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PHENOLOGY, TROPHIC PREFERENCES, AND REPRODUCTIVE ACTIVITY IN SOME DUNG-INHABITING BEETLES (COLEOPTERA: SCARABAEOIDEA) IN EL LLANO DE LAS FLORES, OAXACA, MEXICO

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Abstract.—A study was conducted of dung-inhabiting beetles found in samples of cow and horse dung collected monthly for a year, in El Llano de las Flores, Oaxaca, México. A total of 2,574 dung beetles were collected, including individuals from four Aphodiinae species, one Scarabaeinae species, and one Geotrupinae species. *Planolinus vittatus* (Say) was found most frequently in cow dung; *Cephalocyclus durangoensis* (Bates) and *Liothorax levatus* (Schmidt) were found only in horse dung; and *Gonaphodielus opisthius* (Bates), *Onthophagus chevrolati retusus* (Harold), and *Onthotrupes viridiobscurus* (Jekel) were found equally in the two types of dung. The species studied were active during the rainy period, except for *L. levatus. Phanolinus vittatus* was active 11 months of the year and is bivoltine. The two new generations were observed during the population peaks of June and October. *Gonaphodielus opisthius* was active from June to December and is univoltine. It was most abundant during July, when the population consisted of mature females and males; the new generation emerged from September through December. From January through May, *G. opisthius* was in diapause. *Cephalocyclus durangoensis* was active only during the first two months of the rainy period and is univoltine. During its two active months, this population consisted only of mature females and males. The new generation entered diapause and emerged the following year. *Liothorax levatus* was active only three months at the beginning of the dry period and is univoltine. During this species's active period, only mature females and males were seen. The new generation entered diapause for seven months. *Onthophagus chevrolati retusus* was active from January to March and from June to December. This species was seen in greatest abundance in July and November; while it was in diapause in April and May. *Onthotrupes viridiobscurus* was seen from June through December, showing the highest abundances in June and again in September. This species was in diapause from January through May.

Key Words: phenology, trophic preferences, reproduction, Aphodiinae, Scarabaeinae, Geotrupinae

Dung beetles incorporate large amounts of dung from livestock and other vertebrates into the soil, for the beetles' nesting, egg-laying, and provision of food for adults and maturing individuals (Halffter and Edmonds 1982, Hanski and Cambefort 1991). The incorporation of dung into the soil reduces the loss of nitrogenous elements and increases the fertility and productivity of the soil (Fincher 1981, Rougon et al. 1988, Yokoyama et al. 1991), as well as destroying eggs and cysts of livestock parasites (Bryan 1973, Fincher 1975, Chirico et al. 2003). Moreover, when dung beetles are present, fly mortality is high (Moon et al. 1980, Ridsdill-Smith et al. 1987, Ridsdill-Smith and Hayles 1990).

Unfortunately, dung beetles are susceptible to vermicides administered to livestock and to herbicides applied to pasture, to the extent that lethal effects are seen on populations, perhaps some day up to the point of species extinction (see the review articles by Lumaret and Martínez 2005, Martínez and Lumaret 2006).

Because of the importance of this group of beneficial insects, the little that is known about their biology, and the threats to their diversity and conservation from the indiscriminate use of vermicides and herbicides in managing livestock and pasture, for a number of years we have studied these beetles' phenology and reproductive biology, especially in Aphodiinae species, in various Mexican locations (Martínez and Cruz 1999, 2002; Martínez and Alvarado 2001; Martínez et al. 2000, 2001a, b; Martínez 2001, 2003, 2005; Cruz et al. 2002).

The current study is part of this series of studies. The principal objective here is to gather information on such biological phenomena as trophic preference, phenology, and reproductive cycles of the dung beetle species most commonly found in montane pastures in El Llano de las Flores, Oaxaca, México.

Materials and Methods

The dung beetle species studied were those found in pastures surrounded by pine woods, in El Llano de las Flores, at 17°26′31.1″N, 96°30′13.2″W, and at an altitude of 2,600 m, in Sierra de Juárez, Oaxaca, México.

