Development and Emergence of the Orchard Pollinator *Osmia lignaria* (Hymenoptera: Megachilidae)

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ABSTRACT The solitary bee *Osmia lignaria* Say has been developed as an orchard pollinator in the western United States. Immatures develop through the spring and summer. By late summer, bees become adults and remain in this stage inside their cocoons throughout the winter. In this study, we reared *O. lignaria* at various temperature regimes in the laboratory and outdoors. Developmental rates increased with temperature: bees reared at 18°C took >120 d to complete development, whereas bees reared at 29°C took half that long. Bees reared outdoors under fluctuating ambient conditions took ≈95 d. At 18°C, some bees were unable to complete prepupal dormancy. Different developmental stages responded differently to the various temperature regimes. Fluctuating temperatures averaging 22°C significantly shortened the dormant prepupal stage, and, as a result, bees developed faster than at the equivalent constant temperatures. Bees that developed faster (29°C and fluctuating temperatures) could be wintered as early as August and incubated for emergence in March, 1 mo ahead of bees exposed to natural conditions. These results can be applied to field populations for pollination of early-blooming crops such as almonds, *Prunus amygdalus* Batsch.

KEY WORDS blue orchard bee, development, wintering, emergence, mortality, orchard pollination

Osmia lignaria SAY is a univoltine North American solitary bee that overwinters in the adult stage and emerges early in the year, March–May, depending on the geographical area. After mating, females start building their nests in preestablished cavities such as beetle burrows in timber. Nests consist of a linear series of cells delimited by mud partitions. Each cell is provisioned with a mass of pollen and nectar on top of which an egg is deposited. Completed nests are sealed with a mud plug. Although *O. lignaria* is a polylectic species, females are strongly attracted to flowers from the genera *Prunus*, *Malus*, and *Pyrus* (Rosaceae).

Because of its superiority as a fruit tree flower pollinator, methods to manage *O. lignaria* populations have been sought and developed (e.g., Torchio 1976, 1982a, 1985; Bosch and Kemp 1999). Nesting shelters with nesting materials and adult overwintering bees are placed in orchards shortly before bloom and removed after petal fall. Bee progeny obtained are stored for the remainder of the year. By late spring, the 5th instar completes consumption of the pollen-nectar provision; defecates, and spins a cocoon with silk strands from the labial glands (Torchio 1989). In this stage (prepupa), the bee undergoes a dormancy period (probably diapause-mediated [unpublished data]) that lasts ≈1 mo until it pupates and later becomes an adult in late summer. Adult bees remain inside the cocoon, and a period of cold temperatures is necessary for them to overwinter successfully and emerge the following spring.

Although many aspects of the biology of *O. lignaria* are well known (Phillips and Klostermeyer 1978, Torchio and Tepedino 1980, Tepedino and Torchio 1982, Torchio 1989, Rust 1990), little is known about the effect of temperature on its development. This information is important to effectively manage *O. lignaria* populations for orchard pollination. Rearing temperature not only influences developmental mortality, but also determines emergence time, and therefore synchronization with local fruit tree bloom. The latter aspect is particularly relevant when emergence needs to be advanced to pollinate early blooming crops, such as almonds, *Prunus amygdalus* Batsch.

In 1997, we studied the development, mortality, and emergence of *O. lignaria* at various laboratory temperature regimes and outdoors. The aim of the study was to determine which treatments were adequate for rearing *O. lignaria* populations, and to determine the relationship between rearing temperature and emergence time. Particularly, we were interested in finding 1 or more treatments that would allow us to advance adult emergence without reducing survival or vigor of the bees.

