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A race to the bottom: observations on Pandora moth larvae during the hour(s) of tree descent, dispersal, and prepupal burrowing

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ABSTRACT.—Many montane, pine-dominated forests in the western United States are home to the Pandora moth, *Coloradia pandora*, a large lepidopteran species that has a 2-year life cycle, generally alternating between “moth years” and “larval years.” During the latter, larvae descend from their feeding locations in the pine canopy, disperse across the ground, and burrow in the soil for pupation. This study examines the nature of larval movement on trees as well as on and in the ground; the time required for the various phases during the day of descent; and parasitoid and environmental threats during ground dispersal. Locomotion during descent from trees was relatively slow at 0.64 cm/s (range 0.44–0.93 cm/s). Larvae slowed further as they transitioned from tree boles to the ground and were initially unsteady. Once on the ground, larvae quickly recovered and were able to move significantly faster (1.63 cm/s, range 1.23–2.08 cm/s) than during descent from the boles. About 10% of dispersing larvae were attacked by ovipositing tachinid flies and larvipositing sarcophagid flies. Larvae being attacked by parasitoids or traveling in full sun at high temperatures increased their speed to the point that locomotion appeared poorly coordinated. This apparently stressful locomotion was often followed by the affected animals burrowing only a centimeter below the surface of the loose soil, duff, and pine needles. Shallow burrowing by larvae stressed by heat or parasitoid attack may result in a positive feedback in terms of vulnerability because the resulting pupae would in turn be more exposed to several additional threats. Moreover, a warming climate would likely exacerbate a number of these linked causes of larval and pupal mortality.

RESUMEN.—Muchos bosques montaños dominados por pinos en el oeste de Estados Unidos albergan a la polilla Pandora, *Coloradia pandora*, una especie de lepidóptero grande que presenta un ciclo de vida de dos años, alternando generalmente entre “años de polilla” y “años larvales”. Durante estos últimos, las larvas descienden de sus áreas de alimentación en el dosel de pinos, se dispersan por el suelo y se entierran en él para pupar. Este estudio analiza el movimiento de las larvas en los árboles y sobre y por debajo del suelo, el tiempo requerido para las distintas fases durante el día del descenso, y las amenazas de parasitoides y del ambiente durante la dispersión en el suelo. La locomoción durante el descenso desde los árboles fue relativamente lenta, con 0.64 cm/s (rango 0.44–0.93 cm/s). Las larvas se ralentizaron aún más al pasar del tronco al suelo y mostraron inestabilidad inicial. Sin embargo, se recuperaron rápidamente y pudieron moverse significativamente más rápido (1.63 cm/s, rango 1.23–2.08 cm/s), comparado con el descenso por los troncos. Aproximadamente el 10% de las larvas en dispersión fueron atacadas por moscas tachínidas ovipositantes y moscas sarcófagidas larvipositantes. Las larvas atacadas por parasitoides o expuestas al sol a altas temperaturas aumentaron su velocidad hasta el punto de que su locomoción parecía poco coordinada. Esta locomoción, aparentemente estresante, fue seguida a menudo por el enterramiento superficial a solo un centímetro bajo la superficie del suelo, la hojarasca y las agujas de pino. El enterramiento superficial de las larvas estresadas por el calor o el ataque de parasitoides puede generar un efecto de retroalimentación positiva en términos de vulnerabilidad, ya que las pupas resultantes quedarían más expuestas a varias amenazas adicionales. Además, un clima más cálido probablemente exacerbaría varias de estas causas interrelacionadas de mortalidad larval y pupal.

