Emergence dynamics and bet hedging in a desert bee, *Perdita portalis*

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Bees (series Apiformes, superfamily Apoidea) are most diverse in arid regions of the world. Arid regions (deserts and semi-deserts) are characterized by discrete rainy seasons and extreme temporal variability in rainfall. This paper documents several novel mechanisms by which one desert bee species (*Perdita portalis*) copes with harsh and unpredictable conditions in xeric habitats. These same mechanisms are likely to be present in diverse bee families. First, diapausing *P. portalis* follow a bet-hedging emergence pattern, such that only approximately half of the larvae pupate under optimal conditions. Second, emergence is condition dependent such that larvae with a low average body weight are significantly more likely to emerge than are larvae with a high average body weight under similar conditions. Finally, larval emergence is induced by exposure to high humidity (rainfall). The parallels between bee larvae and angiosperm seeds in arid environments are striking. In both cases there is clear evidence of bet hedging, emergence (or germination) is dependent on larval (or seed) condition and rainfall triggers emergence (or germination). These patterns of emergence are significant for understanding bee species diversity in arid regions.

Keywords: diapause; biogeography; diversity; insect–plant interactions

1. INTRODUCTION

In virtually all natural environments, temporal variation in biotic and abiotic factors can alter the reproductive success of individuals. Because change in gene frequency over time is multiplicative, long-term fitness in temporally variable environments is measured by the geometric rather than the arithmetic mean of fitness across generations. One way to maximize the geometric mean in variable environments is to reduce between-year variance in reproductive success (since the geometric mean increases as the numbers averaged become less variable). Individuals that minimize between-year variance in reproductive success are said to be 'bet hedging' or 'risk spreading' (reviewed by Seger & Brockmann 1987; Philippi & Seger 1989; Hopper 1999). While bet hedgers can have lower reproductive success in some years, some offspring will survive even in catastrophic years and, therefore, the benefits of reduced variance can outweigh the cost of reduced arithmetic mean fitness in variable environments.

Diversified bet hedging ('do not put all your eggs in one basket') has been modelled by numerous authors, including Cohen (1966, 1967), MacArthur (1972) and Venable & Lawlor (1980). These models have been developed to explain seed germination strategies in desert annual plants, but can be applied to diapausing insects (Tauber *et al.* 1986; Hanski 1988) and freshwater copepods (Ellner *et al.* (1999) and references therein). Cohen's (1966) model made specific predictions: (i) seeds that do not germinate under good conditions in the first year should germinate under the same conditions in subsequent years, (ii) the proportion of seeds germinating should be positively correlated with the proportion of 'good' years, and (iii) all genotypes should produce seeds

that germinate both in the first year and in subsequent years. When Cohen's (1966) model is modified to allow for dispersal between local populations (Venable & Lawlor 1980; Metz *et al.* 1983; Bulmer 1984; León 1985; Klinkhamer *et al.* 1987; Venable 1989), one predicts a trade-off between dispersal and bet hedging, as expected if 'escape in space' and 'escape in time' are alternative methods for surviving in harsh environments (Southwood 1977).

One ecological by-product of bet-hedging, life-history strategies is enhanced species richness in temporally variable environments (Levins 1979; Chesson 1986, 1994; Chesson & Case 1986; Strong 1986; Chesson & Huntly 1988, 1989). Species coexistence is thought to be favoured when there is a long-lived, resistant phase that buffers populations from unfavourable conditions, when emergence (or germination) is induced by environmental cues (such as rainfall) and when resources are limited during the period of adult activity such that adults experience competition. Thus, bet hedging can have ecosystem effects.

Deserts are among the most temporally variable and unpredictable habitats on earth. The coefficient of variation of potential evapotranspiration between years in deserts is greater than in any other biome (Frank & Inouye 1994) and the variability in annual precipitation is negatively correlated with overall rainfall in US deserts (Davidowitz 1999). Thus, one might expect desert organisms to show bet-hedging life histories. Desert annual plants have been model organisms for testing the predictions of bet-hedging models and the empirical results support many of the theoretical expectations. For example, many desert annuals have seed banks (Nelson & Chew 1977; Freas & Kemp 1983; Reichman 1984; Price &

Reichman 1987), seed germination is induced by rainfall (Freas & Kemp 1983; Philippi 1993), not all viable seeds germinate in any one year (e.g. bet hedging; Freas & Kemp 1983), seeds that do not germinate under good conditions in the first year germinate under the same conditions in subsequent years (Philippi 1993), germination is age dependent (Philippi 1993), seed germination patterns may be heterogeneous, such that conditions that trigger emergence in one species may not be the same as those that trigger emergence in another species (Venable *et al.* 1993; Pake & Venable 1996) and germination may be 'predictive', such that higher germination occurs in years that are favourable for reproduction (Venable & Lawlor 1980; Pake & Venable 1996).

The seeds of desert annuals and the overwintering larvae of desert bees are similar in many ways. In both cases adult activity and reproduction are limited to a short period of time following the desert rainy season. Seeds and bee larvae are both small, buried in the soil, exposed to high temperature and low humidity and subject to attack by foraging ants, fungal and other pathogens and dessication. Both seeds and bee larvae represent the pool of individuals from which the next generation of adult reproductives will be drawn.