Materials and Methods

Bees were obtained from an actively nesting population managed by our laboratory and released at the beginning of May 1997 in a pear, *Pyrus communis* L., and apple, *Malus domestica* Borkh, orchards in North Logan, UT. Wood blocks with inserted paper straws

(15 cm long and 7.5 mm in diameter) (Torchio 1982b) were used as nesting materials. Every day, a sample of newly plugged paper straws were removed from the wood blocks and taken to the laboratory, where straws were dissected. Within each nest, cells with unhatched eggs were dated assuming an approximate cell production rate of 1 cell per day (Phillips and Klostermeyer 1978, Torchio 1989). Cells with hatched eggs were discarded. In *O. lignaria*, females are ≈1.7 times larger than males, and female eggs are allocated larger pollen-nectar provisions, which tend to be deposited in the innermost cells of nesting cavities (Levin 1966, Phillips and Klostermeyer 1978, Torchio 1989). Using this criterion, cell sex was established initially based on cell position within the straw and provision size, and confirmed in later developmental stages (pupae and adults). Provisions with eggs were transferred to artificial clay cells (Torchio and Bosch 1992) that were labeled with nest number and cell position within the nest and covered with glass slide covers.

Male and female cells were assigned in equal numbers to various temperature treatments, so that no treatment received 2 cells from the same nest and sex. Sample sizes were ≈60 males and 40 females per treatment. Clay wells with eggs and provisions were placed in clear PVC boxes containing 2 additional clay wells filled with water to provide adequate humidity throughout development. Boxes were transferred to temperature cabinets according to the following treatments: 18, 22, 26, 29, and 14:27°C on a 8:16 h daily cycle (mean, 22°C). Clay blocks were checked daily and the dates of hatching, beginning of defecation, beginning of cocoon spinning, and cocoon completion were noted. After cocoon completion, cocoons were placed individually in clear gel capsules, transferred to sticky boards (20 by 25-cm boards with double-sided adhesive tape), and X-rayed every 3 d (Stephen and Undurraga 1976). X-ray plates were used to record the dates when bees pupated and became adults. Upon reaching adulthood, individual bees were progressively cooled down: 10 d at treatment temperature + 10 d at 22°C + 10 d at 18°C, before transfer to 4°C wintering temperature. In treatment 18°C, the 10-d period at 22°C was substituted by 10 d at 18°C, so bees of this treatment spent 30 d at 18°C after adulthood before being transferred to 4°C for overwintering.

Bees were left at 4°C for 215–218 d, after which they were taken out of the cooler. Bees were then removed from the gelatin capsules, individually placed in glass vials, and incubated at 22°C. Glass vials were checked daily and emergence dates were noted. Emerged bees were left at 22°C in the glass vial until they died. Date of death was recorded, and longevity without feeding was used as a measure of vigor.

One additional treatment (orchard) was conducted to imitate naturally variable thermal conditions. Whole nests (n = 47) were left inserted in a wood block placed inside a barn facing north at the edge of the pear–apple orchard in which the parental population had nested. Temperature at the barn was recorded hourly with a temperature logger. Larval development in these nests was checked twice (1 and 20 June). On these dates, nests were brought to the laboratory and a longitudinal flap was cut on the paper straw at the level of each cell. After checking the developmental stage of each individual, the flaps were closed back with adhesive tape to avoid excessive evaporation. After each of the 2 examinations, straws were placed in the original wood block and brought back to the barn. After 20 June, when most bees had either initiated or completed cocoon spinning, nests of the treatment orchard were X-rayed every 3 d, and developmental stages were checked as in the other treatments. Nests of the treatment orchard were kept in the wood block in an unheated barn for the winter. In April, before any bee of this treatment had emerged, nests were dissected and cocoons placed individually in glass vials, which were left in the barn and checked daily for emergence. Emerged bees were transferred to 22°C, and their longevity without feeding was monitored as in the other treatments.

Two-way analysis of variance was used to analyze differences among treatments and between sexes in development time (days to develop from egg to adult), emergence time (days to emerge after incubation at 22°C), and longevity (days from emergence until death at 22°C). Differences in developmental and winter mortality rates were analyzed with chi-square tests.

Results

The first nests were recovered from the orchard on 15 May 1997. By 1 June, virtually all bees of the treatment orchard were 5th instars, and by 20 June, 98.4% of them had either begun or finished cocoonning. By 31 July, all of them had pupated, and by 30 August all of them were adults. Mean development time from egg to adult in the treatment orchard was 97 d (Table 1). Temperatures in the orchard during developmental time (15 May through 30 August) ranged from 1.7 to 45.7°C, with a mean temperature of 19.5°C.