The Pandora moth, *Coloradia pandora* Blake, 1863 (Saturniidae), is widely distributed across the western United States and is one of the larger forest insects of North America, having an adult wingspan of 7–11 cm and a larval (caterpillar) length of 6–8 cm (Ciesla et al. 2010,

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Hoffman 2013; Fig. 1a, b). This species has a 2-year life cycle (Fowler and Walter 1985, Ciesla et al. 2010, Strauss 2017), alternating between “moth years” and “larval years.” The larvae feed voraciously on the needles of Jeffrey pine trees (*Pinus jeffreyi* Balf.; Fig. 1c) as well as other pines, and descend every 2 years to pupate in the ground over a 2- to 3-week period in late June and early July (Fowler and Walter 1985). The prepupal larvae burrow below the surface for pupation; loose soil has long been understood to be an important determinant of Pandora moth distribution (Patterson 1929). A full year is spent in the pupal stage, and the months of snow cover found throughout much of the moth’s range is likely to provide insulation (Marshall and Sinclair 2012). Such coincidence of the pupal stage with overwintering and diapause is common in temperate climates (Brackley 2021). Moths emerge from pupal cases in early July and mate over a 1-month period (Fowler and Walter 1985). Large moth outbreaks occur approximately every 20 to 30 years, hence the specific epithet *pandora* (Patterson 1929, O’Neill et al. 2023); the moths are typically considered to be a nuisance in nearby communities during outbreaks (Ciesla et al. 2010). Eggs are laid, typically on pine bark but on other substrates as well, and first instars eclose after about a month and ascend into the pine canopy for a year of feeding (Fowler and Walter 1985). The larvae overwinter in the canopy, as has been found for some other forest Lepidoptera (e.g., Moise et al. 2023). *Coloradia pandora* larvae form aggregations for protection, but venture away for feeding during periods of mild weather (Ciesla et al. 2010). It should be fully recognized that, although Western scientists have described aspects of the natural history of this species over the last 100 years, Native Peoples have had extensive knowledge of these life patterns since time immemorial.

The abundance of prepupal *C. pandora* larvae, even in nonoutbreak years, can be substantial, and Native Americans, particularly the Nüümü, Mono Lake Kutzadika’a, and other Paiute Peoples, have long used the larvae as a calorically rich and nutritious seasonal food resource (Fowler and Walter 1985, Weaver and Basgall 1986). In addition to larvae, pupae are also gathered and roasted by the Modoc and Klamath Tribes. Larvae are gathered by hand or by trenches that are dug around trees and capture larvae upon descent (Fowler and Walter

1985, Weaver and Basgall 1986). The clearing of branches, needles, and duff during trench construction effectively creates “defensible space” around individual trees, which results in somewhat reduced wildfire damage to the trees (Slaton et al. 2019). Although Pandora moth outbreaks can slow pine growth (Ciesla et al. 2010, O’Neill et al. 2023), and the species has thus been viewed in the past as a pest (Patterson 1929, Carolin and Knopf 1968), the 2-year life cycle of *C. pandora* combined with Traditional gathering activities can combine to mitigate the usually minor negative effects of herbivory (Hoffman 2013) on a local basis (Slaton et al. 2019).

The prepupal wandering phase of lepidopteran larvae is dangerous and physiologically stressful (Brackley 2021). During this time, 3 critical life phases of *C. pandora* occur in rapid succession: descent from the pine canopy, dispersal across the surface of the ground, and burrowing in the loose soil and duff. This journey is likely to be hazardous and energy consumptive; descent is diurnal, and prepupal larvae would be expected to be exposed to predators and stress from the summer sun.

Despite the prominence of outbreaks, concerns about tree damage, the cultural significance of the moth as an ancient Native foodway, and the ecological importance of Pandora moths, there is not much detailed information available about the events occurring during the short, critical period of larval descent, dispersal, and burrowing. This study examines the nature of larval movement on trees as well as on and in the ground; the time required for the various phases during the day of descent; and parasitoid and environmental threats during ground dispersal.

