ECOLOGY, BEHAVIOR AND BIONOMICS

Phenology of *Bombus pennsylvanicus sonorus* Say (Hymenoptera: Apidae) in Central Mexico

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Fenología de *Bombus pennsylvanicus sonorus* Say (Hymenoptera: Apidae) en el Centro de México

RESUMEN - Estudiamos la actividad estacional de *Bombus pennsylvanicus sonorus* Say bajo las condiciones subtropicales de la Meseta Central Mexicana. Mensualmente, durante el año 1998, registramos las castas de abejas activas (infiriéndolo del tamaño corporal medido por la longitud alar), la presencia y actividad de individuos reproductivos y la actividad reproductiva. También se investigaran las plantas florales usadas como recursos alimenticios. Las condiciones Subtropicales de la Meseta Central Mexicana no parecen alterar las características fenológicas de *B. pennsylvanicus sonorus*, ya que la especie presenta colonias anuales y un periodo bien definido de inactividad. El tamaño de los individuos se incrementó progresivamente desde las primeras actividades observadas, a mediados de abril, hasta el fin de la colonia en noviembre. Las abejas reproductivas fueron registradas a partir de la segunda mitad del año. Los machos fueron observados entre julio y noviembre, y las reinas y parejas apareándose fueron registradas en noviembre y diciembre. Seguidamente las reinas fueron observadas buscando lugares para hibernar. La actitidad fue reasumida a partir de febrero del siguiente año. La actividad estacional parece estar mas relacionada a la disposición de recursos florales (los cuales, a su vez, están relacionados al régimen de lluvias), que a cambios en la temperatura y el largo del día. Algunos de los principales recursos alimenticios de las abejas *B. pennsylvanicus sonorus* fueron *Tithonia tubiformis, Cosmos bipinnatus, Anoda cristata, Solanum rostratum y Jacaranda mimosaefolia.*

PALABRAS CLAVE: Abeja, *Fervidobombus*, subtropical

ABSTRACT - We studied the seasonal activity of *Bombus pennsylvanicus sonorus* Say in subtropical conditions of the Mexican Central Plateau. Monthly during 1998, we recorded caste of active individuals (inferred form corporal size measured as wing length), presence and activity of reproductive individuals, and mating activity. Also, we recorded the flower plants used as resources.
Subtropical conditions of the Mexican Central Plateau do not seem to modify phenological features of *B. pennsylvanicus sonorus* since the species presents annual colonies and a clearly defined period of inactivity. The size of individuals progressively increased between the first recorded activity period in middle April and the end of the colonies in November. Reproductive bees were observed since the second half of the year. The presence of males was recorded between July and November and queens and mating pairs were observed during November and December. Then mating queens were noted seeking hibernation places. Activity resumed in February of the following year. Seasonal activity seems to be more related to availability of floral resources (which, in turn, is related to rain regime), than to changes in temperature and day length. Some of the main food resources used by *B. pennsylvanicus sonorus* were *Tithonia tubiformis, Cosmos bipinnatus, Anoda cristata, Solanum rostratum* and *Jacaranda mimosaefolia.*

KEY WORDS: Bumblebee, *Fervidobombus*, subtropical

Bumblebees, with the exception of the social parasites, produce eusocial annual colonies, founded by a mated female or queen. Under arctic and temperate conditions, colonies are founded during the spring (Plowright & Laverty 1984). The first workers are small individuals, morphologically similar to the queen. Later in the season, the colony produces queens and males, which mate usually with individuals from other colonies. The colony ends after producing reproductive individuals (males and females) and the daughter queens mate at the end of the colony cycle. The newly mated queens

hibernate until the following spring. On the other hand, bumblebees of the subgenus *Fervidobombus* are unusual because they exhibit social characteristics (not usually found in bumblebees) more typical of the highly eusocial honeybees and stingless bees. These include large colonies of up to several thousand individuals with unusually well developed defense systems (Dias 1958, Michener y LaBerge 1954, Cameron *et al*. 1999), and perennial colonies that can persist for many years.

Despite *Bombus pennsylvanicus* Degeer being one of the most abundant and widely distributed bumblebee species in North America, there are a few studies on their phenology and behavior (Johnson 1986, Goldblatt & Fell 1987, Todd *et al*. 1991, Visscher & Vetter 1995).

