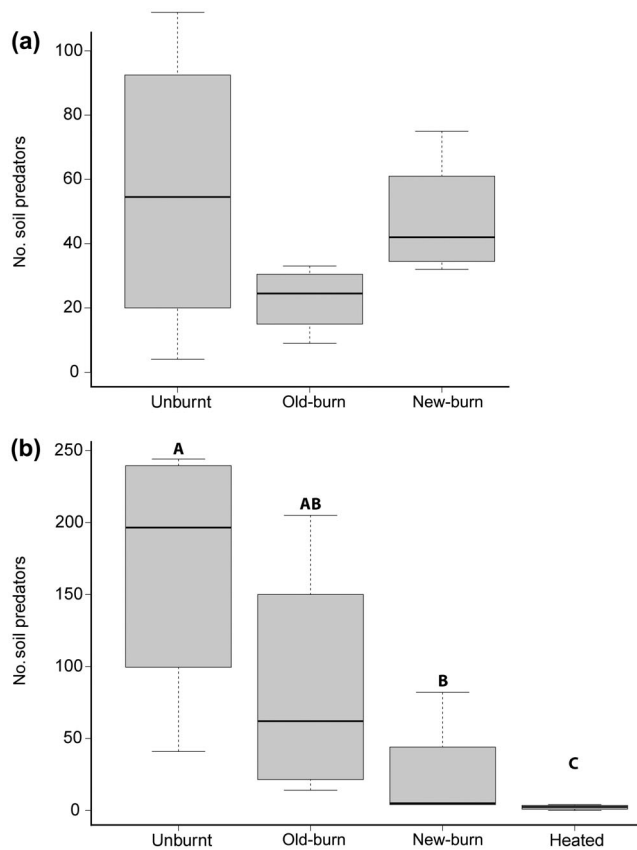


**FIGURE 5** Number of larvae produced by male and female pairs of *Sericoda obsoleta* in each soil treatment (a) and the total number of larvae listed by larval instar per soil treatment (b). For panel (a), boxes represent 50% of values, whiskers represent 95% of values, and the thick line represents the median number of larvae for each treatment. Treatments topped with the same capital letter do not differ ( $p = 0.05$ ) according to post hoc testing.

(median = 62, mean =  $85.8 \pm 43.5$ ) and Unburnt (median = 196.5, mean =  $169.5 \pm 47.0$ ) treatments, which did not differ from each other, according to the post hoc test.

## DISCUSSION

Pyrophilic insects are drawn to the heat, ash, and smoke produced by forest fires and arrive in large numbers at recent burns, often while the fire is still active (Chandler, 2001; Lindroth, 1969; Schmitz et al., 2015). Our experimental findings support our hypothesis that this rapid colonization strategy provides a reproductive advantage via access to heat-sterilized ovipositing substrates that are comparatively devoid of soil-dwelling egg predators. In the first experiment, we found that a wide range of opportunistic predators (mites, spider, springtails, and nematodes; Appendix S1: Figure S3) commonly



**FIGURE 6** Total number of soil predators (mites and springtails combined) by soil treatment extracted from field plots at the English and Cloverdale fires (a) and bulk soil samples leftover from experimental rearing chambers (b). Boxes represent 50% of values, whiskers represent 95% of values, and the thick line represents the median number of larvae for each treatment. Treatments topped with the same capital letter do not differ ( $p = 0.05$ ) according to post hoc testing.

found in forest soils readily preyed on the eggs of *S. quadripunctata*. Indeed, most of the eggs reared in unburnt soils were killed prior to the 72- to 96-h period needed for embryonic development (Burakowski, 1986). In the second experiment, we demonstrated that the median reproductive output of male and female *S. obsoleta* pairs in heat-sterilized soils was 80% higher than that of pairs reared in unburnt soils. Evidence of strong predation pressure in unburnt soils and increased reproductive output in soils where predators were removed by heat sterilization suggests that the reproductive cost of egg laying in unburnt soils is high and that this cost may be reduced by ovipositing in burnt substrates associated with wildfires. These findings are consistent with those in a study by Heessen (1981) who found that egg survival in the non-pyrophilic ground beetle, *Pterostichus oblongopunctatus* (Carabidae), increased 10-fold when eggs were laid in heated compared with

unheated litter, and in a study by Wikars and Schimmel (2001) that showed dramatic declines in soil-dwelling predators, such as mites, immediately after fire.