At constant temperatures (treatments 18 through 29°C), all developmental stages were shortened by increasing temperatures (Table 1; Fig. 1). Differences in development time among these 4 treatments were largest for the active larval (instar I to spinning) and pupal stages, and lowest for the prepupal stage (Table 1; Fig. 1). Total development time (egg to adult) varied among treatments (F = 677.46; df = 5, 621; $P <$ 0.001), and it was almost twice as long at 18°C than at 29°C. Of all 4 constant temperatures tested, only bees at 18°C developed more slowly than bees kept in the orchard. In most treatments, females took a few days longer to complete development than males (F = 37.78; df = 1, 621; $P < 0.001$), but there was a treatment by sex effect (F = 3.93; df = 5, 621; P = 0.002). Differences in development time between males and females were largest (9 d) at 18°C and smallest (0–1 d) at the fluctuating temperature treatments (14:27°C and orchard). Bees of treatment 14:27°C (mean temperature, 22°C) developed faster (mean, 70 d from egg to adult) than bees exposed to constant 22°C (mean, 87 d) (Table 1; Fig. 1). The prepupal stage showed the greatest reduction in the fluctuating temperature

Table 1. Duration (in days) of developmental stages of male and female *O. lignaria* reared at various temperature regimes

Treatment	Sex	Egg		I–IV instars		V instar		Cocoon		Prepupa		Pupa		Egg-Adult	
		n	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE
18°C	♂	60	9.0 ± 0.2	59	8.7 ± 0.1	59	12.4 ± 0.4	55	9.3 ± 0.3	46	34.5 ± 1.3	43	46.7 ± 0.5	43	120.5 ± 1.3
	♀	40	9.8 ± 0.4	40	8.4 ± 0.2	40	13.3 ± 0.3	39	9.3 ± 0.3	17	39.3 ± 2.5	15	48.2 ± 0.9	15	129.5 ± 2.8
22°C	♂	64	6.9 ± 0.1	63	5.1 ± 0.1	62	7.9 ± 0.1	62	4.7 ± 0.1	56	29.2 ± 1.1	50	32.3 ± 0.5	50	84.9 ± 1.1
	♀	39	8.1 ± 0.2	39	5.1 ± 0.1	39	8.8 ± 0.2	37	5.6 ± 0.2	33	28.5 ± 1.3	33	33.1 ± 0.7	33	89.5 ± 1.2
26°C	♂	58	6.0 ± 0.2	57	3.7 ± 0.1	58	5.7 ± 0.1	57	3.9 ± 0.2	54	28.3 ± 1.0	54	23.8 ± 0.5	54	71.4 ± 1.0
	♀	49	7.7 ± 0.3	49	3.8 ± 0.1	48	6.1 ± 0.2	47	3.6 ± 0.2	41	30.3 ± 1.3	39	24.5 ± 0.7	39	75.6 ± 1.3
29°C	♂	59	5.7 ± 0.2	58	3.6 ± 0.1	60	5.8 ± 0.1	60	2.3 ± 0.1	57	25.9 ± 0.7	55	18.1 ± 0.5	55	61.5 ± 1.2
	♀	43	7.1 ± 0.2	43	3.7 ± 0.2	42	6.4 ± 0.2	42	2.3 ± 0.1	34	28.0 ± 1.5	32	19.5 ± 0.7	32	65.8 ± 1.6
14:27°C	♂	65	6.9 ± 0.2	64	4.8 ± 0.1	63	7.6 ± 0.2	63	4.1 ± 0.2	61	17.8 ± 0.7	58	28.2 ± 0.5	58	69.3 ± 0.8
	♀	40	7.9 ± 0.3	38	4.9 ± 0.1	38	8.0 ± 0.2	38	4.7 ± 0.2	35	17.0 ± 0.7	35	28.5 ± 0.5	35	70.8 ± 0.9
Orchard	♂	160	—	—	—	—	—	—	—	—	—	144	32.5 ± 0.3	144	97.0 ± 0.4
	♀	91	—	—	—	—	—	—	—	—	—	75	33.6 ± 0.3	75	97.1 ± 0.6

treatment (18 d on average at 14:27°C, compared with 29 d at constant 22°C or 27 d at constant 29°C).