Our observations were made in Jeffrey pine forest of the Indiana Summit Research Natural Area (Fig. 1d), Inyo National Forest, in east central California, just south of Mono Lake (37.80187, −118.90438). This montane forest is at 2600 m elevation and averages 6 months of snow cover. The overall aspect of the forest is west, and the average slope is 7 degrees, although there is much smaller-scale variability across rock bands and draws (Fig. 1d). Jeffrey pines between 30 and 40 m in height dominate the forest (as determined from data acquired as described in Ramirez 2015; Fig. 1c, d), along with scattered individuals and stands of lodgepole pine (*Pinus contorta* Douglas ex Loudon) and white fir (*Abies concolor* [Gord. & Glend.]

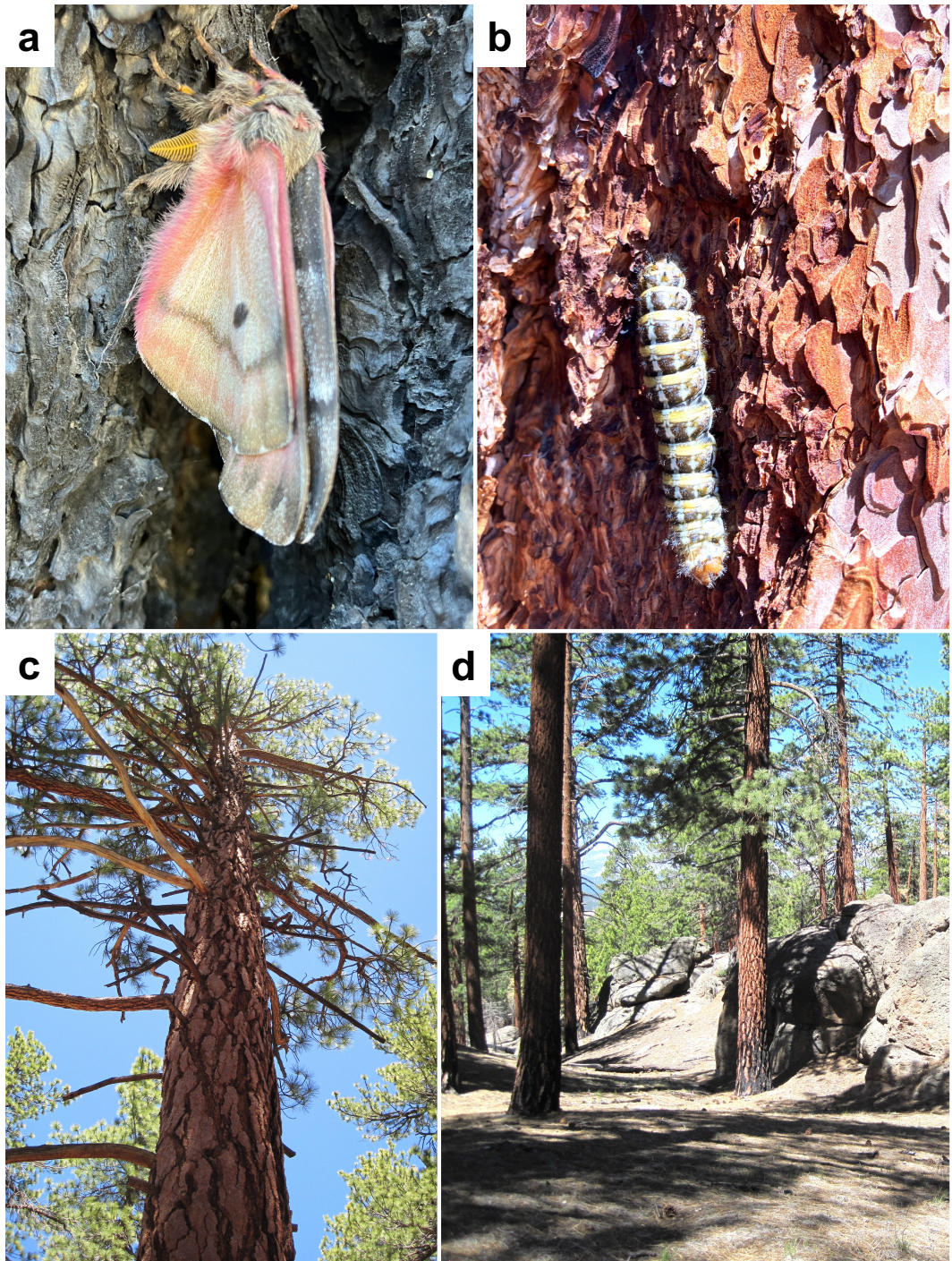


Fig. 1. *a*, Adult male Pandora moth, *Coloradia pandora*. *b*, Pandora moth larva descending a Jeffrey pine (*Pinus jeffreyi*) prior to pupation in the soil. *c*, Large Jeffrey pine. *d*, Jeffrey pine-dominated habitat in Indiana Summit Research Natural Area, Inyo National Forest, California.

Lindl. ex Hildebr.), and there is a sparse understory of shrubs, forbs, and grasses. All observations on larval movements were made without any form of interference in the animals' natural forest habitat. Larvae were observed during daylight hours (08:30–17:30) in the periods 1–6 July 2020, 1–9 July 2022, and 25 June–4 July 2024 during their biennial descent from the pine canopy. Larval locomotory speeds during tree descent and dispersal across the forest floor were estimated with a flexible, fiberglass tape measure while avoiding contact and shadow casting. Each measurement was made on a different larva. We were not able to measure or estimate speeds of descent for larvae observed higher than 10 m from the ground, and we thus have no information about locomotion within the canopy.