Two subspecies, *B. pennsylvanicus pennsylvanicus* and *B. pennsylvanicus sonorus*, are recognized. The former is more frequently found in South West U.S. and the drier areas of the Mexican Plateau, the Sonoran Desert and Baja California; the second subspecies occurs in the moister areas of the Mexican Plateau, up to the highlands of Oaxaca (Labougle 1990).

The seasonal distribution of the species is partially known for Mexico, based on collection dates from museum specimens (Labougle 1990), and some phenological features of this species were studied by MacFarlane *et al*. (1994) in Canada.

With this study we investigate the influence of subtropical conditions on the phenology of *B. pennsylvanicus sonorus*, analyzing the activity and phenology of colonies in Cholula, Puebla, located on the Central Mexican Plateau.

Materials and Methods

Study site. Fieldwork was conducted in three observation points located within and around the campus of the Universidad de las Américas-Puebla, in Cholula, Puebla. The campus occupies 78 ha, and is located at 19°03'13"N 98°16'52"W, at a mean altitude of 2250 m. The climate is classified as C (w2)x', in the system of Köppen with rains predominantly in the summer, and dry and cold winters. The original vegetation was transitional between pine-oak and tropical deciduous forest to the south and southwest, and xerophytic shrub and grasslands to the north and northeast. However, due to intense urban land use and agricultural activities practiced since pre-Columbian times, practically nothing of the original vegetation remains (Rzedowski & Rzedowski 1985).

Sampling. Sampling was performed once a week, between March 26, 1998, when the first active individuals were found, until December 11, 1998, when flying activity was no longer apparent. We captured all bumblebees found in each site during one hour using an entomological net and sacrificed them with Potassium Cyanide. We measured the length of the anterior right wing, from the basal end of the coastal vein, to the apical margin of the wing. Similar measures of wing length have been used for social wasps and were strongly correlated with dry body mass (O'Donnell 1995, O'Donnell 2001).

To estimate the age of individuals (Cartar 1992), the degree of wing wear was semi-quantitatively determined, assigning each individual to a category between 0 (no wear) and 3 (maximum wear observed).

Caste assignation. Female individuals were assigned to either the queen or the worker caste, depending on the measure of wing length. Any individuals with wing length equal to or greater than 1.72 cm were considered queens. Individuals with wing length smaller than 1.72 cm were considered workers. We used this wing length value to differentiate castes because it was the smallest measure obtained during the period when only queens were active. In cases when there was doubt about the caste of an individual, we dissected the reproductive system to determine if the ovaries were developed.

Colony cycle. The colony cycle kind (annual or continuous) was inferred from the presence of individuals in the field and their relative abundance during the observations and samples taken over one year.

First workers emergence. The first workers emergence was determined from the measurements of the anterior wing length of the specimens collected during the observations. The foraging activity of the worker caste began when two groups of individuals were observed, with noticeable different wing length, the queens (bigger bees) and workers (smaller bees). The wing length was chosen because it provides a constant proportion of the size of the insect.

Emergence of reproductive individuals. The production of reproductive individuals of the colony was determined by examining the bees collected. The males usually have a more cylindrical body and fly more slowly. Also, they have an extra antennal segment than females and obvious differences in the reproductive system. Queen-worker differentiation was made as described on "caste assignation".

Mating period. The mating period of the bees was determined from direct observations of individuals in copula in the field and from inferences of the proportion of queen/males during the collections over the course of the year.

Hibernation. The beginning of the hibernation stage was deducted from the decrease in the number of foraging bees and the increase in the size of the active bees. The end of this period lead to the initiation of new queens searching for places to found new colonies.

Plants visited. During our study we collected the most common plant species flowering on the observation sites in which *B. pennsylvanicus sonorus* visitations were observed. Then, samples were identified by the personal of BUAP herbarium.

Results

The queen caste prevails on the first months of the year. Thus, in March, they represent 100% of the samples, and

in the following months (April and May) the proportion decreases gradually until they are absent in the samples at the end of May (Table 1, Fig. 1). In November and December, the queens are again collected in the samples. Moreover, the queens show the lowest variations in wing length throughout the year among the three castes (Fig. 2).