There are scattered anecdotal observations and limited experimental data suggesting that bees in arid regions show some of the same life-history traits documented for desert annuals. For example, melittologists have long suspected that rainfall is a cue that triggers emergence in desert, oligolectic (pollen specialist) bees (Ulrich 1933; Malyshev 1936; Michener & Rettenmeyer 1956; Linsley & MacSwain 1957; reviewed in Linsley 1958; Wcislo & Cane 1996). A frequently cited observation is that of Hurd (1957), who observed a second emergence in a normally univoltine desert bee (*Hesperapis fulvipes* Crawford) following a freak summer rain that induced the bee's host plant (*Geraea*, Compositae) to bloom. He speculated that 'if the maturation process of the bee is initiated when the soil surrounding the bee cells becomes wetted we would have a perfect mechanism to coordinate the bee and plant development' (Hurd 1957, p. 10). Likewise, Rust (1988), based on eight years of emergence data, found evidence that rainfall in excess of 5 cm was sufficient to trigger emergence of *Nomadopsis larreae* Timberlake. Rainfall is likely to be as important a phenological cue as photoperiod and temperature in insects, but has generally been overlooked (Tauber *et al.* 1998). However, melittologists have been reticent to accept the idea of rainfall-triggered emergence (referred to below as 'induced emergence') because there has been no direct, experimental demonstration of the hypothesis. Wcislo & Cane (1996), for example, stated in a recent review that 'detection of any special relationship between oligolecty and phenological tracking of flowers awaits additional, longer-term studies of emergence phenologies' (p. 268).

Likewise, many studies have documented that not all viable larvae of the same generation emerge at the same time in bees. Delayed emergence (including 'parsivoltinism', in which individuals of the same generation emerge in different years and 'partial bivoltinism', in which individuals develop directly into adults or enter diapause and emerge the following year) has been reported for a wide variety of ground- and stem-nesting

bees: *Perdita nuda* Cresson (and its parasite *Sphecodes* sp.) (Torchio 1975), *N. larreae* Timberlake (Rust 1988), *Lasioglossum* (*Sphecodogastra*) *aberrans* (Crawford) (Bohart & Youssef 1976, as *Evylaeus galpinsiae*), *Melissodes robustior* Cockerell (MacSwain 1958), *Diadasia rinconis* Cockerell (Neff & Simpson 1992), *Diadasia afflicta* (Cresson) (Neff *et al.* 1982), *Amegilla dawsoni* Rayment (Houston 1991), *Habropoda depressa* Fowler (Barthell *et al.* 1998), *Dianthidium pudicum consimile* (Ashmead) (Davidson 1896), *Prochelostoma philadelphi* (Robertson) (Krombein 1967), *Osmia marginipennis* Cresson (Parker 1980), *Hoplitis biscutellae* (Cockerell) (Rust 1980), *Osmia montana* Cresson, *Osmia californica* Cresson and *Osmia iridis* Cockerell and Titus (Torchio & Tepedino 1982), *Megachile rotundata* (Fabricius) (Tepedino & Parker 1988) and *Pararhophites orobinus* (Morawitz) (Rozen 1990). While most studies were based on small sample sizes and in some cases inferential data (rather than laboratory-reared larvae), there is clearly evidence of intraspecific variation in diapause length, such that emergence can occur directly or after one or more years in diapause. The duration of diapause may be remarkably long in some bees. For example, Houston (1991) reported a ten-year larval diapause in *A. dawsoni* and Rozen (1990) reported that larvae of *P. orobinus* emerged after a seven-year diapause.

One might expect desert bees to use the same environmental cues for emergence as desert annuals because desert bees are predominantly foraging specialists which rely on one species (or group of species) of plants for pollen (and, sometimes, nectar). Oligolectic bees generally do not switch to alternative pollen sources, even when the preferred host plant is not in bloom (Strickler 1979). Hence, one would expect selection to favour synchrony between bee emergence and host-plant seed germination. Similar responses to seasonally variable abiotic factors, such as rainfall, would be one mechanism of ensuring synchrony.

This study sought to test the hypothesis that bees, like seeds, have rainfall-induced emergence and bet-hedging, life-history patterns.

2. MATERIAL AND METHODS

Perdita includes over 500 species of small, oligolectic bees with peak diversity in the arid regions of North America. *Perdita portalis* Timberlake is a communal, ground-nesting species present in the mixed Chihuahuan desert–grassland habitats of south-eastern Arizona, south-western New Mexico and north-central Mexico (Danforth 1996). Up to 30 reproductively active females share a single nest but do not cooperate in cell provisioning (Danforth 1991*a*). Females collect pollen exclusively from *Sphaeralcea* (Malvaceae) plants, including *Sphaeralcea angustifolia* (Cav.), *Sphaeralcea laxa* Woot. & Strandl. and *Sphaeralcea hastulata* Gray. The larval cells are mass provisioned and larvae complete feeding in approximately eight days (Danforth 1991*b*). The last larval instar (the pre-pupa) enters diapause and remains a pre-pupa until the following year. Emerging females reuse the natal nest, so that nests may persist in one location for many years. The age structure of such nests is not clear and may include larvae of different ages (see below). Males in this species occur in two discrete, non-overlapping male morphs: large-headed, flightless males (LH males) and small-headed, flight-capable males (SH males) (Danforth 1991*b*).