Developmental mortality (bees that died before reaching adulthood) occurred mainly in the prepupal stage (58.5% of those bees that died). There were detectable differences in developmental mortality among treatments for females ($\chi^2 = 13.77$, df = 5, $P = 0.02$), but not for males ($\chi^2 = 9.40$, df = 5, $P = 0.09$) (Table 2). At 18°C, 25.7% of the bees died before adulthood, and another 16.8%, although alive, were still prepupae by 23 October, and had to be overwintered in this stage.

On 29 March 1998, the cooler in which bees were being wintered at 4°C failed temporarily. This caused temperatures to rise for ≈12 h reaching a maximum of 15°C. As a consequence, a total of 42 males from treatments 22, 26, 29, and 14:27°C emerged in the cooler 3–21 d before completing their 215-d wintering period. These bees were counted as surviving the winter, but were not used in calculations of emergence periods or longevity. Temperatures for the September 1997–April 1998 period at the barn where bees of treatment orchard were wintered, averaged 2.6°C and ranged from −17.1 to 29.1°C. Winter mortality (bees that were wintered alive but did not emerge the following spring) was low for treatments 26, 29, 14:27°C, and orchard, intermediate for treatment 22°C, and high for treatment 18°C (Table 2). These differences in winter mortality were statistically significant (males, $\chi^2 = 107.25$, df = 5, $P < 0.001$; females, $\chi^2 = 12.85$, df = 5, $P = 0.03$).

Bees of all laboratory treatments (18, 22, 26, 29, and 14:27°C) emerged promptly upon incubation at 22°C. Most males of treatments 22 through 14:27°C emerged in <24 h, and females of the same treatments took a mean of 2–3 d to emerge (Table 3). There were detectable differences in emergence time among treatments ($F = 38.11$; df = 4, 315; $P < 0.001$) and between sexes ($F = 590.69$; df = 1, 315; $P < 0.001$), with a significant treatment by sex interaction ($F = 2.76$; df = 4, 315; $P = 0.03$). Differences between sexes in emergence time decreased as treatment temperature increased or became fluctuating. Actual emergence dates varied widely among treatments (Table 3). Bees from all laboratory treatments except treatment 18°C emerged earlier than bees kept at the orchard, which emerged naturally around mid-April. Bees from treatments 29 and 14:27°C emerged as early as mid- to late March. Longevity of emerged bees incubated at 22°C was greater for males (around 4 d) than for females (around 3 d) ($F = 83.09$; df = 1, 519; $P < 0.001$) (Table 3). Although no clear trends were apparent, longevity also differed among treatments ($F = 10.59$; df = 5, 519; $P < 0.001$) and showed a significant treatment by sex interaction ($F = 3.34$; df = 5, 519; $P = 0.006$).

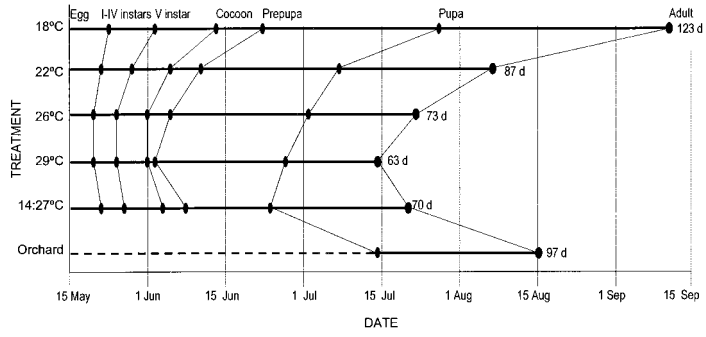

Fig. 1. Developmental phenology of *O. lignaria* reared at various temperature regimes. Black dots represent mean times for each developmental stage (males and females combined). Numbers on the right indicate mean duration (in days) from egg to adult.