Our study is the first to investigate potential reproductive advantages of pyrophilic insects in the post-burn environment, although the tendency for pyrophilic insects to oviposit exclusively in burnt wood or ash suggests that this behavior may be part of a broader pyrophilic strategy (Schmitz et al., 2015; Wickman, 1967). Our findings and those of others (Wikars & Schimmel, 2001) suggest that the reproductive advantages for insects that are associated with heat-sterilized substrates are short-lived due to colonization by other organisms that compete for oviposition sites or that contribute directly to egg mortality. Pyrophilic adaptations that help facilitate rapid colonization of the burn environment, including IR sensors and specialized olfactory capabilities for detecting smoke (Evans, 2010; Kreiss et al., 2007; Schmitz et al., 2016; Schütz et al., 1999), could have evolved as a means of exploiting the reproductive advantages provided by these burned substrates. Although it is still unknown whether *Sericoda* spp. possess IR sensors, pitfall trap studies in burnt habitats have shown that they are exceptionally abundant in the year following fire (Cobb et al., 2007; Koivula et al., 2006; Phillips et al., 2006), possibly because of their increased reproductive output in heat-sterilized soils. Reports of higher numbers of *S. quadripunctata* and *S. bembidioides* Kirby in severely burnt microhabitats than in lightly burnt and unburnt microsites following a single fire (Koivula et al., 2006) provide further support for this hypothesis.

Our results are also consistent with the results of studies demonstrating the vulnerability of insect eggs to predation (Blackman, 1997; Goldberg et al., 2015; Newcombe et al., 2013). Although some mites are well documented as predators of insect eggs (Blackman, 1997; Nguyen et al., 2019), reports of egg predation by nematodes, springtails, and juvenile spiders in the literature are less common and likely reflect instances of opportunistic predation (see Greenslade et al., 2017; Heessen, 1981; Waldorf, 1971; Yousuf et al., 2014). Reproductive costs associated with egg predation in insects have given rise to a wide range of antipredator adaptations including chemical defenses (Eisner et al., 1996a, 1996b; Eisner et al., 2000), parental care (Diehl & Meunier, 2018; Kolesnikov & Karamyan, 2019), development of protective egg cases (i.e., ootheca; Goldberg et al., 2015), and internal incubation of eggs (Nalepa & Bell, 1997; Roth, 1989). The extent of these physiological and behavioral adaptations in insects implies that there is strong selective pressure for minimizing costs associated with egg predation. In the context of pyrophily, such costs may have given rise to adaptations that facilitate



access to ovipositing substrates that are sterilized by the heat of naturally occurring wildfires and that thereby enable the insects to avoid those costs.

The marked differences in egg survival between our two experiments suggest that female site selection (preovipositional care; Kolesnikov & Karamyan, 2019) and the presence of adults are additional factors that influence hatching success. Although differences between the species used in our study prevented direct comparisons of hatch success between the two experiments, egg-rearing studies conducted by Kolesnikov and Karamyan (2019) showed that egg survival in *Pterostichus anthracinus* (Carabidae) doubled when females were present to fend off predators. Further, they showed that the presence or absence of females did not affect egg mortality due to microbes. While we did not observe any direct instances of egg defense in our study, the extensive tunnels and burrows created by adults in the rearing chambers may have improved conditions for egg survival (e.g., aeration of soil) and site selection for ovipositing. Given the constraints of the rearing chamber and observations of extensive burrowing and tunneling at the Cloverdale fire, we suggest that in the field, females may select more severely burnt microsites for egg laying that vary according to fire severity (e.g., depth of burn). Furthermore, because eggs are laid individually over time, as opposed to at the same time in clusters, it is possible that the beetles colonize active hotspots that arise continually as the fire burns, often for several days or even weeks (e.g., 18 days for the English fire).