Table 1. *Localities where nests were excavated and the nearest weather station (and its elevation)*

nest site	weather station	elevation (m)
Rodeo, NM (2 km north)	Portal, AZ	1643
Apache, AZ (2 km east)	Douglas, AZ	1249
Animas, NM (9.2 km east)	Animas, NM	1347
Hachita, NM (30 km north)	Deming, NM	1311
Hatch, NM (20.8 km west)	Hatch, NM	1235
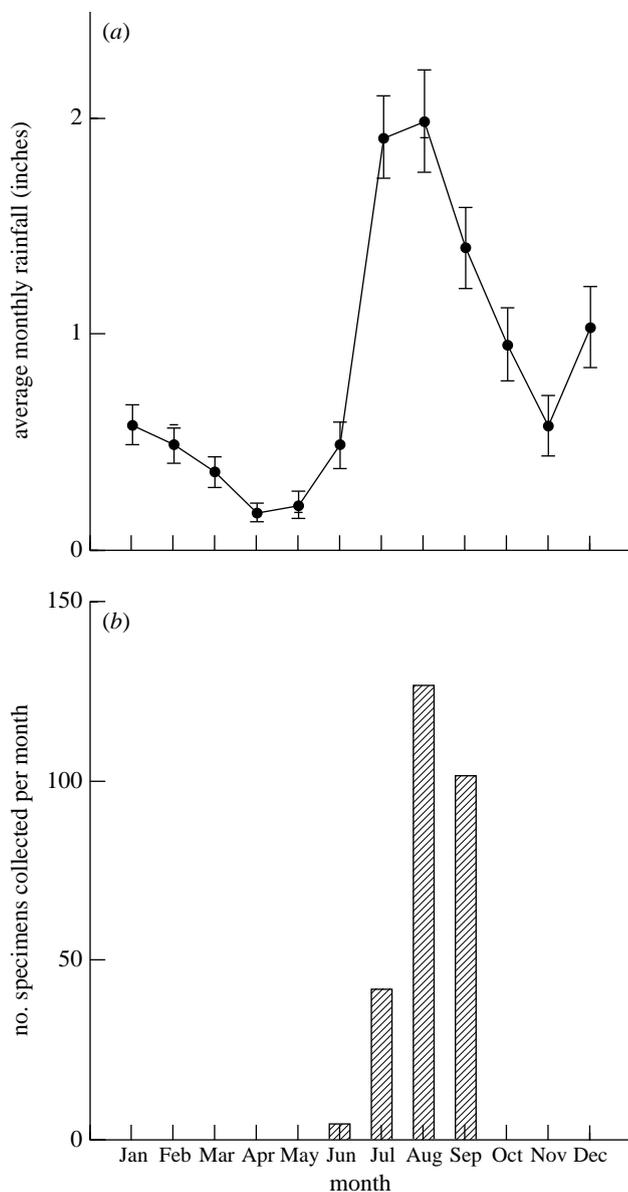
Figure 1. (*a*) Average monthly rainfall at Deming, NM (averaged over 34 years), and (*b*) collection records for museum specimens of *P. portalis* (*n* = 275), shown monthly. The museums surveyed for collection data included the Snow Entomological Museum (University of Kansas), University of California (Riverside), California Academy of Sciences (San Francisco) and the Los Angeles County Museum of Natural History. Rainfall data were available for the period 1962–1997.
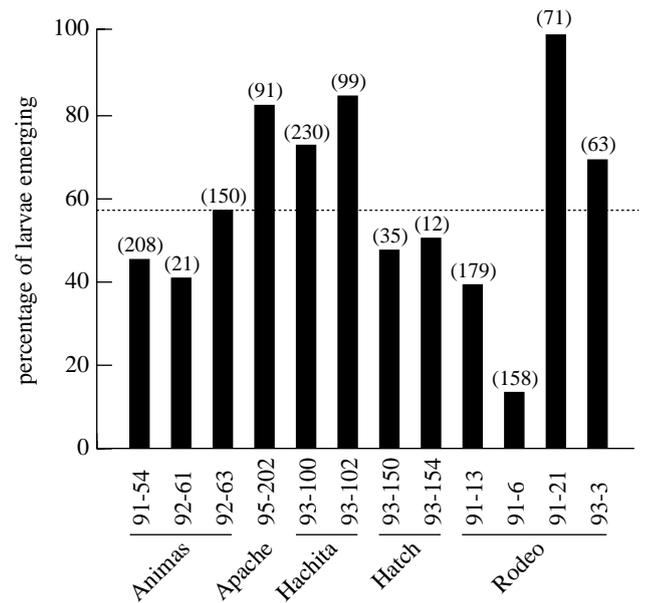
Figure 2. Percentage of larvae emerging per nest from 12 nests excavated over five localities. Sample sizes are shown in parentheses. Overall, 56.7% of the larvae emerged when exposed to high humidity and temperature in environmental chambers (*n* = 1349).

This study was based primarily on fieldwork conducted from 1992 to 1997 (excluding 1994 and 1996). The studies focused on five localities in southern Arizona and New Mexico: 2 km north of Rodeo, Hidalgo Co., NM, 2 km east of Apache, Cochise Co., AZ, 30 km north of Hachita, Grant Co., NM, 9.2 km east of Animas, Hidalgo Co., NM and 20.8 km west of Hatch, Luna Co., NM.

(a) *Rainfall data*

To compare rainfall patterns between and within years I obtained rainfall data for the sites listed in table 1 from the National Climatic Data Center, National Oceanographic and Atmospheric Administration, Asheville, NC, USA. For Deming, NM, I averaged the monthly rainfall over 34 years (1962–1995) in order to characterize the average month-to-month variation in rainfall for mixed Chihuahuan desert–grassland habitats. For all other sites I analysed deviation from the average monthly rainfall in the months during which the majority of the late summer rains come (July–October). These deviations from the average were used to estimate the year-to-year variation in drought stress at all nest sites immediately prior to the year of nest excavation.

