



Predicted fates of ground-nesting bees in soil heated by wildfire: Thermal tolerances of life stages and a survey of nesting depths

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ARTICLE INFO

Article history:

Received 17 March 2011

Received in revised form 15 July 2011

Accepted 16 July 2011

Available online 11 August 2011

Keywords:

Apiformes

Apoidea

Pollinator

Fire

ABSTRACT

Periodic wildfire defines plant community composition and dynamics in many of the world's semi-arid biomes, whose climates and floras also favor wild bee diversity. Invasive flammable grasses, deforestation, historical fire suppression and human ignition are increasing fire frequency and intensifying its severity, as well as introducing fire to previously fireproof biomes. In many of these habitats, bees are key pollinators. Many, often most of the solitary bee species and individuals in these biomes nest underground (so-called "mining" bees). To evaluate their susceptibility to fire, we tested heat tolerances of bees' four life stages using an experimental design that mimicked heat conduction dynamics of natural soils. All life stages survived heating of up to 45 °C for 27 min, but none survived heating at 54 °C for 9 min; the pupal stage survived best. At near-lethal temperatures, more prolonged heating caused more mortality. These data were related to published studies of heat penetration depths in soil during fire and an exhaustive compilation of published nesting depths reported for mining bees. We conclude that a small fraction (9%) of the shallowest-nesting mining bee species is likely to die from soil heating by wildfire. Among these, ground-nesting megachilids (*Osmia*, *Megachile*) will be most vulnerable, owing to their shallow horizontal nests. Because mining bees prevail in most biomes of the temperate zone, any vegetation rehabilitation efforts should therefore expect that bee communities will largely survive the immediate effects of wildfire, and therefore will need pollen and nectar resources in the year(s) after fire.

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1. Introduction

Fire is a major ecological factor in many terrestrial biomes, particularly grasslands, savannahs and Mediterranean-climate shrublands (Bond and van Wilgen, 1996; DeBano et al., 1998). The importance of fire in these semi-arid biomes is readily observed when fire is suppressed. Historically, many of these ecosystems burned periodically, often with fires of relatively low intensity (sensu DeBano et al., 1998). Many plants in these systems have adaptations that enable them to cope with these low intensity cooler fires (Bond and van Wilgen, 1996).

Over the past century, fire intensities and return frequencies have increased in many biomes. In many forests of North America, Europe and Australia, for instance, surface fuels have accumulated as an unintended consequence of many decades of effective fire suppression policies (Neary et al., 1999; Pyne et al., 1996). Additionally, invasions of flammable alien plants are fueling more intense and frequent fires across some semi-arid North American

biomes, as well as other ecoregions of the world (Brooks et al., 2004). A prime example is annual Eurasian cheatgrass, *Bromus tectorum* L., that has escaped into the American sage-steppe, where it greatly increases the horizontal continuity of flammable vegetation (Chambers et al., 2007). These altered wildfire regimes are likely to intensify inasmuch as global warming prolongs growing seasons and magnifies summer heat and droughts (Westerling et al., 2006).

Bees, particularly non-social species, are the most diverse, abundant, and dominant pollinator group in these arid and semi-arid biomes (Michener, 2007) that experience periodic fires (Bond and van Wilgen, 1996). Fire can impact bee faunas in several direct ways. In the short term, flames of surface fires scorch flowering forbs and shrubs, their surface roots (Neary et al., 1999) and any current bloom; crown fires can consume bee-pollinated flowering trees (e.g., Australian *Eucalyptus*). Fire also consumes many potential nest sites (and residents) of twig- and cavity-nesting bees. Indirectly, fire changes the availability of resources for bees, often for the better (e.g., Potts et al., 2003). In the growing seasons following a fire, a pulse of more diverse and abundant bloom sometimes (Seefeldt et al., 2007; Wroblewski and Kauffman, 2003) but not always (Platt et al., 1988) results, as flowering plants resprout or germinate to take advantage of habitats opened by fire. There also may be an increase in water availability and a surge of nutrients that leach from

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the ash (Chambers et al., 2007; Christensen and Muller, 1975), again to the benefit of germinating or resprouting flowering plants and their bee pollinators.