Table 2. Developmental and wintering mortality of male and female *O. lignaria* reared at various temperature regimes

Treatment	Sex	*n*	Developmental mortality		Winter mortality	
			n	%	*n*	%
18°C	♂	60	9	15.0[a]	22	51.2
	♀	41	17	41.5[a]	3	20.0
22°C	♂	64	14	21.9	3	6.0
	♀	39	6	15.4	8	24.2
26°C	♂	58	4	6.9	3	5.6
	♀	49	10	20.4	1	2.6
29°C	♂	61	6	9.8	1	1.8
	♀	43	11	25.6	4	12.5
14:27°C	♂	65	7	10.8	1	1.7
	♀	40	5	12.5	1	2.9
Orchard	♂	160	15	9.4	6	4.1
	♀	91	16	17.6	8	10.7

[a] Developmental mortality in treatment 18°C does not include individuals that were overwintered as prepupae.

Bees from treatment 18°C that were still in the prepupal stage by 23 October (8 males and 9 females) were divided into 2 groups. One group ($n = 8$) was transferred to 22°C (2 d) and then to 26°C to see if bees would eventually complete development and could subsequently be wintered at 4°C. Most of these bees ($n = 7$) pupated and some ($n = 5$) became adults, but none survived the winter. The 2nd group of prepupae ($n = 9$) were wintered for 215 d at 4°C and incubated at 22°C the following spring, to see if they would resume development and could be wintered as adults the 2nd yr. Most of these bees ($n = 6$) never pupated and died in late summer or fall, but 3 reached adulthood and 2 of them could be wintered as live adults on 7 November 1998. The latter 2 males were wintered at 4°C until 3 May 1999, and one of them emerged on 4 May and lived for 3 d at 22°C.

Discussion

Studies on insect development typically show a decrease in development time as temperatures increase to a limit, above which development time can actually increase, often in association with an increased mortality (Ratte 1984). Such an upper limit was not reached for *O. lignaria* in this study. At 29°C, bees completed development in half the time taken by bees at 18°C, with only a moderate increase in mortality compared with intermediate treatments. As expected, the most significant reductions in development time occur during periods in which bees have high metabolic rates: hatching, feeding, cocoon spinning, and pupation.

Table 3. Time to emerge after incubation at 22°C, emergence dates, and longevity at 22°C in male and female *O. lignaria* reared at various temperature regimes

Treatment	Sex	*n*	Time to emerge, d	Median emergence date	Longevity, d
			Mean ± SE		Mean ± SE
18°C	♂	21	1.6 ± 0.1	13 May	4.0 ± 0.3
	♀	12	4.2 ± 0.3	24 May	2.2 ± 0.3
22°C	♂	23	0.7 ± 0.2	30 Mar.	4.1 ± 0.3
	♀	25	3.1 ± 0.2	15 April	3.0 ± 0.1
26°C	♂	39	0.1 ± 0.1	30 Mar.	3.5 ± 0.2
	♀	38	2.4 ± 0.1	1 April	2.6 ± 0.1
29°C	♂	51	0.6 ± 0.1	17 Mar.	4.5 ± 0.1
	♀	28	2.4 ± 0.1	21 Mar.	3.2 ± 0.2
14:27°C	♂	54	0.2 ± 0.1	23 Mar.	3.8 ± 0.2
	♀	34	2.0 ± 0.2	25 Mar.	3.4 ± 0.2
Orchard	♂	139	—	11 April	4.2 ± 0.1
	♀	67	—	23 April	3.7 ± 0.1