(b) *Nest excavation*

For estimates of natural emergence patterns, a total of 21 nests representing 1349 total brood cells were excavated at the five localities. Nest excavations were performed early in the season (during the last week in July or the first week in August), prior to adult emergence. Each nest was dug to completion by carefully scraping away the soil with a penknife. Nests were excavated to a depth of 18 cm and a radius from the central tunnel of 15 cm. When pre-pupae (last instar larvae) were discovered they were placed in 96-well tissue culture dishes and the cell depths and, whenever possible, diameters were measured. Cell depths were measured with a metal ruler to the nearest 0.5 cm. Cell diameters were measured by inserting a machinist's hole
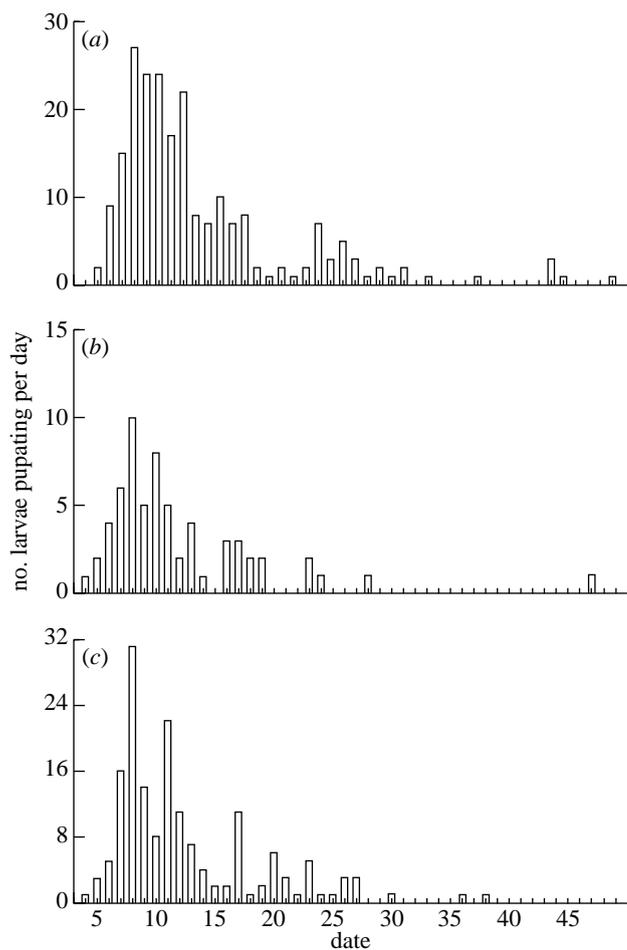
Figure 3. Emergence patterns of laboratory-reared larvae. Day 0 refers to the day the larvae were excavated, weighed and placed into the environmental chamber at high humidity. Data are broken down by morph and sex: (*a*) females (*n* = 219), (*b*) LH males (*n* = 63), and (*c*) SH males (*n* = 166).

gauge (Mitutoyo Small Hole Gauge Set no. 154–901) along the long axis of the ellipsoidal cell and expanding it until it fit snugly against the lateral walls. The hole gauge was then removed and the diameter measured with digital calipers to the nearest 0.01 mm. Diameters could not be measured for all cells, either because the cell was not sufficiently intact after excavation or because the soil was too friable for accurate measurement. Pre-pupae that died in the process of excavating nests (*ca.* 5% of all pre-pupae collected) were placed into vials of Kahle's solution and their sex determined in the laboratory using the methods of Duchateau & Van Leeuwen (1990).

(c) *Laboratory rearing*

All viable pre-pupae recovered from nests were weighed to the nearest 0.01 mg with either a Cahn C-30 microbalance (1993) or a Mettler AT261 Delta-Range balance (1995–1997) on the day the nest was excavated. Following weighing, the pre-pupae were placed into sterile 96-well tissue culture dishes wrapped in moist towels and kept in a Percival environmental chamber set on a diurnal cycle of 12 h at 26 °C (00.00–12.00) and 12 h at 30 °C (12.00–24.00). These conditions mimic those found in the soil during the month of August. The tissue culture dishes were checked once or twice daily for the presence of pupae and freshly emerged adults. This allowed accurate

measurements of the date of pupation, date of eclosion, duration of the pupal stage, the temporal pattern of emergence within each nest and sex and morph ratio for each nest.

Freshly emerged adults were removed from the tissue culture dishes and placed individually in shell vials on the day of eclosion. Thereafter, females were frozen at −80 °C for future genetic analysis and males were dried and later pinned for morphometric analysis.

All pinned voucher specimens were deposited in either the Snow Entomological Museum, University of Kansas (1989–1992) or the Cornell University Insect Collection (1995–1997).

Not all pre-pupae that were collected actually pupated (see below) and so the sex and morph identities of these pre-pupae could not be determined through rearing. The sexes of this subset of non-emerging pre-pupae were determined for all nests in 1995 using the staining methods of Duchateau & Van Leeuwen (1990). In 1997 the pre-pupae that did not pupate in the year of excavation were stored under dry and cool conditions in the laboratory until the summer of 1998, when they were again placed in the Percival environmental chamber and exposed to the temperature and humidity regime described above. This experiment was performed in order to compare first and second year emergence patterns.

In 1997 an experiment was conducted to determine the effect of elevated humidity on the date of pupation. A total of 120 pre-pupae from five nests (Hachita nests 93-104 and 93-102 and Hatch nests 93-150, 93-154 and 95-158) were randomly divided into two treatment groups. One group ('early rainfall') was exposed to high humidity in a Percival environmental chamber set on a diurnal cycle of 12 h at 26 °C (00.00–12.00) and 12 h at 30 °C (12.00–24.00), as described above, shortly after nest excavation. The date of exposure to high humidity was assigned day 0. Pre-pupae assigned to the 'late rainfall' treatment were placed in the same incubator but not exposed to high humidity until 14 days later (day 14). The emergence patterns of the pre-pupae were monitored as above, with daily or twice daily checks.

3. RESULTS

(a) *Habitat distribution*

Based on all the collecting localities recorded for this species, *P. portalis* appears to be restricted to mixed Chihuahuan desert–grassland habitats. To the best of my knowledge no collections have been made in true Chihuahuan desert habitats, based on the vegetation maps presented in Brown (1994). All nesting sites were located within mixed Chihuahuan desert–grassland habitats.