A few studies have characterized bee communities' responses to fire (Campbell et al., 2007; Grundel et al., 2010; Potts et al., 2003). They invariably report bee faunas to be present, along with more bloom, but the fires studied have been small in size (e.g., 10 ha, Campbell et al., 2007). Hence, it is impossible to know whether the bees sampled were residents (or their descendants) that survived the fire or were recent colonists from unburned surroundings. Larger-bodied species could even fly in from beyond the fire perimeter on their foraging rounds; for instance, both *Nomia melanderi* (Cane, pers. obs.) and bumblebees (Osborne et al., 2008) have been seen foraging at distances of 1.5 km or more from their nests. Our study was motivated by a need of land managers to anticipate the match between post-fire pollination services and the choice of wildflowers to be seeded back into large wildfires, where distances from edge habitat are substantial. Seeding pollinator-dependent wildflowers into places where pollinators have been extirpated could be a costly mistake.

Wildfires are most likely late in the dry season due to various combinations of heat, drought, summer lightning and dry vegetation (Pyne et al., 1996). In the temperate zone, this typically is the season that follows the one of flowering and bee foraging. Therefore, the immature stages in their natal nests are the ones most likely to experience fire's heat. Adult bees may be able to escape fires through flight, but their nests with eggs, larvae, pupae and pre-emergent adults are immobile and thus susceptible to fire. Nest residents may die from lethal substrate heating unless the nests are adequately insulated.

We experimentally subjected live bee eggs, larvae, pupae and pre-emergent adults to incremental heat intensities and durations using moist sand substrates and other protocols designed to mimic soil heating by fire via conduction. We also compiled a first-ever database of bee nesting depths for 449 ground-nesting bee species gleaned from the literature and our own unpublished records. We used this database to estimate the proportion of ground-nesting bee species that might be susceptible to lethal soil temperatures from fire. In addition, we used published records to estimate what proportion of the bee fauna nests underground.

2. Materials and methods

2.1. Bee life stages

Most bees are active adults for only 4–6 weeks. Species that are social or multivoltine (multiple annual generations) often develop rapidly from egg through adult, typically in a month. The delicate egg phase is brief, typically less than a week. The larval phase typically lasts 2–3 weeks; most growth occurs at maturity. Among social and multivoltine species, the larva then pupates and a week later, emerges as an adult. However, most bee species and individuals are solitary and univoltine. In these species, the post-feeding larva enters into a resting phase that commonly lasts 10+ months before pupation the following year. Alternatively, some early vernal species pupate in the fall to overwinter as an adult. In either case, most of the life cycle of univoltine species is spent in the natal cell. Given the relative timing and durations of the different life cycle phases of bees, the larval and pre-pupal phases are the most likely to experience fire, followed in likelihood by the adult phase.

2.2. Experimental species and life stages

Two cavity-nesting bees were used for experiments rather than mining bees, as nests and progeny of mining bees are rarely available

in large numbers and are difficult to excavate and transport unharmed. We chose two species of Megachilidae, *Osmia lignaria* Say and *Megachile rotundata* (Fab.). Both species are readily available and have familiar life history parameters (Bosch and Kemp, 2001; Pitts-Singer and Cane, 2011). Moreover, these two genera include other species that, instead of the more familiar cavity-nesting habit, nest shallowly underground (Cane et al., 2007; Eickwort et al., 1981). We measured survival during soil heating in assays that mimicked fire heating of soil so that responses of these two cavity-nesting species would be relevant to their shallow-nesting congeners and ground-nesting bees in general.