The workers did not appear in the samples until mid April. This represents the first worker generation, characterized by their small bodies (Fig. 3). In the following months, there is a trend of increasing body size of the caste. The wing length average in the first months (April and May) was between 1.3 cm and 1.4 cm, whereas in the lasts months (November and December) it was close to 1.6 cm.

On the other hand, the proportion of workers in the samples reach their maximum in mid year (May to July), when they represent 100% of the castes in the samples (Fig. 1).

The first males emerge in July. Their proportion, however, was low (25%) in the first months of their appearance (September and October), until the last months of the year (November and December) when they represent the majority in the samples (75%). These castes also showed a marked trend of increasing body size over the year. The first males produced (May) averaged 1.4 cm, whereas the males of the last months averaged more than 1.6 cm (Fig. 4).

It was also remarkable the overlap between queens and workers in April and May, when both castes were active

Table 1. Number of individuals collected, proportion in the sample, wing average per caste and standard deviation.

Sampling date	Queens				Workers				Males			
	n	% in the sample	Wing aver. (cm)	sd (cm)	n	% in the sample	Wing aver. (cm)	sd (cm)	n	% in the sample	Wing aver. (cm)	sd (cm)
26-Mar	9	100.0	1.983	0.13	0	0.0			0	0.0		
3-Abr	7	100.0	2.019	0.06	0	0.0			0	0.0		
13-Abr	13	81.2	1.976	0.10	3	18.8	1.410	0.03	0	0.0		
21-Abr	10	62.5	2.002	0.07	6	37.5	1.350		0	0.0		
28-Abr	9	50.0	2.041	0.09	9	50.0	1.355	0.09	0	0.0		
6-May	3	57.2	1.957	0.08	3	42.8	1.340	0.16	0	0.0		
11-May	0	0.0			9	100.0	1.463	0.06	0	0.0		
18-May	0	0.0			9	100.0	1.392	0.07	0	0.0		
25-May	1	14.7	1.890		6	85.3	1.429	0.05	0	0.0		
2-Jun	0	0.0			7	100.0	1.424	0.11	0	0.0		
26-Jun	0	0.0			6	100.0	1.478	0.12	0	0.0		
2-Jul	0	0.0			7	100.0	1.550	0.06	0	0.0		
9-Jul	0	0.0			7	100.0	1.531	0.11	0	0.0		
18-Jul	0	0.0			7	87.5	1.517	0.09	1	12.5	1.430	
24-Jul	0	0.0			7	87.5	1.505	0.10	1	12.5	1.420	
5-Ago	0	0.0			8	100.0	1.568	0.10	0	0.0		
19-Ago	1	12.5	1.840	0.03	7	87.5	1.657	0.10	0	0.0		
26-Ago	0	0.0			7	87.5	1.574	0.06	1	12.5	1.490	
4-Sep	0	0.0			7	87.5	1.570	0.08	1	12.5	1.440	
15-Sep	0	0.0			6	75.0	1.547	0.08	2	25.0	1.555	0.04
23-Sep	0	0.0			6	75.0	1.527	0.08	2	25.0	1.620	0.01
30-Sep	1	12.5			5	62.5	1.550	0.05	2	25.0	1.835	0.16
7-Oct	0	0.0			6	75.0	1.638	0.11	2	25.0	1.640	0.04
16-Oct	0	0.0			6	75.0	1.582	0.06	2	25.0	1.750	0.06
24-Oct	0	0.0			5	62.5	1.616		3	37.5	1.698	0.15
11-Nov	1	12.5			5	62.5	1.621	0.05	2	25.0	1.690	0.01
19-Nov	1	12.5	2.140		1	12.5	1.490		6	75.0	1.677	0.08
28-Nov	1	10.0	1.870		2	20.0	1.550	0.04	7	70.0	1.703	0.08
4-Dic	1	25.0	1.770	0.07	0	0.0	1.720		6	75.0	1.670	0.06