Osmia lignaria also developed faster at the 2 fluctuating treatments tested than at equivalent (same mean) constant temperatures (treatments 14:27°C and orchard versus 22 and 18°C, respectively). However, the most significant development time reduction at fluctuating temperatures is found in the dormant prepupal stage. *O. lignaria* and the closely related *Osmia cornuta* (Latreille) (Vicens 1997, Monzón 1998; unpublished data) show minimal weight loss and reduced metabolic rates during the prepupal stage, indicating that prepupal dormancy is probably diapause-mediated (Tauber et al. 1986) in both species. At the lowest temperature tested in our study (18°C), some *O. lignaria* failed to complete prepupal dormancy and remained as live prepupae for >3 mo. This phenomenon also occurs in *O. cornuta* (Bosch 1994), although in this species the temperature threshold to complete dormancy is higher: up to 20% of the *O. cornuta* studied failed to pupate at 22°C, in contrast to 0% at 25°C (J.B., unpublished data). Interestingly, fluctuating temperatures not only shorten the duration of the prepupal stage in *O. cornuta*, but also decrease the incidence of individuals failing to pupate (0% at 17:27°C of 12:12 h on a daily cycle [mean, 22°C]) (J.B., unpublished data). Therefore, high or fluctuating temperatures are necessary to complete prepupal dormancy in these 2 closely related *Osmia (Osmia)* species.

Instances of extended prepupal dormancy are known to occur in other insects (Tauber et al. 1986). In bees, extended prepupal dormancy has been interpreted as either a direct response to adverse environmental conditions (Torchio 1975), or as a species-characteristic bet-hedging strategy (Torchio and Tepedino 1982). In *O. lignaria* and *O. cornuta*, however, we regard prolonged prepupal dormancy as an artifact caused by nonoptimal artificial rearing temperatures. Because of their potential as crop pollinators, *O. lignaria* and *O. cornuta* have been well studied in diverse geographical areas. Both species have always been found to winter as adults and to be strictly univoltine (Levin 1966, Krombein 1967, Taséi 1973, Rust 1974, Asensio 1984, Torchio 1989, Westrich 1990, Krunic et al. 1991, Vicens et al. 1993). In fact, only 3 of the 17 *O. lignaria* undergoing a prolonged prepupal dormancy in this study reached adulthood, and only 1 emerged as a 2-yr form.

Osmia (Osmia) bees enter a 2nd dormancy period, which is also probably diapause-mediated (Monzón 1998; unpublished data) as wintering adults. Wintering adults require a period of exposure to cold temperatures to emerge (Taséi 1973, Maeta 1978, Bosch and Blas 1994). Bees that have not accumulated enough days at cold temperature either do not emerge or take longer to do

so, and are less vigorous than fully chilled individuals (Bosch and Blas 1994, Monzón 1998; J.B., unpublished data). Populations from colder areas require longer wintering periods (Bosch and Blas 1994). The wintering period used in this study (215–218 d) was long enough for our *O. lignaria* population, because emergence periods were short and emerging bees were vigorous. A short emergence period is a desirable trait in managed *Osmia* populations, because it facilitates synchronization between bee nesting and orchard bloom. Although wintering conditions were identical for all laboratory treatments, winter mortality was highest in those treatments that also produced high developmental mortality (18 and 22°C).

In the Cache Valley of northern Utah, *O. lignaria* populations reared and wintered under natural conditions emerge around mid-April, approximately between cherry, *Prunus avium* L., and pear bloom. Emergence can be advanced a few weeks by artificially incubating wintering bees, or delayed by artificially cooling them. An adequate rearing treatment for *O. lignaria* populations should combine low mortality rates with a quick enough development, so that bees can be wintered in time to accumulate enough days at cold temperature during the winter, and emerge in time to pollinate the target crop.

Three artificial temperature regimes tested in this study (26, 29, and 14:27°C) yielded low mortality rates and produced vigorous individuals, even though they emerged ≈1 mo ahead of bees kept under natural conditions (orchard). As explained, this was accomplished through 2 different physiological responses to temperature: either shortening the active immature stages (high temperatures) or shortening the prepupal dormant stage (fluctuating temperatures). These results are potentially important for pollination of early-blooming crops such as almonds. Bees forced to develop quickly can be wintered ahead of time and complete winter dormancy early in the year. A final step to validate this as a viable method to manage *O. lignaria* populations needed to be tested in the field to make sure that bees reared this way would establish and nest in sufficient numbers in early blooming orchard environments. In 1998, the results of this study were applied to late-flying (April–May) *O. lignaria* populations, which emerged and successfully nested in almond orchards blooming in mid-February in 1999 (unpublished data).

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