

Temperature Rise and Its Influence on the Cessation of Diapause in *Plebeia droryana*, a Eusocial Bee (Hymenoptera: Apidae)

Charles F. Dos Santos,¹ Patrícia Nunes-Silva, and Betina Blochtein

Departamento de Biodiversidade e Ecologia, Faculdade de Biociências, Pontifícia Universidade Católica do Rio Grande do Sul, Av. Ipiranga, 6681, Porto Alegre, RS, Brazil (chasanto@gmail.com; patricia.silva@pucrs.br; betinabl@pucrs.br) and

¹Corresponding author, e-mail: charles.santos@pucrs.br

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Abstract

Climate warming in the coming decades may affect diapause in insect species which use it to survive unfavorable winter conditions. *Plebeia droryana* (Fries) (Hymenoptera: Apidae: Meliponini) is a highly eusocial bee species that exhibits reproductive diapause and inhabits southern South America where winter temperatures may fall below 10°C, or even below 0°C in extreme years. In this paper, we evaluate whether *P. droryana* might terminate diapause during winter under laboratory conditions. We initially kept colonies of *P. droryana* at 8°C in a biochemical oxygen demand chamber, and then raised the temperature by 2°C every 3 d until the cessation of diapause was detected, as indicated by the onset of brood cell building and subsequent egg-laying by queens. We found that the termination of diapause in *P. droryana* could be achieved at temperatures between 16°C and 22°C, resulting in typical postdiapause brood cell building and egg-laying rates. Our binomial generalized linear mixed model indicated that only temperature, but no time or temperature–time interaction, explained the probability of termination of diapause in *P. droryana*. Again, only temperature, but no time or temperature–time interaction, significantly affected amount of brood cell built postdiapause in this species. These data suggest that the levels of predicted climate warming in the geographic range of *P. droryana* over the coming decades will probably result in these populations abandoning diapause behavior. These results have important implications regarding the ecological service of crop and wild plant pollination provided by this species.

Key words: Apidae, beneficial arthropod, climate change, diapause, physiological ecology

Extreme, cyclic environmental conditions such as high or low temperatures, heavy rainfall, and severe drought may impose limits on the development of many insects (Tauber and Tauber 1976, Denlinger 1986). However, over evolutionary time most species have evolved important adaptations and behavioral strategies, such as diapause behavior, to cope with these unfavorable conditions (Tauber and Tauber 1976, Denlinger 1986). Diapause has been defined as a gradual, temporary, and genetically programmed arrest of the growth or development of an organism in order to ensure its survival through unfavorable environmental conditions (Tauber and Tauber 1976, Denlinger 1986, Košťál 2006).

However, it is unclear whether insects may be able to evolve changes to their behavior and physiology fast enough to cope with anthropogenic disturbances occurring over relatively short time scales, such as rapid changes in climatic conditions. For example, rapid global warming in some regions have been found to affect insect populations which currently exhibit diapause (Bale and Hayward 2010, Stelzer et al. 2010, Owen et al. 2013, Scaven and Rafferty 2013). They may therefore remain active or shorten their

duration of diapause as temperatures rise within their geographic distributions (Bale and Hayward 2010).

Indeed, the diapause behavior in insects have been observed or likely believed to be affected by warming climates. Thus, some studies have demonstrated that insect species are becoming less likely to enter reproductive diapause, or may shorten the time spent in reproductive diapause due to milder winter temperatures in those study areas (see Table 1 for species and references).

In Brazilian subtropical regions, the reproductive diapause of native, highly eusocial bees is also predicted to be affected by climate warming during the coming decades (Santos et al. 2015). These bees, known as stingless bees (Hymenoptera: Apidae: Meliponini), exhibit reproductive diapause in order to survive periods of colder weather (Santos et al. 2014). The reproductive diapause of stingless bees has been described as a gradual, seasonal, and preprogrammed arrest in the provisioning and oviposition process (POP; Santos et al. 2014). In summary, worker bees stop building brood cells and consequently queens interrupt their egg-laying activities.