2.2.1. Adults

Loose cocoons containing adult male *O. lignaria* from northern Utah were overwintered at 4 °C until mid-March. These were X-rayed to find and discard the few cells that were parasitized, diseased, or with pre-pupae; all live individuals still had fat body reserves (clear zone in X-ray negatives). Immediately prior to experimentation, cocoons were warmed to 9 °C for 18 h, a compromise to lessen thermal shock but without eliciting emergence of this early spring bee. Following an experiment, cocoons were placed individually in gel caps and incubated at 24 °C for a week while daily checking for emergence of live adults.

2.2.2. Immatures

Loose nest cells containing pre-pupae (post-feeding larvae) of *M. rotundata* (mixed sexes) from Canada were overwintered at 4 °C until early April. These were X-rayed to find and discard the few cells that were parasitized, diseased or empty. To elicit pupation, cells were incubated at 30 °C for 12 days prior to experimentation. Ten cells were dissected to confirm that pre-pupae had transformed to young pupae for experimental use. Following an experiment, cocoons were returned to the incubator and, over 28 days, monitored daily for adult emergence.

In July, a nesting population of *M. rotundata* was started in Logan, Utah using standard polystyrene foam nesting blocks with paper straw liners inserted into the holes. Adults had access to alfalfa (*Medicago sativa* L.) and other flowers. Newly completed nests in the straws were held at ambient temperatures and X-rayed to confirm that they contained either eggs or feeding larvae with partly consumed pollen provisions. Following the experiment, these nests were held at 24 °C until post-feeding larvae commenced spinning cocoons. Nests were then X-rayed and cells scored for developing and dead larvae.

2.3. Thermal tolerance experiment

Steel cans (450 ml) were 2/3 filled with loosely packed, fine moist clean sand (15% w/w water). Mining bees place their nest cells at depths with some soil moisture (Cane, 1991). By using moist sand, we also averted possible complications from bee desiccation while improving conductive heating. Cans filled with sand were placed in a programmable shaking hot water bath and warmed to experimental temperatures. Sand heating and later cooling was monitored using a digital recording thermometer. Immature bees were added once the sand reached the desired temperature. Loose cocoons (of *O. lignaria* and *M. rotundata*) were placed in lightweight mesh tea bags; these were laid across the warmed sand surface, one per can, and topped with heated moist sand from another can. For *M. rotundata* eggs and feeding larvae, paper straws with intact nests were implanted vertically in the cans of heated sand.

Cans remained in the hot water bath for a fixed time period (1, 3, 9, 27 min) at a constant temperature (38, 42, 46, 50 and 54 °C). After that, cans were removed and allowed to passively cool to room temperature (24 °C) over about 40 min. Cocoons

or nest cells, including controls, were then transferred to small ventilated paper carton containers held at a constant 26 °C. Egg and larval development were monitored by periodic x-radiography until cocoon spinning by surviving mature larvae was evident. Pupae and adults were likewise held until surviving adults emerged from their cocoons. Survival of treated individuals was calculated as the percent of average control survival for each life stage.

Treatments (20; 4 exposure durations each at 5 temperatures) received 10 adults ($n = 200$) or 15 pupae ($n = 300$) each, or variable numbers of eggs ($X = 4.6 \pm 2.5$, $n = 57$) or feeding larvae ($X = 9.5 \pm 3.9$, $n = 190$) as the latter were used while still in their intact nesting straws. Given the limited numbers of available nests with eggs, we chose not to test combinations of 42 °C (9 and 27 min) or 48 °C (3 and 9 min) or 54 °C. Controls ($n = 10$ –27) for each life stage were handled the same but not heated. Survivors of each of the four tested life stages were counted and adjusted for control mortality. Logistic regression analysis was chosen, as it allows statistical comparison of a proportion (here, mortality) as a function of independent variables (Allison, 1999). Life stage, temperature and duration (main effects) and their interaction were compared for the proportion of surviving bees. Convergence criteria for the model were met. The Wald test was the appropriate overall statistical test, given our small sample sizes.