Most descending larvae (Fig. 1b) were on larger trees (>70 cm diameter at breast height; Fig. 1c). Descent seemed “tentative” for some larvae and was interrupted by quiescent periods. About 10% of the larvae were not in motion when initially spotted from the ground. Some individuals remained motionless on their natal tree for the entire day. Other larvae would occasionally reverse course and begin ascending the tree for about 30 s before either resuming their descent or remaining motionless for up to 15 min. Descent speeds were only estimated for moving individuals and did not include any time while the larva was stopped. Mean descent speed was 0.64 cm/s (SE = 0.08, $n = 6$), and the range was 0.44–0.93 cm/s (video, Supplementary Material 1). Larvae descending at 0.64 cm/s would be expected to descend 17 m in 45 min, but, with stops, 45 min might only be sufficient for 15 m of descent. Canopy base height of the larger pines that support larvae is approximately 10 m (Slaton et al. 2019), and thus 45 min of descent time would be sufficient for a larva to reach the ground from the lower portion of the canopy. We did not observe any descending larvae being attacked by parasitoids; we would have been able to observe attacks that took place within 4 m of the ground, but not higher.

Larvae slowed as they transitioned to the ground, and about half of the observed individuals tumbled to their sides as they attempted to navigate the new terrain (video, Supplementary Material 2). The larvae recovered within 1 min and attained a greater speed than was observed during descent (video, Supplementary Material 3). Movement was no longer tentative but

rapid and seemingly driven, and larvae often appeared to orient toward the sun. Larvae on the ground moved at 1.63 cm/s (SE = 0.09, $n = 13$), which is significantly faster than the speed observed during tree descent (2-tailed independent t test on $[\log + 1]$ -transformed data: $P < 0.001$, $t = -8.87$, $df = 17.0$). The absolute range was 1.23 to 2.08 cm/s. Several larvae that encountered rocks >2 m in diameter continued crawling straight across these substrata that were clearly unsuitable for pupation, rather than altering course. Larvae moving across the soil and duff were never observed to stop, unless the animals had rolled off of rocks several times in succession, in which case the larvae would lie still for several minutes before continuing.