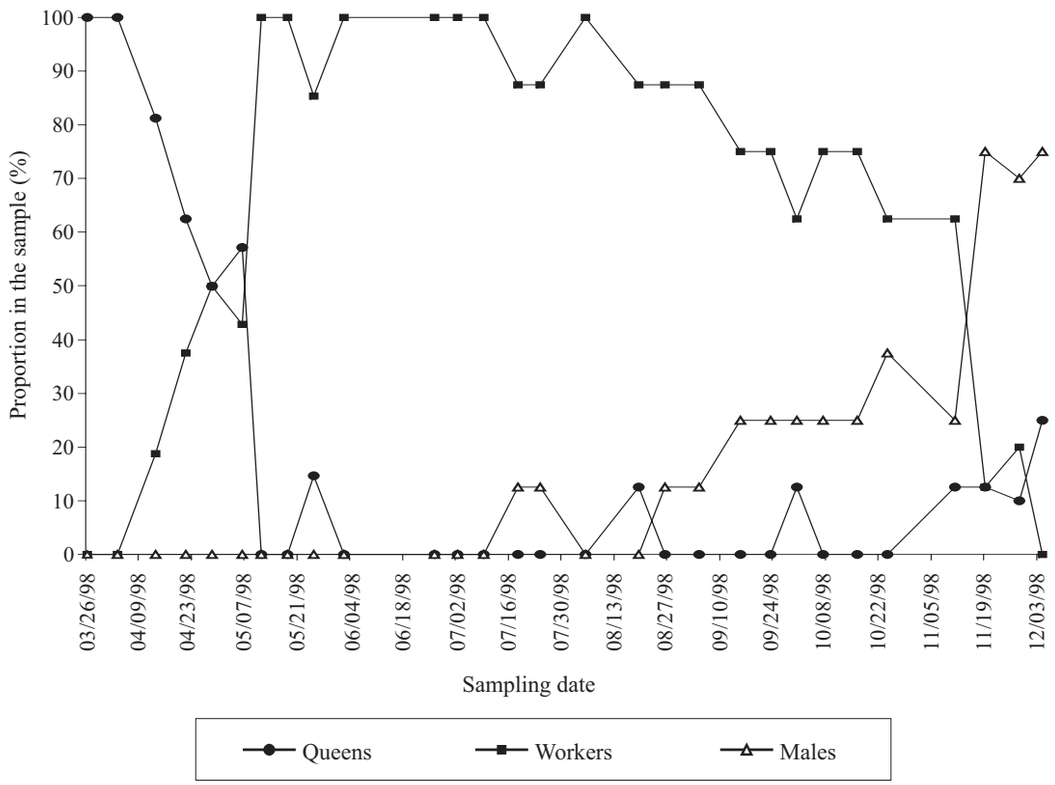

Fig. 1. Caste proportion per date from March 26 to December 3, 1998.