Table 1. Some examples of solitary, gregarious, and social insect species known (or believed in future decades) are being affected by climate warming

Species	Order	Common name	Importance	Locality	Reference
<i>Calliphora vicina</i> Robineau-Desvoidy	Diptera	Blowflies	Forensic entomology	United Kingdom	Vaz Nunes and Saunders 1989
<i>Sesamia nonagrioides</i> Lefebvre	Lepidoptera	Moths	Agricultural pest	Greece	Fantinou and Kagkou 2000
<i>Nezara viridula</i> L.	Heteroptera	Bugs	Agricultural pest	Japan	Tougou et al. 2009
<i>Nezara antennata</i> Amyiot & Serville	Heteroptera	Bugs	Agricultural pest	Japan	Tougou et al. 2009
<i>Bombus terrestris</i> L.	Hymenoptera	Bumblebees	Pollinator	United Kingdom	Stelzer et al. 2010, Owen et al. 2013
<i>Plebeia droryana</i> (Friese)	Hymenoptera	Stingless Bees	Pollinator	Brazil	Santos et al. 2015

In general, stingless bee species (mainly *Plebeia* Schwarz genus) commence prediapauses behavior (gradual decrease of POP) at the end of the summer and mid-autumn (February–May, at ~24°C) while environmental conditions are still mild and favorable so that by the colder months (June–July, at ~14°C) all of the colonies are in reproductive diapause which then ceases at the end of the winter and mid-spring (August–September, at ~16°C; Santos et al. 2014).

Thus, if climate warming is predicted to terminate reproductive diapause in stingless bees during the coming decades (Santos et al. 2015), it would be necessary to understand how such bees would behave if temperature extremes already occurred somewhat in current time.

In this paper, we look at whether experimental temperature rise under laboratory conditions could interrupt reproductive diapause in colonies of the stingless bee *Plebeia droryana* (Friese). This stingless bee species is widely distributed in the Neotropical region (Camargo and Pedro 2013). In the southern part of its South American distribution, where temperatures are relatively moderate (i.e., not subject to prolonged extremes of hot or cold weather), its colonies remain in reproductive diapause for at least 3 mo of the year usually from May to July (Santos et al. 2014). We discuss our findings in the light of the potential effects of climate change on the biology of *P. droryana*.

Materials and Methods

Colonies

Seven *P. droryana* colonies, A–G, of standardized size were housed in boxes measuring 17 by 17 by 12 cm³. Each colony (A–G) initially comprised one egg-laying queen and about 300 workers. All the colonies were initially in reproductive diapause, i.e., no brood combs were being built and no oviposition had occurred for at least 1 to 2 mo (May–June 2014), that is, since mid-autumn to the beginning of winter in southern Brazil. Colonies A–G received approximately three honey and pollen pots from conspecifics as well as a small propolis pellet.

The experiment to interrupt reproductive diapause in the *P. droryana* colonies was conducted during July 2014, at the peak of winter in the study area, when the minimum average temperature was 10°C, with occasional falls to near zero degrees (National Institute of Meteorology [INMET] 2014). The experiments were carried out at the Laboratory of Entomology in the Museum of Sciences and Technology at the Pontifícia Universidade Católica do Rio Grande do Sul, in Porto Alegre, Brazil (30° 1'58" S, 51° 13'48" W).

Diapause Termination Experiment

The colonies were placed inside a biochemical oxygen demand chamber (B.O.D., model Luca-161/04, LUCADAMA, São Paulo,

Brazil), with a controlled relative humidity (RH) 70%, constant darkness (0L:24D regime), and an initial temperature of 8°C. The temperature was then raised by 2°C every 3 d until brood cell construction and subsequent queen oviposition was detected. The temperature inside the B.O.D. was recorded using datalogger devices (model U23-001 HOBO Pro v2, version 3.6.2, ONSET, Mato Grosso, Brazil).