No institutional review was required or available for experiments with common insects. Deaths of the several hundred bees incurred during these experiments will be more than offset if practices to rehabilitate plant communities after fire addresses our prediction that wild bee communities will largely survive the fire and so be in need of suitable bloom in the year after fire or face starvation.

2.4. Survey of nest cell depths

Our coverage of the available literature is most complete for the Americas, less so for Europe and quite limited for Asia, Australia and Africa. Where multiple reports were available for a single species, we used the shallowest and deepest cell depths reported. In a few cases, cell depths were not given but nest drawings with scales were provided, by which cell depths could be measured. Reported depths are given as the distance from the nest entrance to the cells along a line perpendicular to the soil surface (e.g., vertical for most species, horizontal for bank nesters). Both mean and median cell depths for each species would have been useful for estimating fire susceptibility, but they are rarely reported.

3. Results

3.1. Thermal tolerances

Buried *O. lignaria* adults and *M. rotundata* eggs, larvae and pupae survived heating at 38 °C and 42 °C for as long as 27 min (Fig. 1). Conversely, no stages survived heating of the damp sand substrate for 9–27 min at 54 °C. All three independent variables contributed significantly to the regression, thus: life stage (Wald $X^2_{[3]} = 79.2$, $p < 0.0001$), temperature (Wald $X^2_{[1]} = 76.8$, $p < 0.0001$), duration (Wald $X^2_{[1]} = 5.5$, $p = 0.02$), and the interaction of temperature and duration of heating (Wald $X^2_{[1]} = 9.08$, $p < 0.003$). At the intermediate heating temperatures, greater durations resulted in more mortality (Fig. 1). Control survival was good for eggs (90%), larvae (96%) and pupae (87%) but not male adult *O. lignaria* (67%). When adult data were removed from the logistic regression analysis, life stage and temperature remained significant in the regression, and maximum likelihood estimates showed that pupae survived heating better than did eggs (Wald $X^2_{[1]} = 4.086$, $p < 0.043$) but not larvae (Wald $X^2_{[1]} = 0.092$, $p < 0.092$).

3.2. Nest cell depths

Our compilation of the available nesting data for bees indicates that 64% of all non-parasitic bees (55% of all bees) excavate their own nests in the soil (Appendix A). This estimate is necessarily imprecise as so few species have been studied. Because some additional species, mostly megachilids, adopt pre-existing cavities in the soil for nesting, the total percentage of bees that nest underground is slightly greater. Reported cell depths of mining bees range from 1 cm to 530 cm (Appendix B). The average minimum cell depth is 17 ± 26 cm (1–270 cm, $n = 447$, median = 10 cm) while the average maximum cell depth is 35 ± 49 cm (2–530 cm), $n = 448$, median = 20 cm). Variation among species within families is substantial. Of these 449 species, 26% had at least some cells at depths of ≤ 5 cm, but only 9% of the species had all their cells in such shallow nests (Fig. 2). Moreover, half of the species had at least some of their cells 10 cm deep or less and 24% of the species had all of their cells at ≤ 10 cm. The Megachilidae (species studied herein) are notable for consistently shallow nests, with mean cell depth ranging from a minimum of 5.3 ± 6.4 cm (1–16, $n = 50$) to a maximum of only 8.4 ± 5.9 cm (1.5–25, $n = 50$). Lethal fire heat often penetrates mineral soils to depths of 5 cm (see Sections 4.2 and 4.3), putting progeny in such shallow nests at high risk; conversely, those deeper than 10 cm are at zero risk (Fig. 2).