From January through December 2003, 10 dung samples were collected each month from a pasture area of approximately 800 m^2. Each collection included 5 samples of cow dung, and 5 samples of horse dung, with similar characteristics: a weight of approximately 250 grams, and with a semi-pasty consistency in the interior and a hard crust.

All the 120 dung samples collected were analyzed for type of sample and dung beetle species. To characterize the phenology of each species, the number of individuals of each of the species was counted monthly, and these counts were then considered in the context of environmental factors.

To determine each species' preference for dung type, the total number of individuals found in each type of dung was counted for all 60 samples of that type of dung collected during the year. These data were then analyzed by Student's t-test.

To determine the relative proportion of sexually immature, maturing, and mature females and males, 10 individuals of each sex for each species were separated and examined for each monthly sample. All reproductive apparatus was placed in saline solution; later, organs were fixed in AFATD (ethyl alcohol 96°–formaldehyde–trichloracetic acid–dimethylsulfoxide), drawn to scale in stereomicroscope with camera lucida, and completely stained with Feulgen green light technique (Martínez 2002). State of sexual maturity for all species was determined with reference to the following characteristics: for females, the number, length, and characteristics of basal eggs in each ovariole; for males, the length of testis follicles and the volume of secretions contained in each of the

Table 1. Total annual abundance of dung beetle individuals, by species, in monthly samples of cow and horse dung, El Llano de las Flores, Atepec, Oaxaca, during 2003.

Species	*Planolinus vittatus*	*Gonaphodielus opisthius*	*Cephalocyclus durangoensis*	*Liothorax levatus*	*Onthophagus chevrolati*	*Onthotrupes viridiobscurus*
Total Number	1,238	436	379	164	312	45

glandular reservoirs, using the morphometric technique described by Martínez (2002).

To describe the reproductive cycle of each species, we determined the proportions of females and males in different states of sexual maturity found each month. Reproductive cycles were characterized with reference to monthly population levels and to climatic factors observed over the course of the study.

Results

Over the period of the study, four Aphodiinae species were encountered: *Planolinus vittatus* (Say 1825), *Gonaphodielus opisthius* (Bates 1887), *Cephalocyclus durangoensis* (Bates 1887), and *Liothorax levatus* (Smichdt 1907) (sensu Dellacasa et al. 2002). One Scarabaeinae species was also found, *Onthophagus chevrolati retusus* (Harold 1869), and one Geotrupinae species, *Onthotrupes viridiobscurus* (Jekel 1865).

Species phenology.—The active periods of the different species varied, occurring in different months of the year. The most abundant species was *P. vittatus*, represented by 1,238 individuals (Table 1). This species was active 11 months of the year; the only month during which it was not found was January. *P. vittatus* showed three population peaks, in June, August, and October (Fig. 1).

Gonaphodielus opisthius was the species second in abundance 436 individuals were collected. This species was active only from June to December, showing its highest abundance by far in July.

Cephalocyclus durangoensis was the third most abundant species, with 379 individuals collected. This species was active from June to August, with its highest abundance seen in July. Just 6 individuals were found in June, and only 2 in August. No individuals were seen from January through May or from September through December.

Liothorax levatus was one of the least abundant species, with a total of 164 individuals collected over 2003. This species was encountered only in January, November, and December, showing the highest abundance in January. Only 9 individuals were collected in November, and just 30 in December. No individuals were collected from February through October.

The *Onthophagus chevrolati retusus* collected totaled just 312 individuals. This species was found throughout 10 months of the year, from January through March, and from June through December, with the highest abundances seen in July and November (Fig. 2).

Only 45 individuals of *O. viridiobscurus* were collected over the entire year. This species was found only from June through December, showing the highest abundances in June (17 individuals) and September (11 individuals) (Fig. 2). Very few individuals of this species were seen except during these active periods. The number of individuals found in pasture samples was small, but in zones bordering the pine woods, population levels were much higher, with up to 30 individuals collected from one dung pat. However, no monthly samples were taken at these locations.