During the experiment, we fed the colonies with honey syrup (one honey:one water, 5 ml) and pollen (0.50 g) at 0800 hours daily. Observations were made of the absence or presence of brood cells and queen oviposition activity three times a day (at 0800, 1300, and 1800 hours) during the entire experiment. Observations were made in a darkroom under red light, and sufficient amounts of the wax involucre were removed from the brood comb to enable accurate observations. Whenever any brood cell building was detected, we recorded the previously programmed temperature inside the B.O.D. After the cessation of diapause, the number of brood cells under construction was recorded three times a day (period like above) during 3 d. Then these colonies were moved to another B.O.D. at a steady temperature of 25°C in order to assure that they would not enter reproductive diapause again after detection of maximum critical temperature for this behavior (see Results).

Statistical Analysis

Because we made multiple repeated measures across time (longitudinal data) for each colony, it matters to account for possible variation among random-effect predictors (here, colonies; Bolker et al. 2009, Pirk et al. 2013). Therefore, we carried out two generalized linear mixed models (GLMM) for assessing these hierarchical data.

In first model, we estimated the probability for the termination of reproductive diapause (no = 0; yes = 1) in *P. droryana* colonies by assuming temperature, treatment days, and interaction between them as fixed-effect predictors and *P. droryana* colonies as random-effect predictors. Such model was fit with a binomial distribution (logit) for binary data. This mixed model was adjusted fit by maximum likelihood (Adaptive Gauss-Hermite Quadrature, nAGQ = 10) using function *glmer* in lme4 package (Bates et al. 2015). Yet, in second model, we assessed whether temperature, treatment days, and interaction between them (fixed effects) could explain the number of brood cells built per POP by assuming again *P. droryana* colonies as random effects. For this, we employed a negative binomial family using function *glmer.nb* from lme4 package (Bates et al. 2015). This model was fit by maximum likelihood (Laplace approximation).

For both models we evaluated for overdispersion data using function *overdisp.glmer* from “RVAideMemoire” package (Hervé 2015). Significance tests were done using χ^2 -test as follows: 1-pchisq (residual deviance/ degree of freedom).