4. Discussion

4.1. Heat tolerances of bees

All buried individuals of *O. lignaria* and *M. rotundata* of every life stage died from conductive heating of the damp sand substrate for 9 min at 54 °C (Fig. 1). For temperatures that approached this lethal limit (46–50 °C), prolonged heating (27 min) was more deadly than brief heating (60 s). Note, however, that even the 60 s treatment was followed by a gradual soil cool-down meant to mimic the passage of a flame front over a soil surface (DeBano et al., 1979). Pupae of *M. rotundata* were more heat tolerant than eggs in our assays, most individual pupae surviving 1–9 min heating at 50 °C and even brief exposure to 54 °C. The biological relevance of such small temperature differences are not interpretable for now because the few reported instrumental recordings of soil heating by fire are quite imprecise (e.g., DeBano et al., 1979; Hartford and Frandsen, 1992).

Comparable thermal limits have been reported for a few bee species, albeit under different heating regimes. Specifically, all published studies used dry, still, hot air of an incubator to heat later life stages for longer time periods. Air transfers heat much differently than moist sand. Pre-pupae and pupae of *M. rotundata* survived 1–3 h exposures to air heated at 45 °C, but all died after 0.5–3 h at 50 °C (Undurraga and Stephen, 1978). Barthell et al. (2002) compared this species with *M. apicalis*. After 3 h at 50 °C, 40% of *M. apicalis* pre-pupae survived to finish development to adulthood, but only 20% of *M. rotundata*; nearly all survived heating at 49 °C. That study was unusual in finding small but meaningful differences in thermal tolerances among congeneric bees. Adults of two species of honey bee (*Apis mellifera*, *Apis cerana*) survived slow stepwise heating to 49 °C but died after 20 min at 52 °C (Ken et al., 2005). These results were broadly predictive of our findings for heat tolerances of eggs, larvae, pupae and overwintering adults of solitary bees that we buried in hot damp sand for shorter durations.

4.2. Fire risk predictors for mining bees

We propose that four factors taken together should predict the fates of progeny of mining bees during fire: soil moisture, surface