Larvae were attacked by insects during dispersal on the ground; we did not observe attempted avian or mammalian predation. We observed ants (*Formica sibiyla* Wheeler, 1913) attacking larvae and consuming dead larvae, but we did not observe the ants successfully killing larvae. Parasitoids appear to be a more formidable threat. About 10% of observed moth larvae carried 1 or more tachinid fly eggs dorsally and/or were being pursued by 1 or more sarcophagids (flesh flies) attempting to larviposit first-instar larvae, not eggs, on the caterpillars (Fig. 2; video, Supplementary Material 4). A tachinid captured while depositing eggs on larvae is believed to be in the *Chetogena claripennis* (Macquart, 1848) complex (John Stireman III personal communication). Sarcophagid females, identified as *Blaesoxipha* sp. (Greg Dahlem personal communication), were observed perching on nearby fallen pine needles between rapid forays for attempted or realized larvipositing (Fig. 2; video, Supplementary Material 4). The sarcophagids would often shake violently on a needle for a fraction of a second between larvipositing attempts. We did not observe hymenopteran parasitoids.

Pandora moth larvae increased speed (1) when being attacked by parasitoid flies, (2) when dispersing in direct sun during the warmest part of the day (up to 30 °C), or (3) after traveling for 20–25 min. This faster locomotion seemed less efficient: there was less slowing when the larvae encountered obstacles and more frequent tumbling awkwardly to one side. There was a decrease in speed if larvae traveling in sun encountered shade.

The prepupal larvae that we observed began burrowing 1.5–30 min after dispersing away

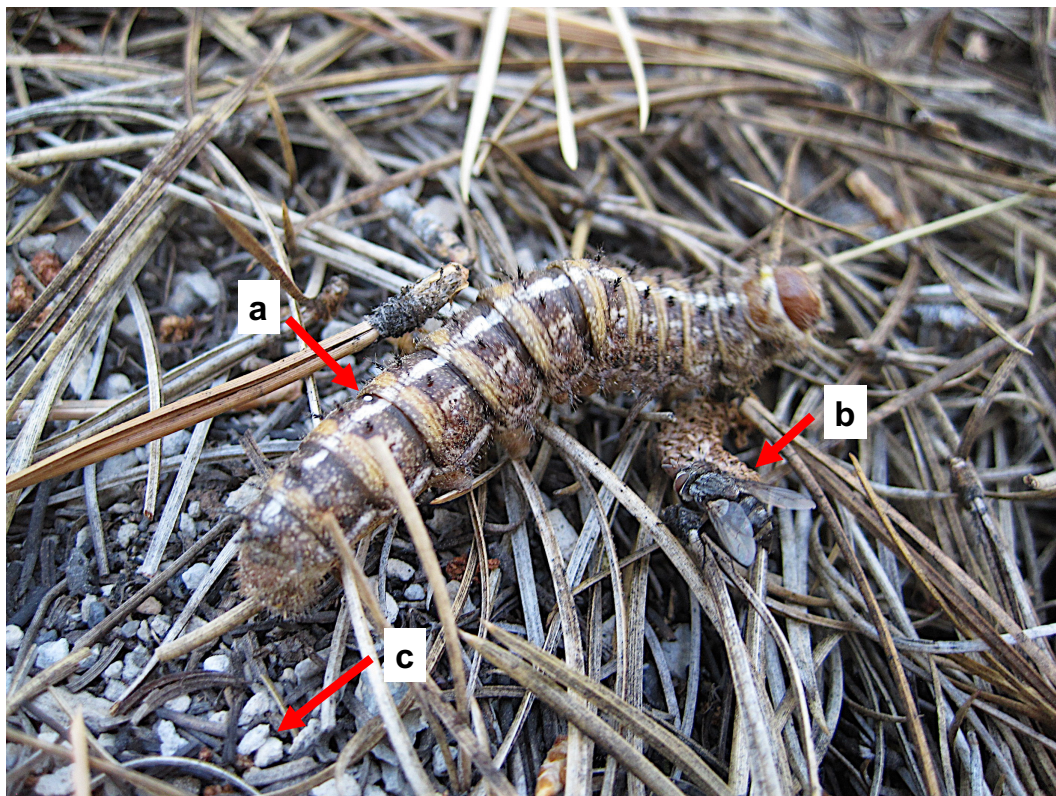


Fig. 2. Pandora moth larva bearing a tachinid fly egg (a) and being pursued by a sarcophagid fly attempting to larviposit (b). Also visible is a substrate of needles, duff, and loose soil, including pumice particles (c).