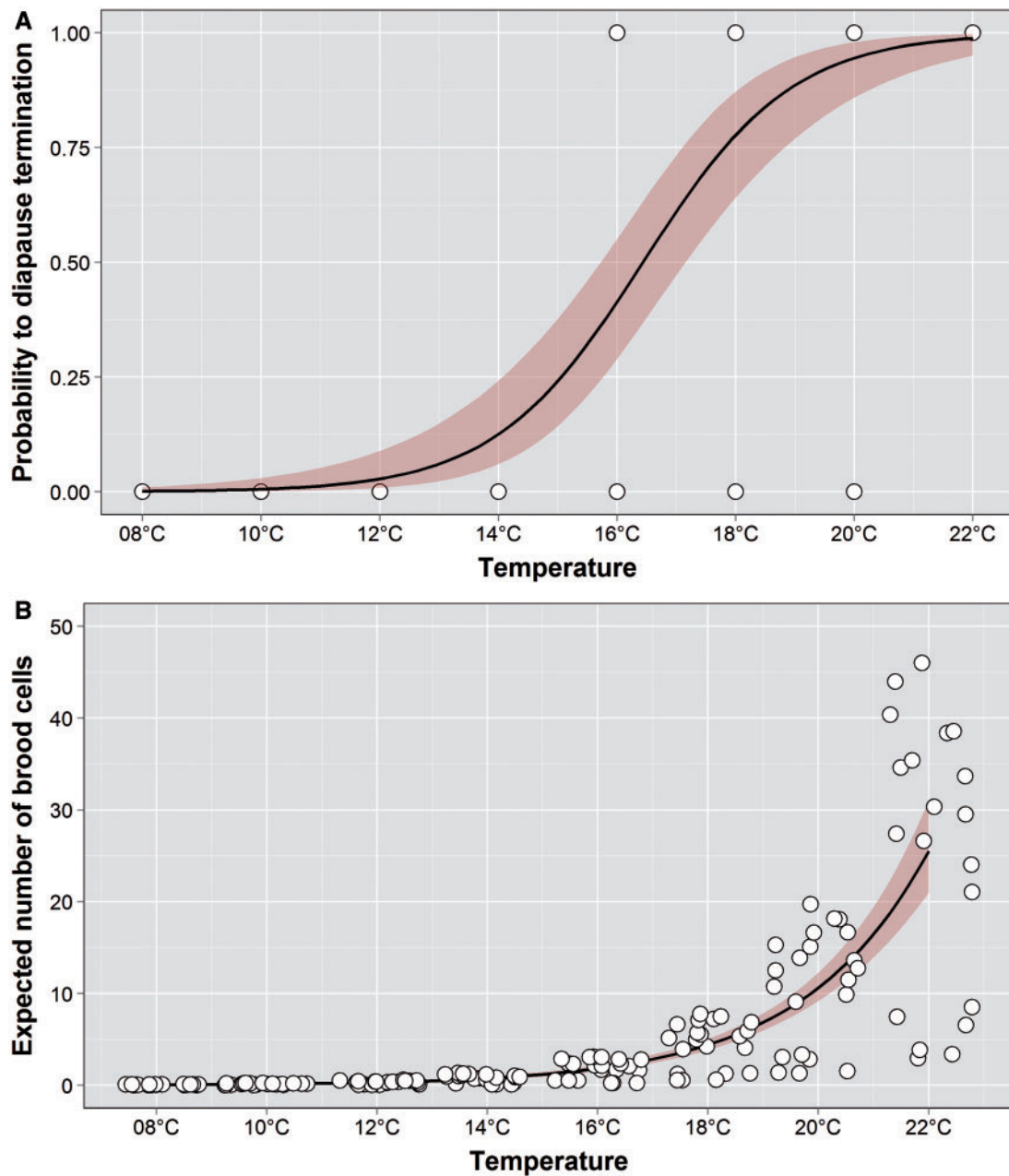


Fig. 1. Effect of temperature over *P. droryana* colonies. (A) Probability of reproductive diapause cessation: binomial GLMM fit with maximum likelihood (Adaptive Gauss-Hermite Quadrature). (B) Number of brood cell built per colony for each temperature: negative binomial GLMM fit with maximum likelihood (Laplace approximation). Notes for both models: dots—total observed values; solid line—predicted model; shaded area—confidence interval (95%), $P < 0.001$.

To test whether there were any differences between the numbers of brood cells built and consequently egg-laying rates by each postdiapause colony, we analyzed the data for their normality and homogeneity of variances using, respectively, the Shapiro-Wilk test and the Bartlett test with 999 permutations. Confirmed the normality and the homogeneity (see results), we conducted a one-way analysis of variance (ANOVA) with 999 permutations, followed by a post hoc Tukey honest significant difference (HSD) test with 95% confidence level.

We also tested power and effect size analyses to assess the ANOVA results for reliability. For this, we used the function *pwr.anova.test* from the package *pwr* (Champely 2012). The input data were: $k=7$, $n=9$, $f=0.8$, $sig.level=0.01$, $power=x$, where, k is

the number of groups, n is the number of observations per group, f is the effect size (quantitative measure of the strength of the mean difference among samples), $sig.level$ is the significance level, and $power$ is the statistical power analysis (Champely 2012). All statistical analyses were carried out using the R program (R Core Team 2015) and plotted using *ggplot2* (Wickham 2009) and *gridExtra* (Auguie 2015), as applicable.