(b) *Emergence phenology*

(i) *Phenology based on museum specimens*

Perdita portalis emergence patterns occur in synchrony with the late summer rains in the south-western deserts (figure 1). Based on a total of 275 museum specimens examined, all specimens were collected during the late summer rainy season, from late July until early September. No specimens were found that would indicate *P. portalis* is active in the spring, in spite of the fact that *Sphaeralcea* plants bloom in both the spring and summer in the Chihuahuan desert (Martin & Hutchins 1981).

(ii) *Phenology based on laboratory rearing*

For the entire data set of over 1300 laboratory-reared bees, the percentage of healthy larvae pupating in the

Table 2. *Comparisons among LH males, SH males and females for various morphometric and developmental variables*

(Mean ± standard error (*n*).)

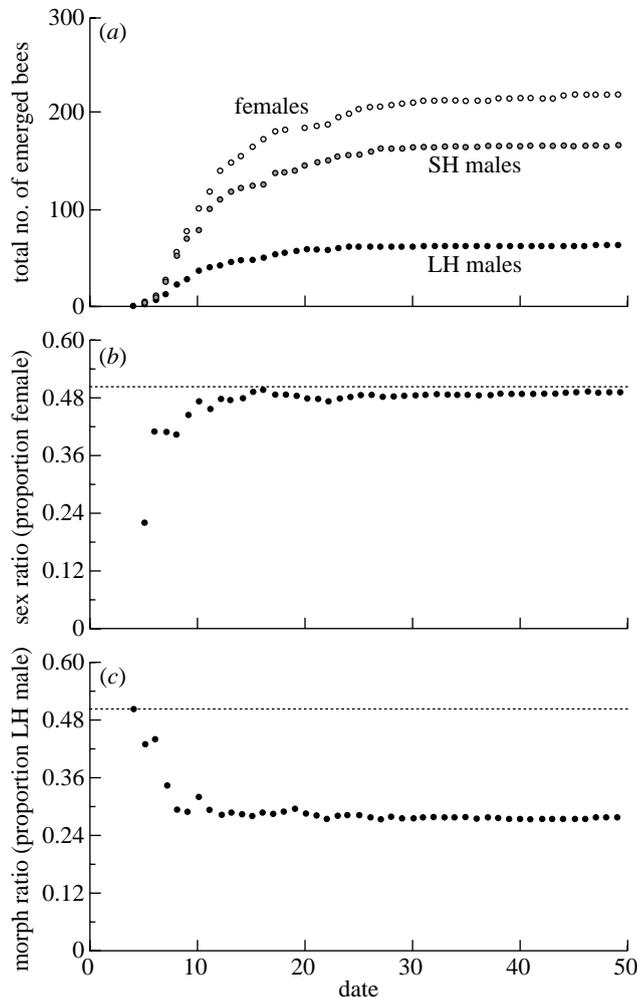| variable	females	LH males	SH males
cell diameter (mm)	3.360 ± 0.013 (81)	3.380 ± 0.074 (9)	3.351 ± 0.026 (26)
cell depth (cm)	9.108 ± 0.095 (348)	9.507 ± 0.223 (71)	9.105 ± 0.133 (174)
larval weight (mg)	7.448 ± 0.050 (439)	7.281 ± 0.088 (83)	5.634 ± 0.074 (212)
date of pupation	13.530 ± 0.527 (219)	11.873 ± 0.856 (63)	12.488 ± 0.483 (166)
development time	8.635 ± 0.065 (137)	8.853 ± 0.105 (34)	8.754 ± 0.066 (122)

Figure 4. (*a*) Cumulative emergence patterns for females (*n* = 219), LH males (*n* = 63), and SH males (*n* = 166). (*b*) Temporal change in the sex ratio (females:total adults) over the period of adult emergence. (*c*) Temporal change in the morph ratio (LH males:total males) over the period of adult emergence. In (*b*) and (*c*) the dotted line indicates the 50% emergence mark.

year of nest excavation was 56.7% (figure 2). This value varied widely between nests, from 13.1% (nest 91-6) to 98.1% (nest 91-21; figure 2).

The temporal pattern of emergence is depicted graphically in figure 3. For females and both male morphs,

emergence reached a peak at around eight days following exposure to high humidity and gradually tapered off thereafter. Based on the data presented in table 2, there was no difference between LH and SH males ($p = 0.533$) or between LH males and females ($p = 0.146$) in date of emergence. Overall, males emerged slightly earlier than females (more than one day on average), but this difference was not significant ($p = 0.075$). There was no significant difference between males and females in the duration of the pupal stage, which lasted, on average, eight to nine days ($p = 0.098$).

Overall (based on both laboratory-reared larvae and larvae sexed by the staining methods of Duchateau & Van Leeuwen (1990)), the sex ratio of the pre-pupae was slightly female biased. Of the 1078 pre-pupae whose sex was determined, 587 (54.5%) were female. This was significantly different from an equal sex ratio ($\chi^2 = 8.55$, $p < 0.005$ and d.f. = 1). Figure 4 presents the cumulative emergence data for larvae reared to adulthood in the laboratory. The sex ratio is initially male biased but quickly (within the first ten days) reaches an equilibrium sex ratio of slightly less than 50% (figure 4).

Likewise, the morph ratio (as per cent LH males) declines quickly within the first ten days. Overall, the morph ratio was significantly biased towards SH males. Out of the 302 males successfully reared to adulthood, only 87 (28.81%) were LH males, a significant deviation from equal proportions of LH and SH males ($\chi^2 = 54.25$, $p \ll 0.001$ and d.f. = 1). All nests of more than ten cells produced at least one LH male, indicating that LH males are likely to be present in all nests except those that have been recently founded (Danforth 1991*b*). These data indicate that, in *P. portalis*, there is both slight protandry and a slight tendency for LH males to emerge before SH males.