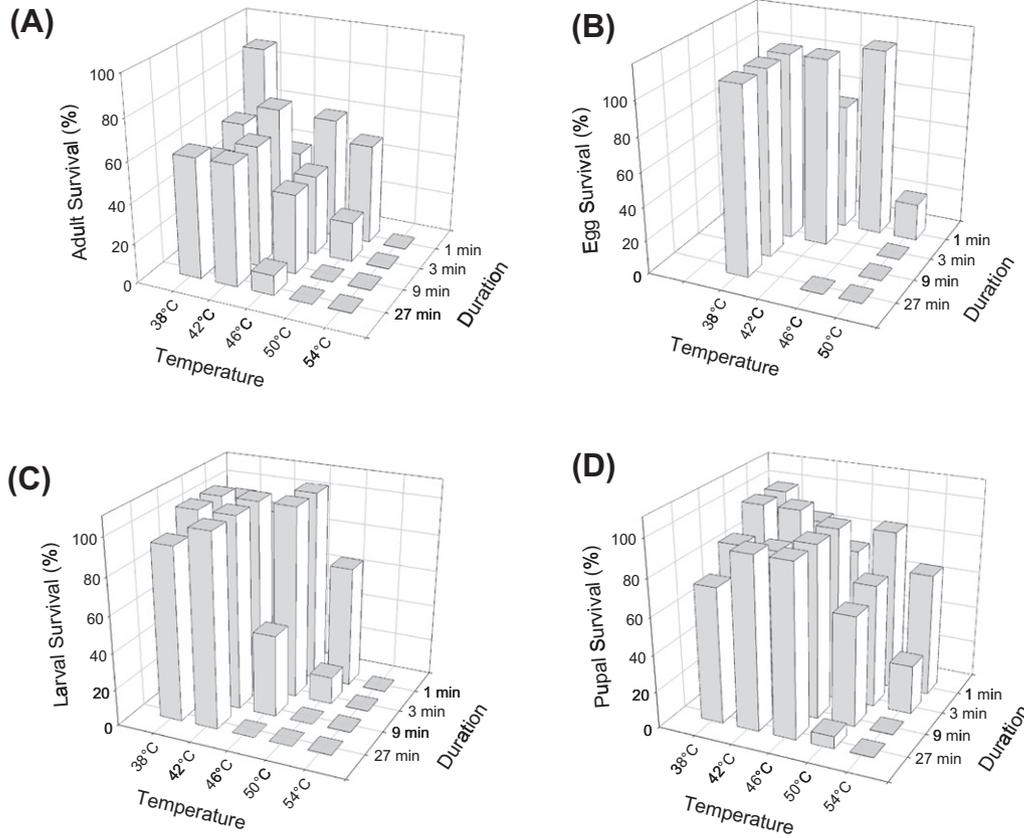


Fig. 1. Percent survival of cohorts of overwintering adult *Osmia lignaria* bees (A), and eggs (B), feeding larvae (C), and pupae (D) of *Megachile rotundata* held different temperatures and durations of soil heating, followed by gradual cooling. No eggs were tested at 42 °C (9 and 27 min) or 48 °C (3 and 9 min) or 54 °C owing to insufficient live material.

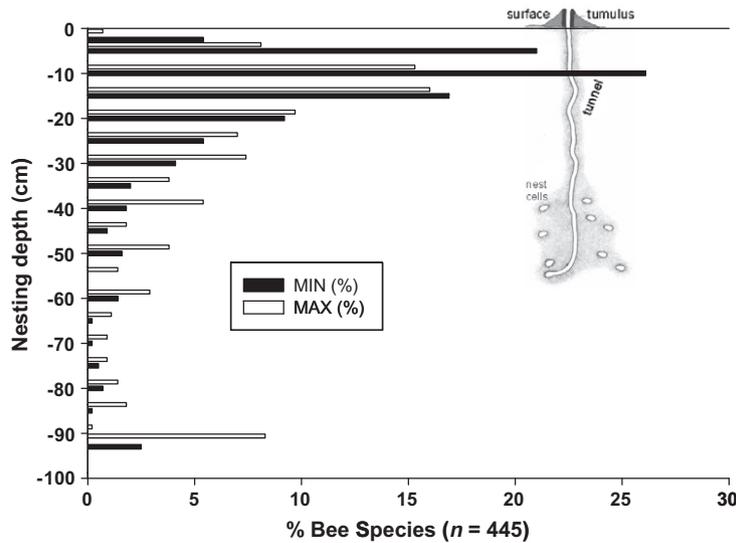


Fig. 2. Frequency distribution of nest cell depths reported for 449 species of mining bees, depicting depths of their shallowest and deepest nest cells. Data compiled in Appendix B. Inset drawing of a representative subterranean nest of a solitary bee adapted from Fig. 5 in Rozen (1984). Nest cells <5 cm deep are at high risk from fire, those from 5 to 10 cm depth are at low risk, and those >10 cm are at no risk.

fuel loading, preferred nesting surface, and especially, nest cell depth. Grassland combustion can generate intense heat, but because surface fuels are sparse, these fires do not linger long, so soil warming is minimal (DeBano et al., 1998). Shrublands offer more woody fuel and therefore burn hotter (Neary et al., 1999). Surface temperatures exceeded 500 °C during some fires in California

chaparral, but remarkably, the soil barely warmed at 5 cm depth (DeBano et al., 1979). Fires can heat mineral soils more deeply when the surface has thick dry layers of combustible leaves, needles, or woody debris (e.g., Busse et al., 2005). When these undergo a smoldering burn, a surface layer of ash forms that insulates smoldering organic matter below, driving heat deep into mineral soils

(DeBano et al., 1979). In general, mining bees forgo nesting amid thick duffs anyway (but see Cane, 1994), preferring patches of bare ground or soil banks, or at most, thin surface duffs (Malyshev, 1935). Mining bees also typically place their cells at depths with some soil moisture (Cane, 1991); by moistening the sand for our experiments, we enhanced heat transfer by conduction, both in warming and later cooling. At higher temperatures, evaporation of moisture from decaying surface duffs and the mineral soils beneath, a “latent heat of vaporization”, can significantly retard soil heating during fire (DeBano et al., 1979; Hartford and Frandsen, 1992). Under surfaces with little or no duff (e.g., in grasslands or shrub-steppe), the lethal heat of above-ground combustion is largely lost to the atmosphere; at depths >5 cm in these soils, reported temperatures do not exceed 50 °C, as reviewed above.