Results

Termination of Reproductive Diapause

The cessation of reproductive diapause in *P. droryana* colonies could be explained by rising temperature (binomial GLMM; Wald

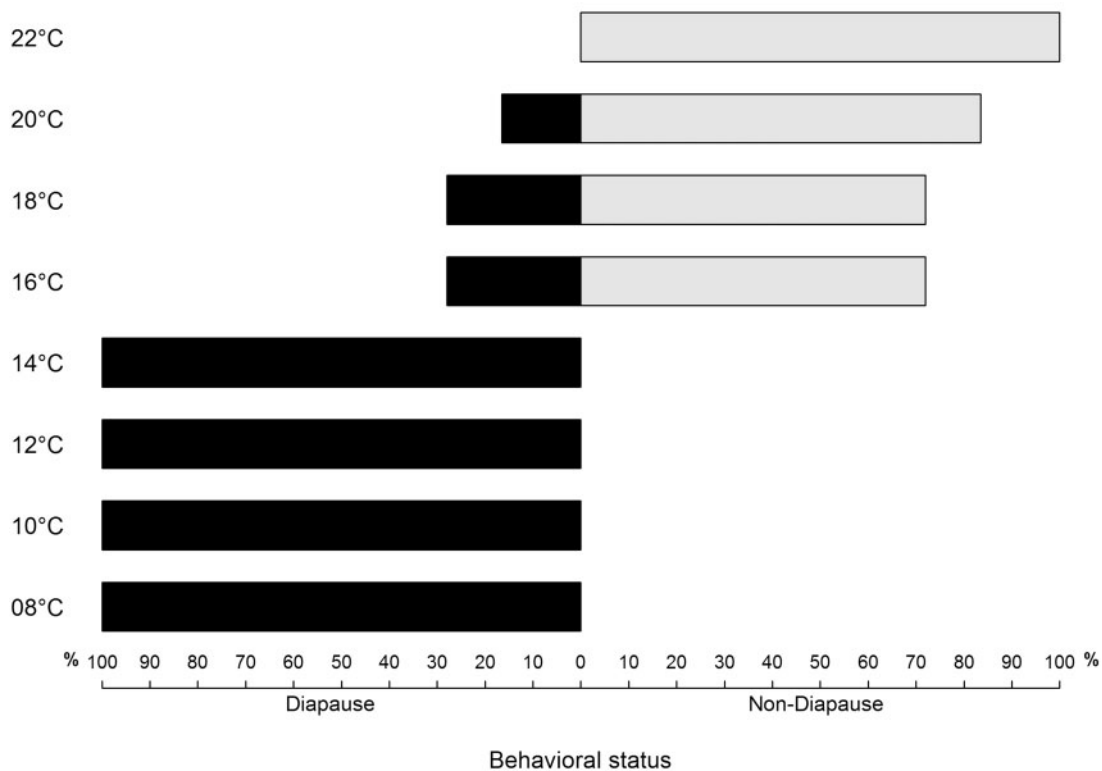
Effect of temperature rise on *Plebeia droryana* colonies

Fig. 2. Proportion of observed *P. droryana* colonies in reproductive diapause or nondiapause as temperatures were progressively increased from 08°C to 22°C during the peak of winter (July) in southern Brazil.

z -test = 4.146; $P < 0.0001$), but not by time or temperature–time interaction (binomial GLMM; Wald z -test = 0.0; $P > 0.05$, Fig. 1, Supp Table 1 [online only]). There was not data overdispersion for this first model (ratio: 0.003, $p > 0.05$). Similarly, temperature rise resulted in larger number of brood cell built within colonies (negative binomial GLMM; $z = 4.050$; $df = 162$; $P < 0.0001$), but time and temperature–time interaction had not any effect over it (negative binomial GLMM; Wald z -test = -0.493, 0.528; $P > 0.05$; Supp Table 1 [online only]; Fig. 1). Again here, there was not data overdispersion for this second model (ratio: 0.741, $P > 0.05$). The *P. droryana* colonies ceased reproductive diapause from 16°C (c.a. 72%) to 22°C (Fig. 2).