(iii) *Comparison between emerging and diapausing pre-pupae*

Because only slightly over half of the overwintering larvae actually pupate (figure 2), it was worthwhile comparing the groups of larvae that did and did not pupate in the year of nest excavation. Using the staining methods of Duchateau & Van Leeuwen (1990), I was able to determine the sex of larvae that did not emerge in a given year and, thus, compare the sex ratio, larval body weights and cell depths between the two groups.

For both males and females the pre-pupae that emerged in the year of nest excavation were significantly ($p \le 0.001$) lighter than those that remained in diapause for an additional year (table 3). For both males and

Table 3. *Comparison of emerging and diapausing larvae at end of season: relationship between larval weight and emergence*

(Mean ± standard deviation (n).)

	females	males
larval weight		
emerged	7.237 ± 0.0681 (265)	6.034 ± 0.0761 (270)
not emerged	7.792 ± 0.704 (139)	6.878 ± 0.944 (90)
t-test	$p \leqslant 0.001$ (d.f. = 379)	$p \leqslant 0.001$ (d.f. = 200)
larval cell depth		
emerged	9.209 ± 0.125 (213)	9.216 ± 1.156 (233)
not emerged	8.821 ± 0.147 (120)	8.560 ± 0.193 (81)
t-test	$p = 0.046$ (d.f. = 272)	$p = 0.006$ (d.f. = 141)

Table 4. *Sex ratio of pre-pupae that pupated after exposure to high humidity and those that remained in diapause*

($\chi^2 = 11.36$ and $p < 0.001$.)

	female (n = 404)	male (n = 360)	total	percentage female
emerged	265	270	535	49.53
diapausing	139	90	229	60.70

females this difference is substantial. For example, emerging females were 7.7% lighter than females remaining in diapause and emerging males were 14.0% lighter than males that remained in diapause. These results indicate that, if pre-pupae have sufficient fat and/or water reserves to overwinter an additional year, they do so, leaving the lighter (and presumably older) pre-pupae to emerge in the current year.

In addition, the bees that emerged were significantly deeper in the soil than those that remained in diapause (table 3). This result is difficult to interpret, but could reflect different average ages for emerging and non-emerging pre-pupae.

The sex ratio of the emerging and diapausing bees was also significantly different. For emerging bees the sex ratio was 49.5% female while for the overwintering bees it was 60.7% female (table 4; $\chi^2 = 11.36$ and $p < 0.001$). This indicates that females are significantly more likely than males to overwinter multiple years or, alternatively, a male is significantly more likely to emerge in any one year than is a female. This same pattern (a larger proportion of females undergoing prolonged diapause than males) was observed in three species of *Osmia* (Torchio & Tepedino 1982), in which female larvae are almost twice the weight of male larvae (table 7 in Torchio & Tepedino (1982)).

The heterogeneous pattern of emergence between nests (figure 2) results in part from between-nest variation in larval condition at the time of nest excavation. There is a significant negative correlation between the percentage of larvae emerging per nest (for nests with >20 cells, $n = 12$) and the average body weight of either males (figure 5a; $p = 0.020$) or females (figure 5b; $p = 0.038$) within the nest. There is also a negative (though not significant; $p = 0.079$) correlation between the percentage of bees emerging and the departure from the average annual rainfall for the previous year (based on the

$$Y = -19.89(X) + 187.43$$
$$p = 0.020$$
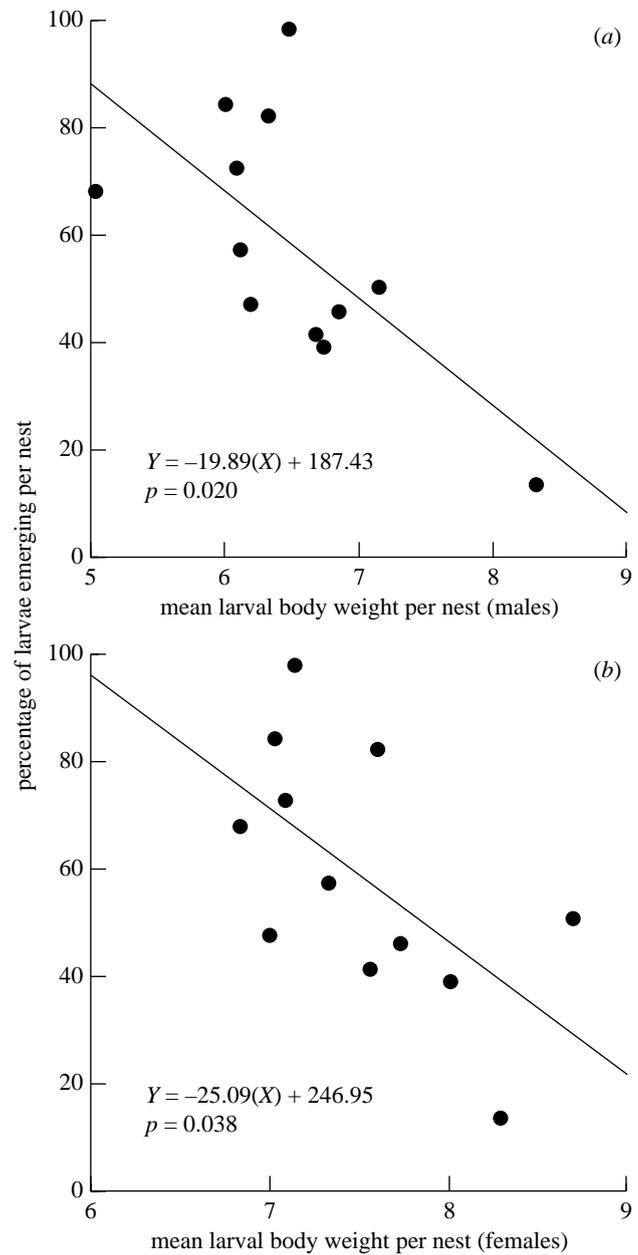
$$Y = -25.09(X) + 246.95$$
$$p = 0.038$$