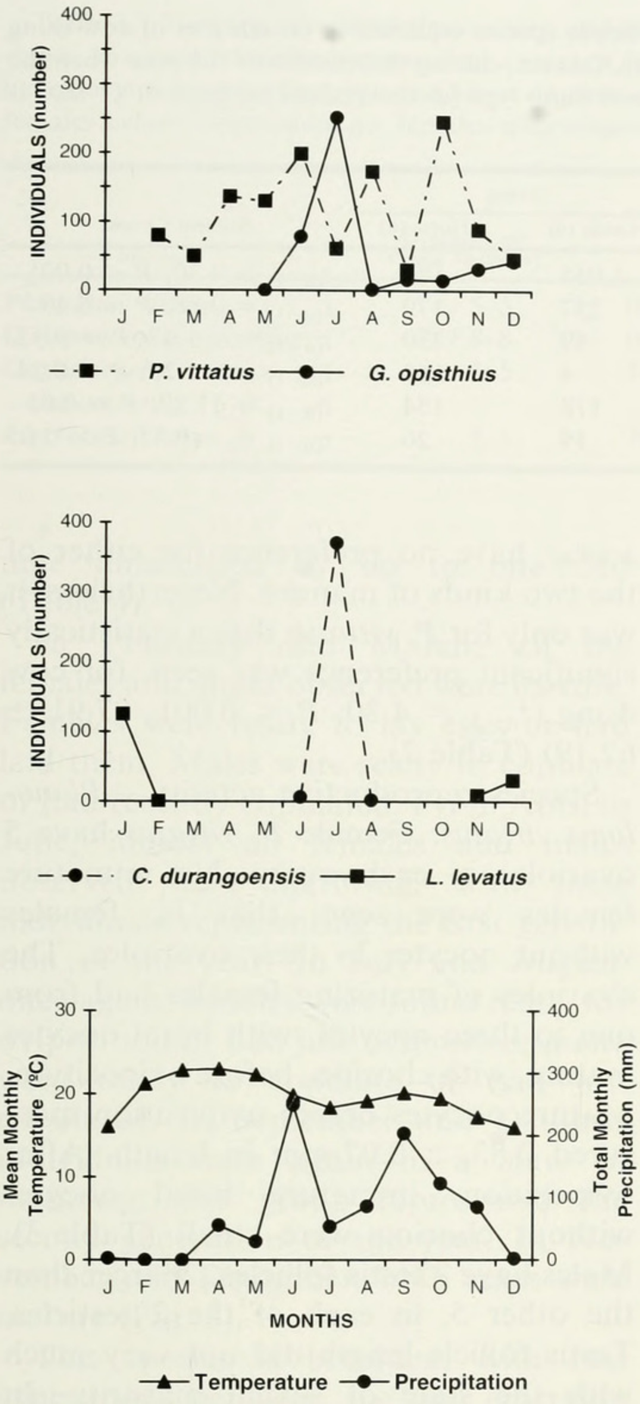

Fig. 1. Monthly population levels, in numbers of individuals, for each of the four Aphodiinae species found in cow and horse dung samples in El Llano de las Flores, Oaxaca, January–December 2003; and mean monthly temperature and total monthly precipitation (data taken from the climatological station of San Juan de Atepec, Oaxaca, provided by the National Water Commission).