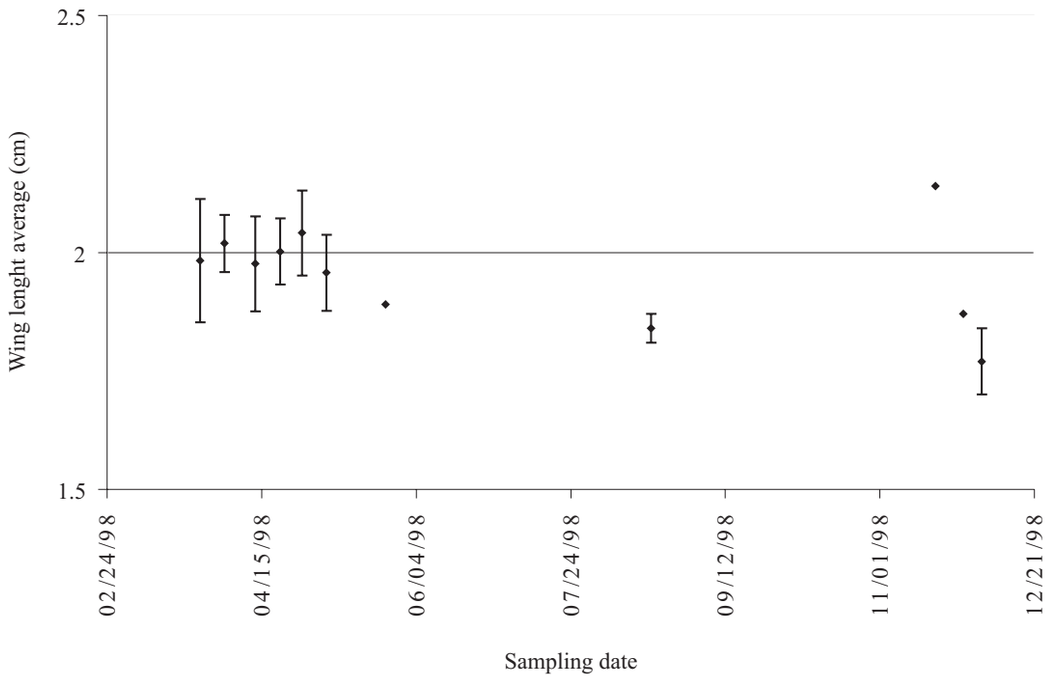

Fig. 2. Wing length average for queens.

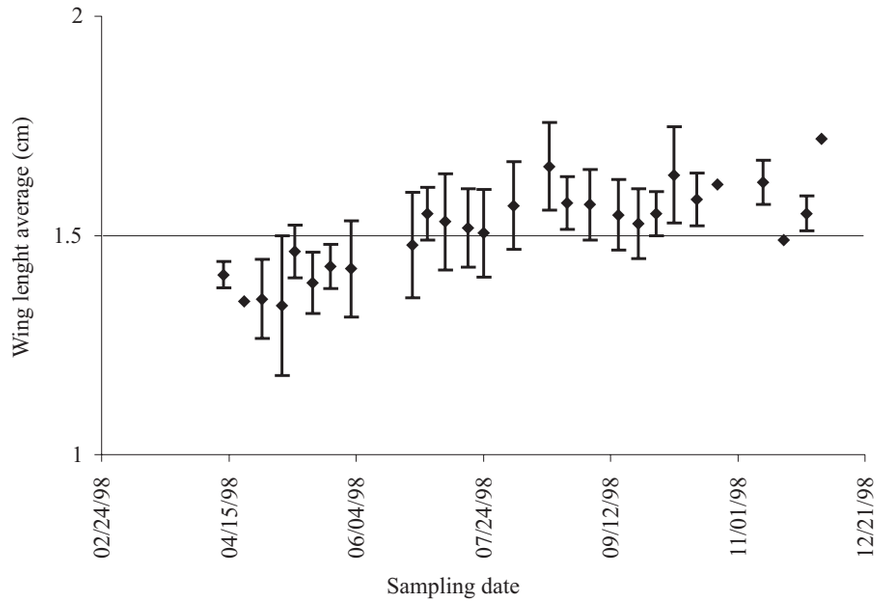

Fig. 3. Wing length average for workers.

(Fig. 1). Another superposition occurred between workers and males from July to December, and workers, males and queens in November and December. These last months are the only period of the year in which all the castes are active.

Discussion

Our results are congruent with the literature regarding the biology of *B. pennsylvanicus sonorus* in temperate zones (Johnson 1986, Goldblatt & Fell 1987, Todd *et al*. 1991). Our study suggests that living in a semitropical zone, as Puebla (Central Mexico), does not notoriously alter the typical phenology of the species. Probably the bees form annual colonies beginning activity in mid or late February and ending in late November or the beginning of December.

As the colony evolved, the size of the bees increased significantly. This phenomenon has been extensively reported (Heinrich 1979, Duchateau 1991, Ribeiro 1994).

The bees reach a maximum wing length in March and April as a result of being queens dominant caste, and they are typically the largest bees of the colony. The samples taken in April show the higgest standard deviation during the year,