from the natal tree. Dispersal distance was shorter (<10 m), and thus burrowing began sooner, in high temperatures or when larvae were being pursued by parasitoid flies. If ~ 45 min are required for descent and 1.5–30 min are spent in travel before burrowing, then the entire process could be completed in 50–75 min if the larva was not in the upper half of the canopy at the beginning of descent. Additional descent time would be required for larvae feeding in the top of the canopy. Dispersal distance from the natal tree was observed to be 10–30 m unless the larva was being attacked relentlessly by parasitoids. It is worth noting, however, that we occasionally saw larvae crossing dirt roads >30 m from pines. Although we did not observe the entire transit of these larvae, some animals must have traveled farther than 30 m and probably for longer periods of time.

The burrowing that we observed appeared to be generally peristaltic in nature (Supplementary Material 5). Larvae burrowed 1–5 cm below the

surface. Burrowing was often shallow (1 cm), even in full sun on a hot day, if the larva had been attacked by parasitoids or had been traveling for longer periods of time (20–30 min).

Peristaltic motion is in general a key component of locomotion in lepidopteran larvae. There is a peristaltic wave of contraction and relaxation that causes the body to move forward in an approximately linear fashion (Dethier 1989, Brackenbury 1999), but there are many complexities and refinements at the scale of individual body segments (Trimmer and Issberner 2007). Further, grip and propulsion by the prolegs and legs have been found to be important as well, and gut movements may also contribute to propulsion (van Griethuijsen and Trimmer 2014). *Coloradia pandora* has a greater body length and is faster than a number of other species (Berger 1992, Brackenbury 1999), although the eastern tent caterpillar, *Malacosoma americanum*, can be faster still at high temperatures (Joos 1992).

Some lepidopteran larvae increase crawling speeds significantly as the temperature increases (Dethier 1989, Joos 1992). Dethier, studying 3 species of arctiid caterpillars, noted, “Obstacles impede them less; there is an indomitable drive forward until shade is encountered,” which matches our observations of Pandora moths in high temperatures and full sun. Heat stress and desiccation are known to be dangerous for lepidopteran larvae (Dethier 1989). Larvae of some other lepidopteran species are known to respond to predation attempts (Dethier 1989, Brackenbury 1999) in a manner similar to our observations. Pursuit by parasitoids on hot days is likely to be particularly stressful.

Larval descent from trees was 2.5 times slower than horizontal ground travel in our study. Descent appeared to be tentative relative to travel on the ground, and larvae became motionless at times, occasionally for long periods. It is possible that the stops were because downward travel was tiring, but the stops, and even reversal to climbing, were more suggestive of unfamiliar orientation and navigational processing than exhaustion. Indeed, Vaughan et al. (2018) found only subtle behavioral and biomechanical alterations as tobacco hornworms, *Manduca sexta* (Linnaeus, 1763), transitioned from horizontal travel to climbing.

Population outbreaks are one of the defining characteristics of the Pandora moth, and a variety of parasites and predators may contribute to population control. A polyhedrosis virus (Hoffman 2013) and a variety of birds are known to attack larvae (Patterson 1929, Ciesla et al. 2010). Ground squirrels (*Callospermophilus* spp.) and chipmunks (*Neotamias* spp.) are thought to contribute to control of *C. pandora* populations by feeding on pupae (Patterson 1929, Gerson 1995, Ciesla et al. 2010). Pupae may be eaten immediately or cached by these rodents. Patterson (1929) observed a chipmunk caching pupae in a hollow log, which, when examined, yielded 54 pupae.