Figure 5. Relationship between the percentage of larvae emerging per nest per year and (a) the average body weight of male larvae in the nest and (b) the average body weight of female larvae in the nest.
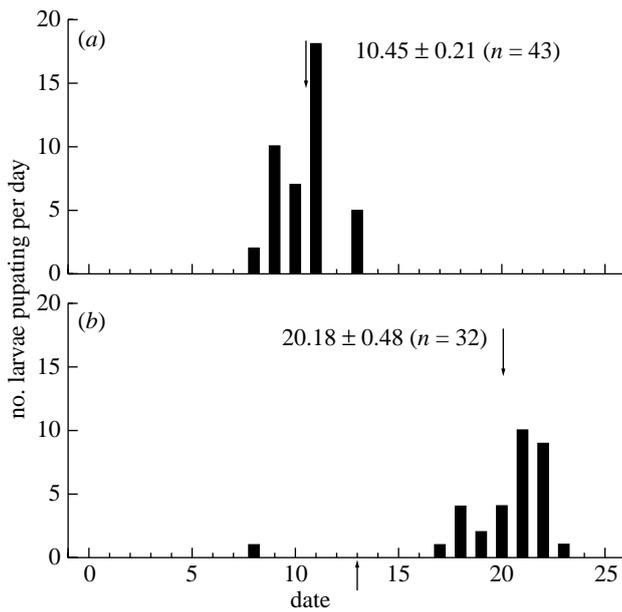
Figure 6. Experimental manipulation of emergence. (*a*) In the early rainfall treatment ($n = 60$), the pre-pupae were exposed to high humidity shortly after collection (day 0). (*b*) In the late rainfall treatment ($n = 60$), the pre-pupae were exposed to high humidity 14 days later. Average emergence dates are shown for each treatment.

rainfall records for the localities listed in table 1). In other words, when the previous rainy season was dry, the proportion of emerging larvae increased (but not significantly). Nest 91-21, in which over 98% of the pre-pupae emerged, was excavated following the year with the lowest average late summer rainfall for all three years examined and contained larvae that had nearly the lowest average body weight. These correlations indicate that the variation between nests in emergence is not random, but is related to pre-pupal condition and the likelihood of surviving an additional year.

(iv) *Emergence after prolonged (three-year) diapause*

In 1997 a total of 211 viable pre-pupae were collected from ten nests. One hundred and sixty-one (76.3%) of these pupated the first summer, while the remaining 50 overwintered an additional year. In early August 1998, 46 out of these 50 pre-pupae were still viable and these 46 pre-pupae were again placed in the Percival incubator and exposed to high humidity and a diurnal temperature cycle as described above. Forty-three (or 93.5%) of these pupated within 45 days while the other three remained in diapause. These results indicate that the proportion of pupating larvae increases over time and that some larvae are capable of overwintering for as long as three years.

(v) *Experimental manipulation of emergence*

The pre-pupae experimentally exposed to high humidity at different times showed markedly different patterns of emergence (figure 6). The pre-pupae in the early rainfall treatment emerged significantly earlier than those in the late rainfall treatment ($p \leqslant 0.001$ and d.f. $= 42$). As expected, there were no significant differences between treatments in any other variable measured, including cell
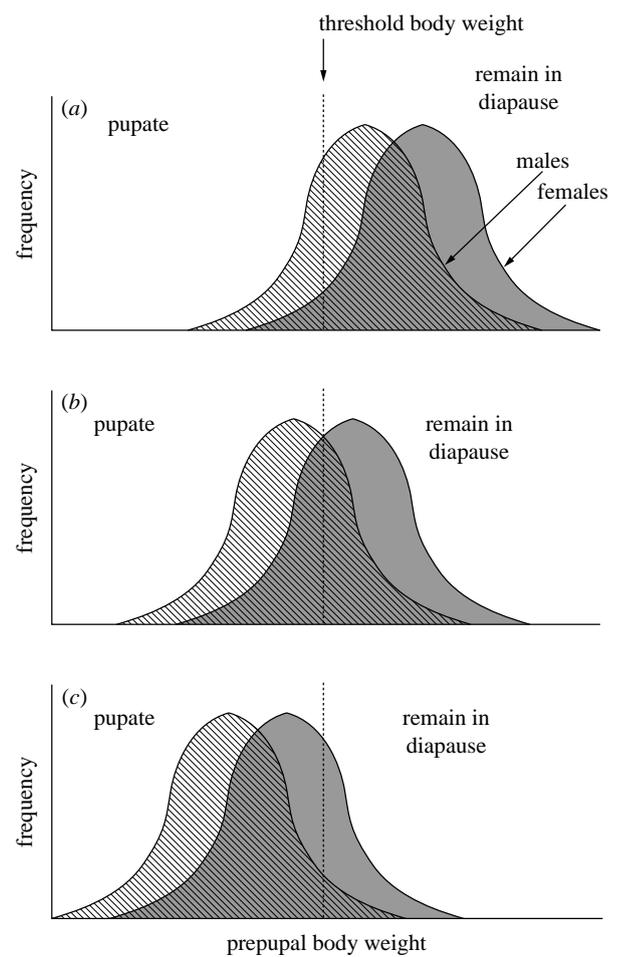