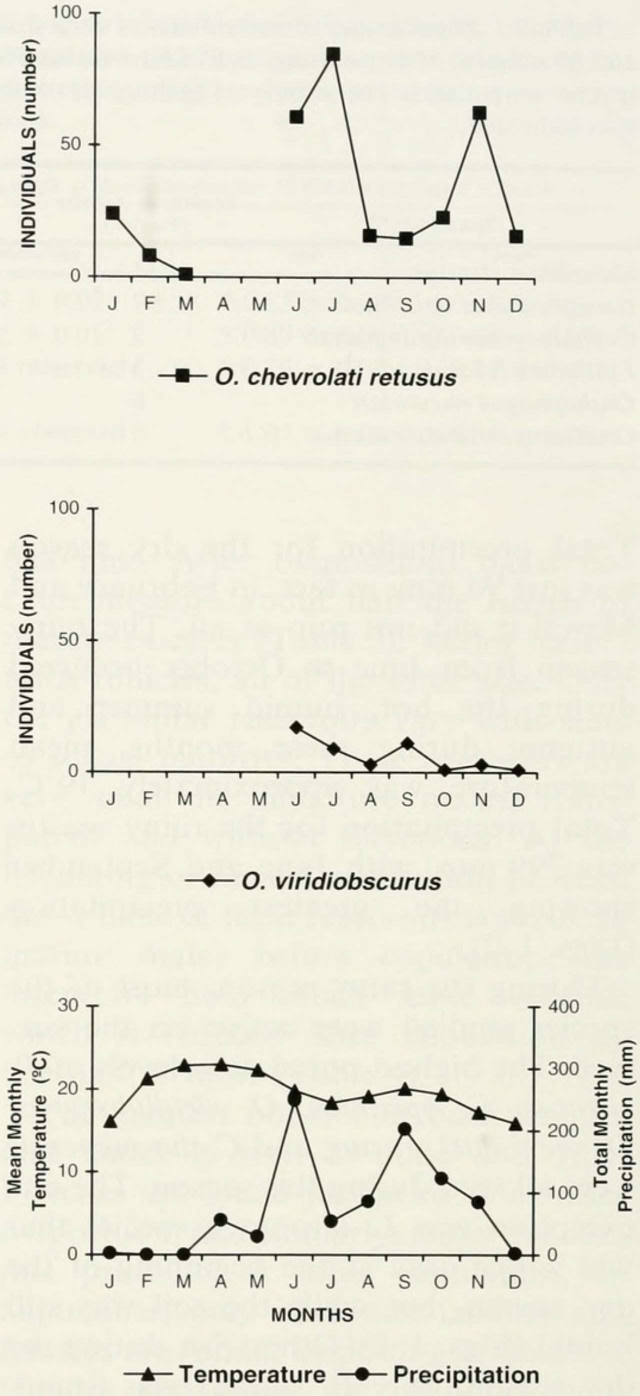

Fig. 2. Monthly abundances of individuals of *Onthophagus chevrolati retusus* (Scarabaeinae) and *Onthotrupes viridiobscurus* (Geotrupinae) found in samples of cow and horse dung from El Llano de las Flores, Oaxaca, January–December 2003; and mean monthly temperature and total monthly precipitation (data taken from the climatological station of San Juan de Atepec, Oaxaca, provided by the National Water Commission).

Over the course of the study year, the area under study experienced alternating dry and rainy periods. Dry periods occurred from January to May and November to December, corresponding to winter and spring. During the study year, mean temperature was 20°C, although from March to May mean monthly temperature was almost 23°C.

Table 2. Number (n) of individuals of each dung beetle species collected in 60 samples of cow dung and 60 samples of horse dung, in El Llano de las Flores, Oaxaca, during the months of the year when the species were active. The affinity of each species with each dung type (as determined by Student's *t*-test) is also indicated.

Species	Months of Activity (number)	Dung		Student's *t* test
		Cattle (n)	Horse (n)	
Planolinus vittatus	11	1,055	183	$t_{(n-1)} = 4.30$; $P < 0.001$
Gonaphodielus opisthius	7	257	179	$t_{(n-1)} = 0.88$; $P = 0.40$
Cephalocyclus durangoensis	2	49	330	$t_{(n-1)} = -1.03$; $P = 0.32$
Liothorax levatus	3	4	160	$t_{(n-1)} = -1.25$; $P = 0.24$
Onthophagus chevrolati	6	178	134	$t_{(n-1)} = 11.27$; $P > 0.05$
Onthotrupes viridiobscurus	5	19	26	$t_{(n-1)} = -0.53$; $P > 0.05$

Total precipitation for the dry season was just 90 mm; in fact, in February and March it did not rain at all. The rainy season from June to October occurred during the hot, humid summer and autumn; during these months, mean temperature was approximately 19°C. Total precipitation for the rainy season was 799 mm, with June and September showing the greatest precipitation (Figs. 1–2).