4.3. Fire-susceptible ground-nesting bees

As a consequence of soil heating dynamics, shallowly placed bee nest cells (≤ 5 cm) could be at risk of deadly heating, but those deeper than 10 cm should be safe from fire in nearly all nesting contexts. Our literature survey, though large, only represents 4% of the ground-nesting fauna. To the extent that our survey represents all mining bees, then only 9% of the soil nesting species of bees would be in significant danger of population loss from wildfires. Another 44% (those with some cells ≤ 10 cm deep) could lose some progeny to more intense wildfires but populations would persist (Fig. 2; Appendix B). Nearly 75% of mining bee species place at least some of their nest cells deeper than 10 cm. (Fig. 2) where they should be safe from soil heating by wildfire. Deeper nest cells should also be safe from wind and water erosion of soils laid bare by fire. Confirmation of our predictions awaits comparative sampling of bee communities from far within the perimeters of large wildfires.

The few bee species that nest shallowly enough to be at risk from fire-generated soil heating are not merely tiny bees too feeble to dig deeper. The list of non-social bees with shallow nests does include small-bodied panurgines (Rozen, 1967), but there are also larger-bodied megachilids plus a mixed lot of anthophorines, emphorines and centridines (Apidae) of a size comparable to the honey bee. Many of the latter three groups nest shallowly but in vertical soil banks (Michener et al., 1958; Rau, 1926) where they could be less affected by wildfires than bees nesting in flat ground (but see Maynard and Rao, 2010). In addition, a number of species of *Osmia* and *Megachile* nest underground, in contrast with their relatives' more familiar habit of nesting above-ground in existing cavities (Cane et al., 2007; Eickwort et al., 1981). These megachilids comprise only 6% of all ground-nesting bee species (and 11% of our nest depth survey) but represent 2/3 of the shallowest-nesting species ($n = 39$) that have all of their nest cells within 5 cm of the surface (Appendix A). Most habitus descriptions of ground-nesting megachiline and osmiine nests report a shallow main burrow that runs horizontally just beneath the soil surface (e.g., Cane et al., 1996; Eickwort et al., 1981; Gordon, 2003). Among ground-nesting bees, we contend that only these shallowest nesters will sometimes suffer lethal heating during wildland fires.

As an aside, we also note that bees nesting shallowly underground can be overheated by mere solar insolation in places with hot summers. Thus, for grasslands of the Vaira Ranch 35 km south-east of Sacramento California USA, soil temperatures at 2-cm depth exceeded 48 °C for 30 h in the summer of 2006 (Dennis Baldocchi, Ameriflux program, *pers. comm.*). Amid the creosotebush desert scrub of the Santa Rita Experimental Range in southern Arizona USA, afternoon summer soil temperatures in 2009 exceeded 50 °C for 100 h and 54 °C for 15 h at 5-cm depth (Russell Scott, Ameriflux program, *pers. comm.*). Conceivably, such intense solar heating (or frequent fire cycles) might select for greater heat tolerance among

shallow-nesting bee species that reside there, and so greater fire heat tolerances than we found in our study. Alternatively, excessive solar heating might exclude shallow-nesting species, or restrict them to shaded microsites.