Figure 7. Condition-dependent emergence model. The pre-pupal body weight in *P. portalis* (and many bees) is significantly different for males and females, with males being lighter on average than females. Assume that there is a threshold body weight for emergence, such that individuals below that body weight are likely to pupate when exposed to high humidity (rainfall) and individuals above that body weight are likely to remain in diapause and assume that larval body weight declines over time. (*a*) In nests with relatively young (and heavy) larvae, rainfall will tend to induce only a small proportion to emerge. (*b*) In nests which have not experienced heavy rainfall for two years, the average body weight of the pre-pupae will have decreased and a larger proportion of larvae will emerge when exposed to high humidity. (*c*) In nests which have experienced long-term drought conditions, the larvae will tend to be substantially smaller and, hence, a large proportion will be likely to pupate given a heavy late summer rainfall. Note that in all nests there will tend to be a bias towards males among the pupating larvae, since males are lighter than females on average.

diameter (insufficient data), cell depth ($p = 0.509$ and d.f. $= 50$) and pre-pupal weight ($p = 0.523$ and d.f. $= 116$).

As expected, not all the pre-pupae emerged in the year of the experiment. Overall (for both treatments) only 75.8% (75 out of 99) of the pre-pupae emerged, while the rest remained in diapause. The proportions of emerging pre-pupae for the two treatments were also significantly different. For the early rainfall treatment 84.3% (43 out of 51) of the larvae pupated, whereas for the late rainfall treatment 66.7% (32 out of 48) of the larvae pupated ($\chi^2 = 11.26$ and $p < 0.001$). Earlier exposure to high

humidity led to a greater proportion of larvae pupating, as would be expected if early monsoon rains were a predictor of good summer flower bloom. Interestingly, the delay time between exposure to high humidity and peak pupation differed significantly between the two treatments. Bees in the early rainfall treatment pupated on average 10.45 ± 0.21 days ($n = 42$) after exposure, whereas for bees in the late rainfall treatment pupation occurred only 6.19 ± 0.48 days ($n = 32$) after exposure ($p = 0.000$ and d.f. $= 42$).

This experiment shows that pupation in *P. portalis* is induced by high humidity. These are the same conditions that overwintering pre-pupae would experience during the late summer rainy season in the south-western deserts. Furthermore, the response of bees to high humidity is altered over time, such that later exposure leads to a lower overall proportion of bees pupating and more rapid pupation relative to the onset of heavy rain.

4. DISCUSSION

The present study provides the clearest evidence of bet-hedging life-history patterns in ground-nesting, oligolectic bees, provides the first experimental evidence of emergence triggered by rainfall (high soil humidity) and indicates that emergence during any given year is dependent on larval condition. To a striking degree the empirical results obtained from desert annuals parallel the results observed here in a desert bee. First, larvae that did not pupate in the first year did pupate in the second or third year. Second, as in some desert annuals (but not all; Philippi 1993), the proportion of pupating larvae (or germinating seeds) increased between the first and second years, as would be expected if metabolic resources are limiting. Third, pupation, like germination, is condition dependent (either based on age, as in the case of desert annuals or weight, as in the case of diapausing bee larvae). Age and pre-pupal weight are probably correlated in *P. portalis* (and in annual seeds), since larvae do not feed once they have reached the pre-pupal stage.

A simple model is presented in figure 7 which accounts for the heterogeneity between nests in the proportion of larvae emerging, the correlation between average larval body weight and proportion of larvae emerging and the sex ratio bias in the emerging larvae (relative to those remaining in diapause).

(a) *Significance for bee diversity*

One should be very cautious about inferring that life-history patterns in one species may explain large-scale patterns of community diversity. However, the anecdotal and limited experimental evidence suggests that both delayed emergence and induced emergence triggered by rainfall occur in many species of oligolectic, desert bees distributed among a wide variety of distantly related bee families (including Andrenidae, Melittidae, Megachilidae and Apidae). These behaviours are ecologically significant in that they provide bees with a strategy for surviving in harsh arid environments by timing emergence with plant bloom and by minimizing catastrophic losses in drought years. This would be particularly true for desert oligolectic bees, which require the presence of one genus or even one species of plant for successful reproduction.

These traits would be particularly important in areas where rainfall is least predictable.

Bee diversity is highest in arid regions (Michener 1979; Neff & Simpson 1993), in contrast to most groups of insects and the proportion of oligolectic (specialist) bees is highest in xeric regions (Moldenke 1979). Oligolectic bees comprise up to 66.5% of the species in the desert regions of North America, as compared to only 17.1 and 23.6% in forested and boreal regions, respectively (Moldenke 1979; table 1). These same patterns are evident on a smaller scale in one cohort of oligolectic bees; the *Larrea* (creosote bush) bees. Minckley *et al.* (2000) showed that the greatest proportion of *Larrea* oligoleges occurs in the region of the south-western deserts with the lowest and the most variable rainfall patterns (the lower Sonoran and Mojave deserts).

Such a pattern of species diversity could only be achieved if oligolectic bees have mechanisms (like those described above) for tracking host plant bloom and surviving unfavourable years. Indeed, it is likely that rainfall-induced emergence may provide a mechanism for disrupting gene flow between populations, if heavy rainfall triggers emergence at one locality, but neighbouring localities with low rainfall fail to emerge. Hence, induced emergence could be one explanation for the extremely high diversity of bees in arid regions. Our preliminary estimates based on six microsatellite loci indicate that there is substantial genetic differentiation between populations (Danforth *et al.* 2000), consistent with the hypothesis that induced emergence could be a novel isolating mechanism in desert bees.

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