During the rainy season, most of the species studied were active on the surface. The highest population levels of *P. vittatus*, *G. opisthius, O. viridiobscurus, O. chevrolati retusus,* and *C. durangoensis* were all seen during this season. The one exception was *L. levatus*, a species that was active only at the beginning of the dry season, but while the soil was still humid (Figs. 1, 2). Otherwise, during the dry season, only *P. vittatus* was found, and only in small numbers. *O. chevrolati retusus* was also found at the beginning of the dry season, but not in April or May, when precipitation is very low and temperature is high (Fig. 2).

Species trophic preferences.—The total number of individuals obtained were just those encountered during the months the species were active (Table 2). Apparently, *P. vittatus* prefers cow dung, and *C. durangoensis* and *L. levatus* prefer horse dung. It may be that *G. opisthius, O. chevrolati retusus*, and *O. viridiobscurus* have no preference for either of the two kinds of manure. Nevertheless, it was only for *P. vittatus* that a statistically significant preference was seen, for cow dung ($t_{n-1} = 4.30$; $P < 0.001$, 87.91 ± 62.19) (Table 2).

Species reproductive activity.—*Planolinus vittatus:* Female *P. vittatus* have 5 ovarioles in each ovary. No immature females were seen, that is, females without oocytes in their ovarioles. The ovarioles of maturing females had from one to three oocytes, with basal oocytes mature, with chorion, before oviposition. Mature oocytes before oviposition measured 0.83 ± 0.07 mm in length. After oviposition, immature basal oocytes without chorion were small (Table 3). Males have 7 testis follicles, 2 larger than the other 5, in each of the 2 testicles. Testis follicle length did not vary much with the state of sexual maturity. In contrast, the volume of glandular secretions stored in the two glandular reservoirs, representing the greatest part of the seminal liquid of the spermatophore, varied significantly depending on sexual maturity. Few immature males of these species were seen as well, that is, those without secretions in their glandular reservoirs. Males at the beginning of maturation showed the smallest glandular reservoirs. Mature males before copulation showed the greatest volume of secretions; after copulation, this vol-

Table 3. Number of ovarioles per ovary, and basal oocyte length in Aphodiinae females, in different stages of sexual maturity (representing a total of 15 females for each species). Immature females do not have oocytes in their ovarioles, and hence do not appear in the table (*, mature oocytes with chorion; bo, females before oviposition; ao, females after oviposition).

Species	Ovarioles per Ovary (number)	Length of Basal Oocytes (for 15 females/species) $\bar{x}$ ± ds (mm)		
			Mature	
		Maturing	bo	ao
Planolinus vittatus	5–5	0.19 ± 0.07	* 0.83 ± 0.07	0.36 ± 0.11
Gonaphodiellus opisthius	7–7 8–8	0.02 ± 0.01	* 0.80 ± 0.06	0.46 ± 0.07
Cephalocyclus durangoensis	5–5	Not observed	* 0.79 ± 0.06	0.27 ± 0.05
Liothorax levatus	5–5	Not observed	* 1.05 ± 0.06	0.34 ± 0.14

ume diminished by up to one-third (Table 4).

In February and March, all the females and males observed were mature. Females were ready to lay eggs or had laid them. Males were ready to copulate or had recently copulated. From April to June, almost all females and males observed were maturing, with these individuals representing the first generation of the year. In July and August, once again, females were found ready for oviposition or had just oviposited; males were ready to copulate or had just copulated. In September and October, individuals were again in a state of maturing; this group represented the second generation of the year. In November and December, both sexes were mature (Fig. 3).

This species is bivoltine, with two generations per year, the first emerging from April through June, and the second from September to October (Fig. 3). The emergence of the two new generations occurred during those periods that experience the highest population levels of this species, in June and October (Fig. 1).