Parasitoids have a well-deserved reputation for controlling high-amplitude population cycles in other forest Lepidoptera (Berryman 1996; see also Marino et al. 2006, Salim et al. 2016), and parasitoids may have an important role in controlling Pandora moth populations as well (Patterson 1929). In addition to the tachinid and sarcophagid parasitoids that we observed directly attacking larvae, the tachinid *Leschenaultia adusta* (Loew, 1872) is known to partially

consume *C. pandora* larvae and pupate nearby (Patterson 1929). This tachinid lays eggs on vegetation that is consumed by caterpillars; consumed eggs are ingested along with the vegetation, and some eggs successfully produce larvae within the caterpillar gut, which then proceed to consume the caterpillar (Jackson et al. 1970). Several wasps and other insects are also known parasitoids of *C. pandora* and could further contribute to population control and the observed cycling of outbreaks (Hoffman 2013). These parasitoids are probably more likely than vertebrate predators to exhibit density-dependent interactions with the Pandora moth hosts.

Nonlethal effects of parasitoid attack and heat may ultimately result in larval death through positive feedback mechanisms, which could in turn be exacerbated by climate change. We observed shallow burrowing by *C. pandora* prepupal larvae that had been stressed by rapid travel in response to heat and parasitoid attack. High soil temperatures can cause mortality among Pandora moth larvae after they burrow for pupation (Ciesla et al. 2010), and larvae that only burrowed a centimeter below the surface should be particularly vulnerable. Thom et al. (2015) found that hairstreak butterfly pupae in forest soils were more susceptible to wildfire mortality when only shallowly buried, and wildfire is an integral part of the studied Jeffrey pine forest–Pandora moth ecosystem (Slaton et al. 2019). Shallow burrowing can also expose insect pupae to attack by pupal parasitoids (Frederickx et al. 2014). Thus heat and/or parasitoid attacks on *C. pandora* larvae can create positive feedback such that exhausted larvae that have survived travel in heat or escaped without successful larval- or oviposition by parasitoids are only able to burrow shallowly in the duff, making them yet more vulnerable to heat, wildfire, or attack by rodents or pupal parasitoids. The warming climate is likely to reduce survivorship of *C. pandora* larvae and pupae in a number of ways: (a) warmer temperatures would be expected to make ground travel by larvae faster and more stressful; (b) faster, less efficient travel in response to parasitoid attack should be more stressful in warmer temperatures; (c) if larvae are only able to burrow to a shallow depth due to the above 2 factors, then ensuing pupal parasitoid attack would be more likely; (d) rodent predation would be expected to increase for shallow pupae; (e) soil temperatures would be more likely to be too hot for pupal survival after

shallow burrowing; (f) higher intensity wildfires that are expected to become more frequent would result in attendant mortality for shallowly buried pupae; and (g) drought-related mortality of pines (Moore et al. 2024) would reduce forage for larvae. Even if only some of these hypothesized climate effects occur, warming temperatures would be expected to exert an overall negative influence on Pandora moths.

SUPPLEMENTARY MATERIAL

Five online-only supplementary files accompany this article (<https://scholarsarchive.byu.edu/wnan/vol86/iss1/17>).

SUPPLEMENTARY MATERIAL 1. Video of Pandora moth larva descending Jeffrey pine (11.5 MB, .MOV).

SUPPLEMENTARY MATERIAL 2. Video of Pandora moth larva transitioning from tree descent to ground travel. The observed tumbling to the side occurred in about half of the observed tree-to-ground transitions (4.2 MB, .MOV).

SUPPLEMENTARY MATERIAL 3. Video of Pandora moth rapid travel across ground during brief dispersal phase (5.9 MB, .MOV).

SUPPLEMENTARY MATERIAL 4. Video of sarcophagid fly attempting to larviposit on Pandora moth larva (18.4 MB, .AVI).

SUPPLEMENTARY MATERIAL 5. Video of Pandora moth larval burrowing behavior in soil and duff (27.4 MB, .MOV).

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