Most studies of *Sericoda* spp. have been conducted in the year following fire, long after the burnt site has already been colonized by pyrophilic and non-pyrophilic species alike (Cobb et al., 2007; Koivula et al., 2006; Phillips et al., 2006). Our observations in the aftermath of the Cloverdale fire indicate that while *S. obsoleta* had likely colonized the fire prior to our first visit approximately 5 days after peak fire intensity, the arrival of *S. quadripunctata* was delayed. Additional visits to three other burnt areas around the Cloverdale fire during our initial visit also revealed the apparent absence of *S. quadripunctata*, although in each case *S. obsoleta* was present. The reason for the delayed arrival of *S. quadripunctata* is unclear, but it may be due to large distances from source populations located at other recent burns (see Figure 1). The English fire, located approximately 27 km east of the Cloverdale fire, is a likely candidate source of *S. quadripunctata* at the Cloverdale site. However, extensive collecting at the English fire only located a single specimen of *S. obsoleta*, suggesting that the English fire location was not the only source for *S. obsoleta* found at the Cloverdale fire. Dispersal capability of *Sericoda* spp. has not been studied; however,

indirect estimates of dispersal ability for other pyrophilic insects (i.e., Buprestidae) suggest that they are capable of colonizing burns 64–130 km from source populations (Linsley & Hurd, 1957; Schmitz & Bousack, 2012). Additional studies focusing on dispersal and immigration/emigration of pyrophilic insects to and from recent burns are needed.

Previous studies have suggested that the rapid disappearance of *Sericoda* spp. in the years following fire is the result of increasing interspecific competition (Holliday, 1991; Wikars, 1995) or changes in understory conditions due to post-fire regeneration of vegetation (Koivula et al., 2006). Our findings are consistent with the view that once the burn is recolonized by other organisms, suboptimal reproductive conditions lead to fewer numbers of *Sericoda* within the burn and increasing local emigration in favor of more recent burns elsewhere on the landscape. Considering these findings and the narrow habitat specificity of pyrophilic insects, maintenance of their populations is likely dependent on a patchwork of recently burned forests (i.e., Nappi et al., 2004). Given climate-change-related implications for natural fire regimes at local (Parisien et al., 2004) and global scales (Moritz et al., 2012), there is a growing need to better understand the spatial dynamics of these insects and the extent to which they form metapopulations.

## CONCLUSION

Our study showed that egg predation by soil-dwelling microarthropods imposes a significant reproductive cost to ground beetles that oviposit in soil and that these costs can be offset by laying eggs in soils that are sterilized by the extreme heat of naturally occurring wildfires. Our findings shed light on the possible adaptive significance of pyrophily in insects and the evolution of pyrophilic adaptations (e.g., IR sensors) that help facilitate rapid colonization of the fire and access to heat-sterilized substrates. Although the timing of arrival and peak abundance in the post-burn environment varied between the two species investigated in our study, the potential factors contributing to this pattern (e.g., dispersal ability and distance to source populations) are generally poorly understood among pyrophilic insects. Whereas most studies of pyrophilic insects are initiated at least a full year after fire, our study demonstrates the importance of studying these insects in the immediate aftermath of the fire, once the sites are safely accessible.

Pyrophilic insects depend on recurrent fire to the extent that the ongoing changes to natural fire regimes are likely contributing to habitat loss and fragmentation for some species. Although the impact of climate

warming on fire activity is likely to increase habitat for pyrophilic insects in the future (Moritz et al., 2012), extensive fire suppression and forest management practices throughout the 20th century have contributed to declines in many forest-dwelling insects in some regions (Koivula & Vanha-Majamaa, 2020). While it is challenging to disentangle the individual effects of loss of fire and removal of deadwood on insect biodiversity, strategies aiming to increase deadwood volume in these forests (e.g., Seibold et al., 2016) are unlikely to conserve pyrophilic insects in the absence of fire. Prescribed burning may serve as an additional tool for effective conservation in regions where natural fire is rare, as has been shown in pyrophilic flat bugs (Heikkala et al., 2017).

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data (Bell, 2022) are available from Dryad: <https://doi.org/10.5061/dryad.931zcrjn0>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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