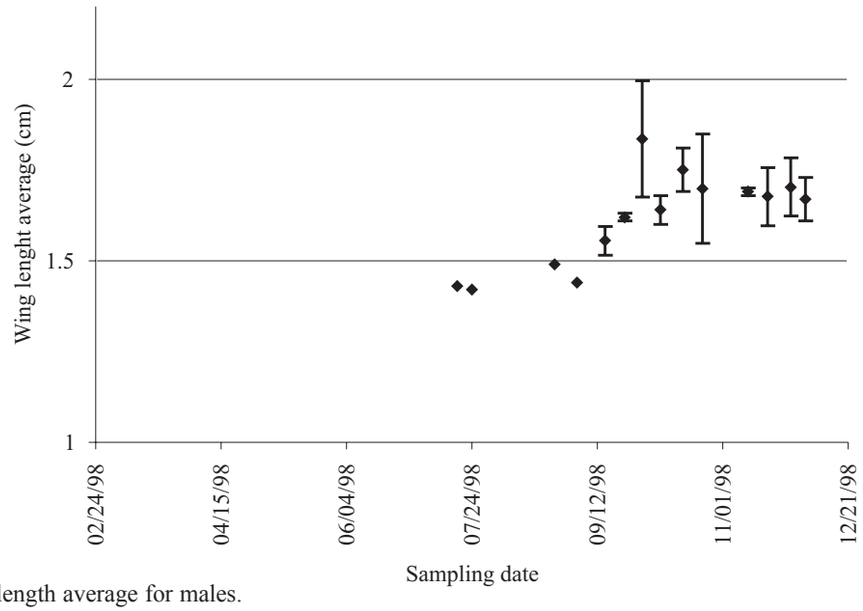

Fig. 4. Wing length average for males.

and it could be attributed to the overlap between queens and the first worker generation. In the following months the wing length average decreases since the number of queens decrease and the workers become the dominant caste.

The most stable period (lower Standard Deviation) was between August and September (Table 1, Fig. 5), when workers, males, and even queens were observed. The characteristic stability from these lapse could be attributed to the size of the colony (number of individuals), which was big enough to produce large quantities of food, in order to support larger bees.

The workers were absent in the samples taken in March because the colonies had just formed and the only foraging bees were queens. Then in April the first workers were collected but their proportion was still low, because the bulk of the foraging activity was still done by the queens. These first workers are characteristically very small bees that represent the first or second generation of the colony. At this stage of the colony the queen is the only foraging bee, so the food supply is typically scarce. In the subsequent months, until July, the workers became the only active foraging caste and their body size increased notoriously. Thus, the last workers produced in the colony were quite large, reaching sometimes the size of the queens. The proportion of workers decreased again when the reproductive individuals appeared, and by the end of the year they had disappeared completely.

The turning point of the colony – when the reproductive individuals were produced – was between July and August, when the first males were produced. These medium sized males were similar to workers (on wing length), and could not mate because queens were produced a couple of months later. In the subsequent months the proportion of the samples and the male size increased until they represented the majority of the active bees and reached the queens size on November and December.

Queens were the most stable caste in the colony (lesser Standard Deviation on wing length average). It could be a result of queens being produced in a relatively short time frame, in which the food resources of the colony have reached their maximum. The queens were the only surviving individuals of the previous season because they spent the last months of the year hibernating. Then, in February and March they were the only active caste, when they were looking for a location to found a new colony, or foraging for the first worker larva. When these bees completed their development they assisted the queen foraging until they gradually assumed all the foraging work. This explains the decrease of the queens in the samples of the subsequent months: the queens were only dedicated to tasks inside the nest whereas the workers did all the foraging work. It is not until November and December when the queens appear again in the samples. These are new queens, which once emerged, made some foraging trips, mated and found a place for hibernating.

The mating period for *B. pennsylvanicus* in Cholula seems to be restricted to November and December. This is inferred from just one observation of individuals in copula, and this is the only interval in which there were active males and queens.

Once the queens are fertilized they are buried for hibernation. The length of this period is determined by environmental conditions such as temperature and