Number of Brood Cells in Postdiapause Colonies

Neither the Shapiro–Wilk normality test nor the homogeneity of variance test were significant ($W = 0.988$; $P > 0.05$ and Bartlett's $\chi^2 = 9.430$; $df = 6$; $P > 0.05$). It was therefore necessary to employ a parametric test to evaluate brood cell building after reproductive diapause termination. The number of brood cells built and provisioned after termination of diapause was 8.01 ± 3.47 (mean \pm SD) per POP, reaching up to 17 brood cells at colony G (Fig. 3).

The number of brood cells built in the colonies did differ significantly (ANOVA, $F = 4.166$; $df = 6, 56$; $P < 0.001$). The number of brood cells built by colony G was significantly different from colonies A and B (Tukey test [HSD]: $P < 0.05$, Supp Table 2 [online only]; Fig. 3). Our power test calculation indicated a high power analysis (0.98) showing great accuracy in the ANOVA results, with differences among colonies in which we can be confident.

Discussion

Our findings indicate that the temperature rise during colder period of winter in southern Brazil (July) may terminate reproductive diapause in *P. droryana* colonies. Here, only temperature explained the cessation of reproductive diapause in the studied species rather than elapsed time or interaction between temperature and elapsed time (days) of experiment. In fact, temperature is an important environmental cue used by many insects to decide whether to initiate, maintain, or terminate diapause (Tauber and Kyriacou 2001, Saunders 2014). In our case, *P. droryana* demonstrated to be a species also highly sensitive to changes in temperature irrespective if temperature tends to increase (like here) or decrease (Santos et al. 2015).

However, the different temperatures to terminate reproductive diapause may be related to distinct temperature thresholds among colonies, as registered also for *Plebeia remota* (Ribeiro et al. 2003), as the colony size, food income, and number of workers per colony were similar in these cases.

Yet, the difference in number of brood cells built per colony postdiapause may be due to specific features within each colony, like those several aspects linking complex *Plebeia* queen–worker interactions (Zucchi 1993; Drumond et al. 1996, 2000). In fact, the different responses provoked by temperature inside bee colonies like productivity and reproduction are difficult to understand because it enfold a series of variables (Vollet-Neto et al. 2014, Holland and Bourke 2015). But it is possible to infer that presence of *P. droryana* queens more genetically productive, as well as faster resumption in optimal physiological conditions postdiapause, may also have

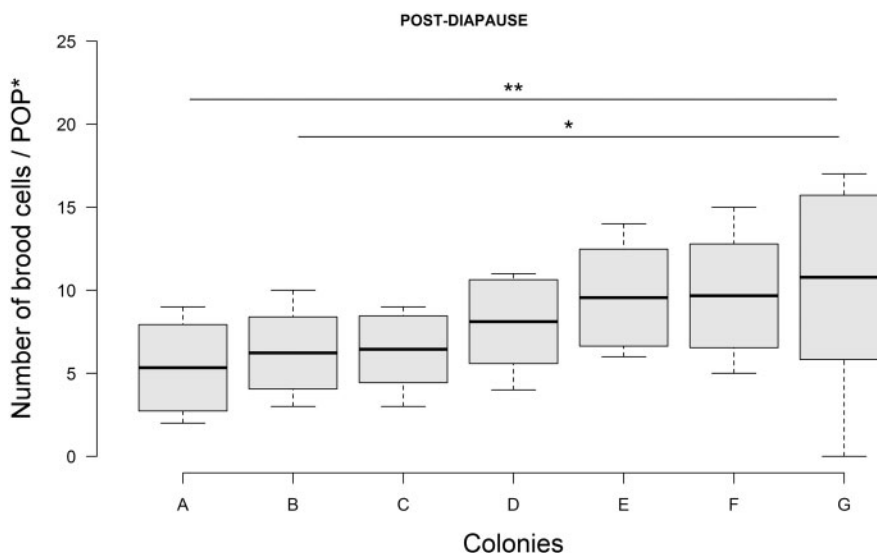


Fig. 3. The number of brood cells built per *P. droryana* colony after experimental termination of diapause under laboratory conditions. Notice: POP—provisioning and oviposition process; Boxplot: mean \pm SD, upper and lowest lines show maximum and minimum, respectively; asterisks indicate significant difference between colonies.