Gonaphodielus opisthius: Female *G. opisthius* have 7 to 8 ovarioles per ovary. Maturing females have small basal oocytes. In mature females, each ovariole has from one to three oocytes. Prior to oviposition, each ovariole has a basal oocyte with chorion, measuring 0.80 ± 0.06 mm. After oviposition, basal oocytes measure about half the length of mature oocytes (Table 3). Males have 7 testis follicles, all of the same size. Only the glandular reservoirs vary with state of sexual maturity. These reservoirs are very small in immature males, transparent and without secretions. At the beginning of males' maturation process, the volume of these reservoirs is small. In mature males before copulation, the reservoirs hold much more volume, which is reduced after copulation by one-half or more (Table 4).

The greatest number of both females and males is seen in June and July. Females are found just prior to or after oviposition, and similarly, males are seen just prior to or after copulation. In September, only immature females and females are found. Beginning in October, females and males are found in both immature and maturing stages (Fig. 3).

Gonaphodielus opisthius is univoltine, emerges at the point that the rainy season begin, and reproduces to found the one new generation of the year, emerging from September to December. The species is in diapause from January to May. The emergence of mature individuals coincides with the period of highest species abundance, in July (Fig. 1).

Cephalocyclus durangoensis: Female *C. durangoensis* have 5 ovarioles per

Table 4. Number (n) and length of testis follicles per testicle, and volume of glandular reservoir, in males of various Aphodiidae species (10 males sampled per species) in different stages of sexual maturity. Immature males do not have secretions in their glandular reservoirs, and no data are shown on this group (bc, males before copulation; ac, males after copulation).

	Testis Follicles Length (mm) $\bar{x}$ ± ds		Glandular Reservoir Volume (10^{-3} mm^3) $\bar{x}$ ± ds		
				Mature	
Species	Same Size	Large and Small	Maturing	bc	ac
Planolinus vittatus	(2) 0.456 ± 0.05	(5) 0.183 ± 0.03	7.5 ± 2.1	35.7 ± 6.8	13.7 ± 2.70
Gonaphodielus opisthius	(7) 0.31 ± 0.03		1.09 ± 0.66	116.1 ± 11.3	65.64 ± 13.14
Cephalocyclus durangoensis	(2) 0.440 ± 0.04	(4) 0.31 ± 0.03	Not observed	232.84 ± 43.2	97.52 ± 46.11
Liothorax levatus	(2) 0.470 ± 0.09	(5) 0.28 ± 0.05	Not observed	27.77 ± 6.07	13.26 ± 3.93

ovary. Neither immature or maturing females were found. Mature females had 3 or 4 oocytes per ovariole. Before oviposition, the basal oocytes, and the second, and often the third, oocyte were mature, with chorion. Basal oocytes measured a mean 0.79 ± 0.06 mm. Following oviposition, basal oocytes were observed to be small (Table 3). Males have 6 testis follicles in each testicle, with 2 of the follicles larger than the other 4. No immature or maturing males were found. All the males collected were mature, with maxium glandular reservoir volume seen immediately before copulation; after copulation, volume was reduced, by up to more than half from this value (Table 4).

The species is univoltine, with the population emerging in the first months of the rainy season, and reproductive activity declining just a little more than a month after the beginning of this active period. The new generation was not seen at the surface, possibly passing through diapause, from January to May and September to December (Fig. 3). The only high population levels seen in this species corresponded to the emergence of mature females and males principally in July, in June only 6 specimens and in August another 2, where find (Fig. 2).

Liothorax levatus: Female *L. levatus* have 5 ovarioles per ovary. Neither immature or maturing females were observed. All the females collected were mature, showing one or two oocytes per ovariole. Mature females before oviposition showed the largest oocytes of all species observed; after oviposition, the following basal oocytes measured far less (Table 3). Males have 7 testis follicles. All males observed were mature. Prior to copulation, males had the most voluminous glandular reservoirs; after copulation, this volume declined by more than half (Table 4).

This species is also univoltine, and only active during three months, after which it appears to enter into diapause for nine months of the year (Fig. 1). All individuals observed were mature females or males (Fig. 3).

The reproductive cycles of *O. chevrolati retusus* and *O. viridiobscurus* were not studied.