4.4. Fates of bees that nest above ground

Twig- and stem-nesting species of bees are unlikely to survive the flames of wildland fire. Typical flame temperatures resulting from pyrolysis of natural fuels range from 500 to 1400 °C (900–2500 °F) (DeBano et al., 1998). Bee nests in twigs, stems, small limbs and snail shells have negligible insulation to counter such ferocious heat. Those that do not burn outright will quickly overheat. Susceptible bees with this nesting habit in North America includes: all species of *Ceratina* and some *Xylocopa* (Apidae); all *Hylaeus* and *Chilicola* (Colletidae); various smaller-bodied species of Megachilidae, including some *Megachile* (Eickwort et al., 1981) and species scattered among several genera of the Anthidiini (Grigarick and Stange, 1968), and Osmiini (Cane et al., 2007). Those few bee species that make free-standing nests of mud, leaf pulp or resin against rock or plant surfaces will likewise be very susceptible to the heat of wildfire, unless their nest substrates are distant from flammable debris.

Tunnels chewed by larvae of large wood-boring beetles (typically Cerambycidae and Buprestidae) in tree boles, logs and large limbs are adopted by other species of Megachilidae for nesting. Bee species with this nesting habit include some members of the megachilid genera *Lithurgus*, *Megachile*, *Osmia* and others (Malyshev, 1935). Predicting their fates from the heat of wildland fire is difficult, for although dry wood readily burns, wood is also a good thermal insulator. Furthermore, once it chars over, larger diameter wood can resist further burning (DeBano et al., 1998). Susceptibility of bee nests in wood that is not burned up by a fire will be a complex function of variables related to the substrate and not the bee *per se*. These should include tunnel depth, wood moisture and diameter, bark thickness, log placement (standing or on ground), and duration and intensity of fire (DeBano et al., 1998). Fire also can kill the cambium layer beneath without burning away the bark of standing trees (Bond and van Wilgen, 1996), leaving the tree bole seemingly intact yet rendering it unsuitable for attack by the wood-boring beetles whose holes cavity-nesting bees would later use. Alternatively, shrubs and trees that are merely injured and weakened by fire can later yield an abundance of dead pithy twigs and tunnels of wood boring beetles, and so more nesting opportunities for cavity-nesting bees. In contrast with most mining bees, which will escape the heat of fire unharmed, fire can be destructive to wood- and twig-nesting bees in the short term, but potentially benefit their subsequent generations in the following years and decades, owing both to more floral resources and more nesting opportunities.

4.5. Conservation implications

In contrast to these twig- and wood-nesting bees, we conclude that most ground-nesting bees should survive wildfires, even intense ones, protected by the soil depths where they place their nest cells. Some, perhaps many, bee species' pollination services will be important for sexual reproduction of many of the showier flowering species found in nearly all plant communities. These wildflower species are often desirable when rehabilitating fire-damaged ecosystems, such as the US Great Basin (e.g., Cane, 2008; Wroblewski and Kauffman, 2003).

The ability of bees to accommodate the short term effects of fire on floral resource availability varies widely between species. Many bee species have no extended dormancy and all of their progeny will emerge the next year, regardless of available floral resources.

For a few species, it has been shown that some progeny can remain quiescent through the following growing season to emerge 2 years later (Torchio and Tepedino, 1982). Others, particularly species of arid habitats, exhibit extended dormancy that allows immatures to wait out unfavorable years. These bet-hedging species may not be able to take full advantage of wet years but will not be devastated by a dry one (Danforth, 1999). The extent of these bet-hedging emergence strategies are little known among bees.

To fully retain and conserve the ground-nesting bee communities that we predict will survive fire, a functional diversity of suitable bloom should be available the next growing season. Bloom can result either naturally or through planted seed mixes that include species that flower during the following growing season (typically annuals or short-lived perennials) and that are useful to bees. Pollination by subsequent resident generations of mining bees can contribute to the long-term recovery of these burned plant communities.

Acknowledgments

We are grateful to Drs. Jim Hanula, Leonard DeBano, Glynn Maynard and three anonymous reviewers for their valuable improvements to this manuscript. Data for soil heating by solar insolation comes from the Ameriflux Project.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2011.07.019.

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