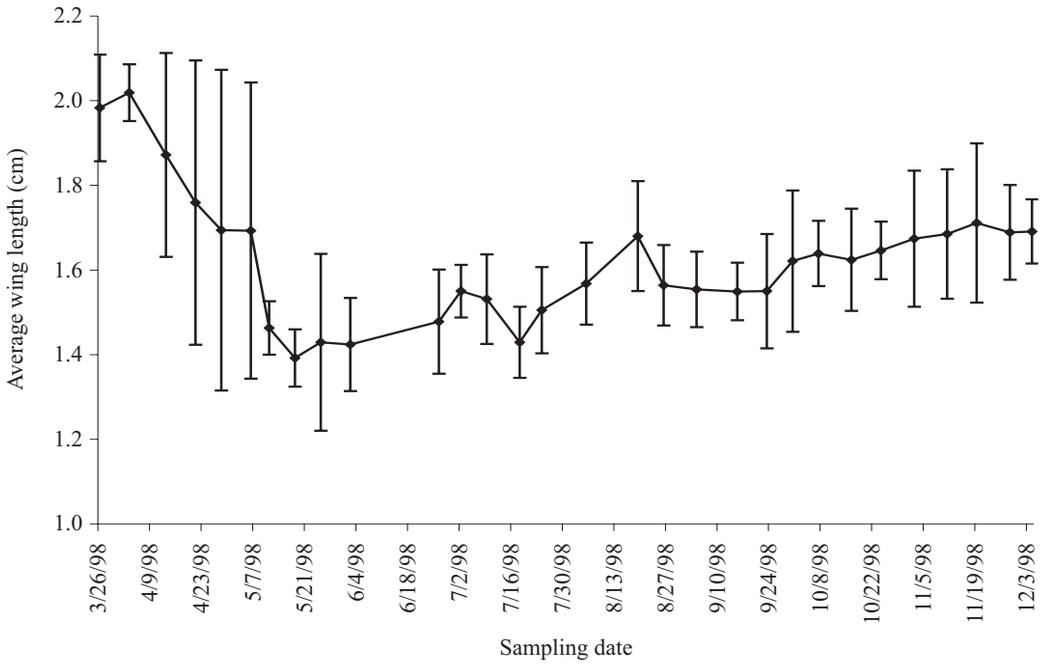

Fig. 5. Combined average wing length of all casts from March 26 to December 4, 1998.

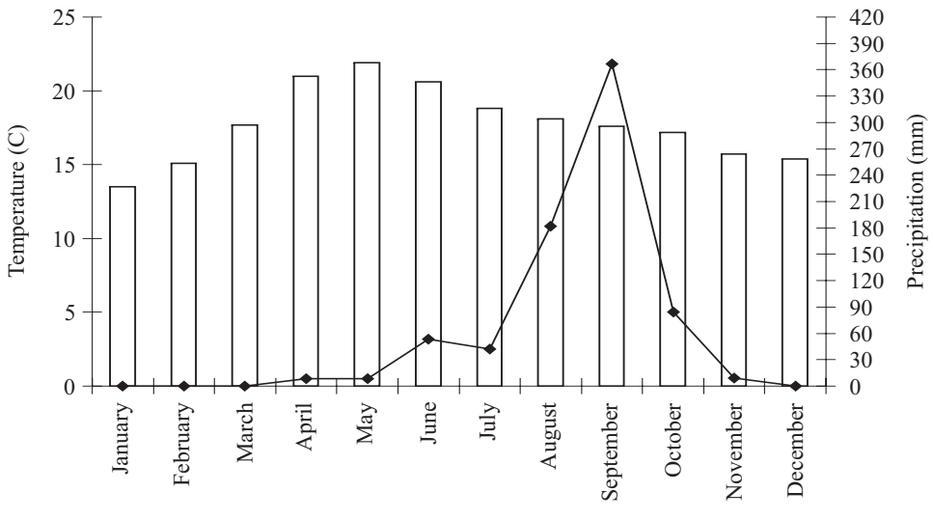

Fig. 6. Rain regime for Puebla, Mexico, in 1998 (BUAP Meteorological Station).

humidity. Laverty & Plowright (1985) indicate that *Bombus* of neartic have long hibernation periods, extending for eight months. On the other hand, the tropical species does not hibernate (Michener 1974). Our study showed *B. pennsylvanicus* in Cholula, a subtropical zone, behave as typical species do in temperate zones. It can be concluded that they have hibernation periods that extend from mid December to mid February, a period of time in which there were not active bees. Finally, the bulk of the food resources used by the species came form annual herbs, native and very common in the mid and lowlands of Mexico Valley (Rzedowski 1985). Some of them were *Solanum rostratum*, from May to July, and *Tithonia tubiformis*, *Cosmos bipinnatus*, *Anoda cristata*, from August to November. The shape of these flowers indicate they are visited by general pollinators. Also important in the diet of the bees is *Jacaranda mimosaefolia,* a caducifolium introduced tree from South America, blooming from March to May. From December to February we could not find any flowering plants in the sampling zone. The availability of resources used and environmental factors such as temperature and rain (Fig. 6) seems to determine the cyclic progression of the colony.

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