Discussion

Trophic preferences.—Several species appeared to prefer either cow or horse dung, while other species showed no preference. Nevertheless, a statistically significant preference (for cow dung) was seen only in *P. vittatus*. Another study based on a larger number of individuals would be needed to obtain sufficient data to analyze whether other species' apparent preferences are real. Recent studies

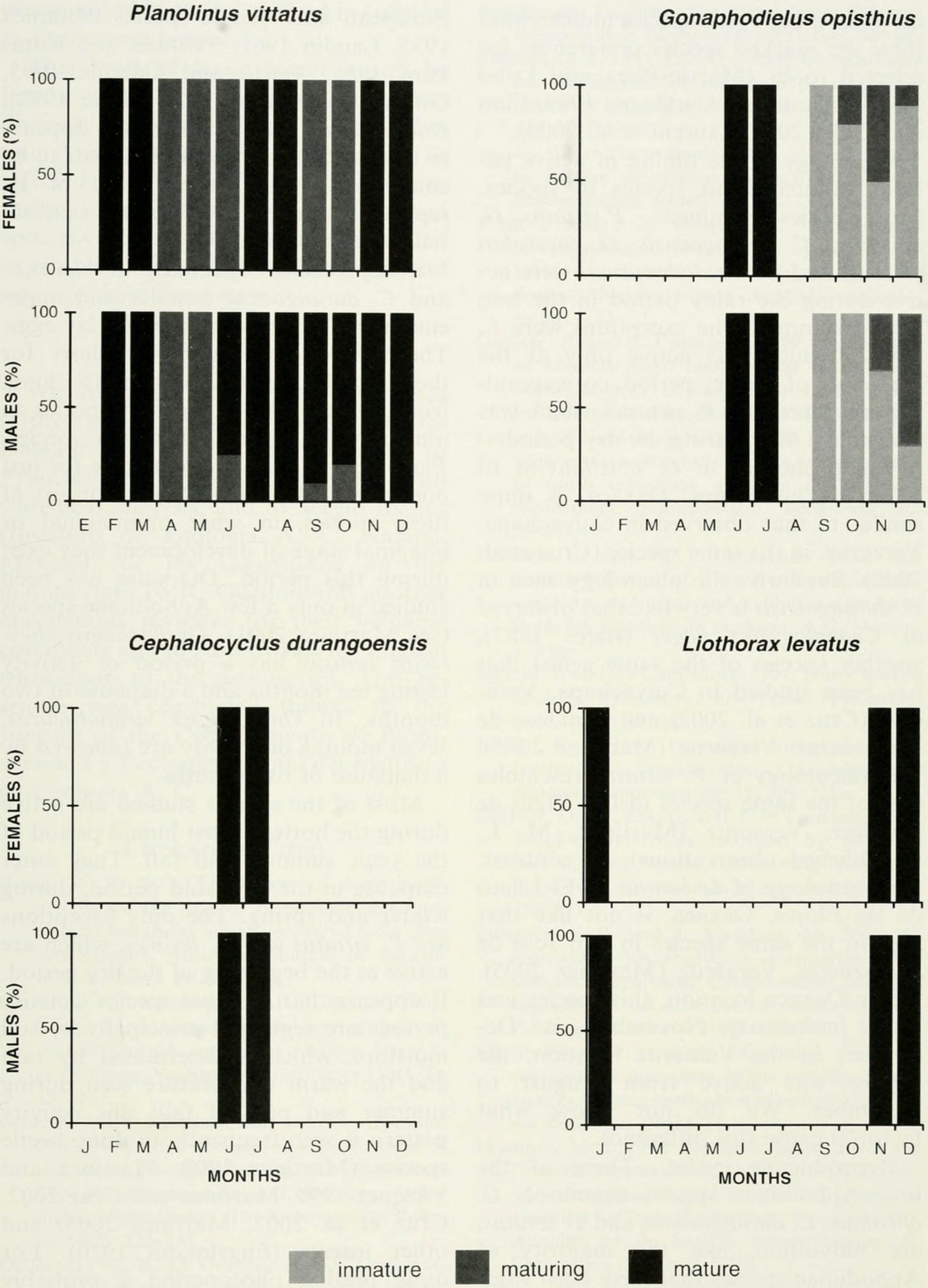

Fig. 3. Monthly percentages of sexually immature, maturing, and mature females and males, for Aphodiinae species found in El Llano de la Flores, Oaxaca, January–December 2003 (with 10 females and 10 males of each species examined each month).

on other dung beetle species indicate that there are marked species preferences for selected foods (Martín-Piera and Lobo 1996, Galante and Cartagena 1999, Finn and Giller 2002, Laurent et al. 2004).