contributed for observed differences in building brood cells in present study.

Importantly, our results beg the question as to whether *P. droryana* bees would cease reproductive diapause under natural conditions during same period on studied area if climate warming indeed to occur in their geographic range in coming decades (Santos et al. 2015). It has been predicted that a significant part of the *P. droryana* population in this region may be active in milder winter months in southern Brazil in 2080 if the current minimum winter temperature (10.1°C, median) rises to 13.4°C (median) as suggested (Santos et al. 2015). Our findings somewhat corroborates this scenario, as can be observed in our predicted model.

Therefore, although reproductive diapause in *P. droryana* is an adaptive behavior that increases the chances of these bees survive to unfavorable environmental conditions (extreme cold), milder winters may induce part of the *P. droryana* population to avoid entering reproductive diapause. Apparently, it could not be a problem itself because these bees could dedicate this time to forage and invest in brood production. However, actually there is increasing concern on whether and how the impact of extreme climatic events such as heat or cold waves may affect organisms in several planet's regions (Vose et al. 2005, Wang and Zeng 2015). Thus, if *P. droryana* colonies were active during predicted milder winters (Santos et al. 2015), but there are sudden extreme cold waves, then we can foresee that it may put at risk several colonies of this bee species if they were not physiologically and behaviorally ready for this.

Although our data should be used with caution because they are results of experimental data, we have evidences that worldwide natural insect populations are already undergoing considerable modifications in their diapause behavior due to milder winter temperatures (Vaz Nunes and Saunders 1989, Fantinou and Kagkou 2000, Tougou et al. 2009, Stelzer et al. 2010, Owen et al. 2013). In other words, insects like moths, blowflies, bugs, and bumblebees are avoiding to enter diapause because temperatures during colder months on their geographical range are actually hotter than in past (Vaz Nunes and Saunders 1989, Fantinou and Kagkou 2000, Tougou et al. 2009, Stelzer et al. 2010, Owen et al. 2013).

In specific case of pollinator insects that strongly need floral resources for survival, like bumblebees and *P. droryana* stingless bees, the consequences for a nondiapause behavior under climate warming are still unclear (Stelzer et al. 2010, Owen et al. 2013, Santos et al. 2015). However, many studies have gathered evidences that climate change may disrupt plant–pollinator interactions as, e.g., by modifying both plant and pollinator phenologies or still to alter production pattern of nectar and pollen (Hegland et al. 2009, Schweiger et al. 2010, Gilman et al. 2012, Scaven and Rafferty 2013). Other studies also indicate that bee-dependent crops may be affected in future because actual suitable habitats for these pollinator insects may be reduced or inadequate, among other things, because of climate warming (Giannini et al. 2012, 2013; Polce et al. 2014).

To what extent *P. droryana* population in southern Brazil will avoid entering in reproductive diapause (Santos et al. 2015), or if they enter would terminate diapause because of predicted milder winters (as seen here), is still unclear. Nevertheless, in both cases many *P. droryana* colonies may be lost if they were active during extreme cold waves. It is therefore necessary to plan ahead to find a means of managing this important pollinating bee species and to find solutions for potential problems regarding shortage of food (nectar and pollen), and potential forage plants for worker bees in future milder winters.

Supplementary Data

Supplementary data are available at *Annals of the Entomological Society of America* online.

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