Phenology.—The timing of active periods differed from species to species. Most species examined— *P. vittatus*, *G. opisthius*, *C. durangoensis*, *O. chevrolati retusus*, and *O. viridiobscurus*—were active during the rainy period in the hot, humid summer. The exceptions were *L. levatus*, which was active only at the beginning of the dry period, corresponding to winter, and *P. vittatus*, which was also active only during the dry period.

The phenology at *G. opisthius* at El Llano de las Flores, Oaxaca, is quite similar to that observed in Cuiyachapa, Veracruz, in the same species (Cruz et al. 2002). Similarly, the phenology seen in *C. durangoensis* is very like that observed in *Cephalocyclus hogei* (Bates 1887), another species of the same genus that has been studied in Cuiyachapa, Veracruz (Cruz et al. 2002) and San José de Aguazuelas, Veracruz (Martínez 2005). The phenology of *P. vittatus* resembles that of the same species in Las Vigas de Ramírez, Veracruz (Martínez, M. I., unpublished observations). In contrast, the phenology of *L. levatus* in El Llano de las Flores, Oaxaca, is not like that seen in the same species in San José de Aguazuelas, Veracruz (Martínez 2005). In the Oaxaca location, this species was active in January, November, and December; in the Veracruz location, the species was active from August to December. We do not know what factor(s) cause this difference.

Reproductive cycles.—Three of the four Aphodiinae species examined, *G. opisthius*, *C. durangoensis*, and *L. levatus*, are univoltine, like the majority of Aphodiinae species that have been studied (Martínez 2001, Cruz et al. 2002, Martínez 2005). *Planolinus vittatus* was the only bivoltine species, as are other European and Asiatic species (Schmidt 1935, Landin 1961, Yoshida and Katakura 1985, Verdú and Galante 1995, Gittings and Guiller 1997, Vitner 1998). *Onthophagus chevrolati retusus* appears to be bivoltine, although this needs to be confirmed with further study of its reproductive cycle. *Onthotrupes viridiobscurus* is univoltine.

Gonaphodielus opisthius, *L. levatus*, and *C. durangoensis* females and males emerge mature to copulate and lay eggs. The reproductive period is short for these species, and the diapause long, from five months in the first species to nine months in the other two species. *Planolinus vittatus* is in diapause for just one month. We do not know, for any of these species, in what preimaginal or imaginal stage of development they exist during this period. Diapause has been studied in only a few Aphodiinae species (see Martínez 2001). *Onthophagus chevrolati retusus* has a period of activity lasting ten months and a diapause of two months. In *Onthotrupes viridiobscurus*, seven months of activity are followed by a diapause of five months.

Most of the species studied are active during the hottest, most humid period of the year, summer and fall. They enter diapause in the dry, cold period, during winter and spring. The only exceptions are *P. vittatus* and *L. levatus*, which are active at the beginning of the dry period. It appears that all these species' activity periods are regulated principally by soil moisture, which is determined by rain and the warm temperature seen during summer and part of fall; this activity pattern is seen frequently in dung beetle species (Martínez 1992, Martínez and Vázquez 1995, Martínez and Cruz 2002, Cruz et al. 2002, Martínez 2005) and other insects (Engelmann 1970). For dung beetles, photoperiod is probably not a significant determinant, given that these species live the greater part of their lives buried; and seasonal variation in photoperiod is not as marked in tropical as in temperate zones.

This kind of basic research can be highly useful for understanding insect diversity in pasture, how species' phenology or reproductive cycles might be affected by agronomic or veterinary residuals, and the behavior of introduced species. All this information is essential in establishing measures to conserve and manage these ecosystems.

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