POPULATION ECOLOGY OF TWO SPECIES OF *PASIMACHUS* (COLEOPTERA: CARABIDAE) IN THE SANDHILL HABITAT OF FLORIDA

EARL D. MCCOY[1] AND BRIAN W. WITZ
Department of Biology and [1]Center for Urban Ecology
University of South Florida
Tampa, FL 33602

ABSTRACT

The population ecology of *Pasimachus subsulcatus* Say and of *P. strenuus* LeConte was studied with beetles captured by pitfall trapping. We searched for patterns in: (1) activity/density, (2) reproduction, (3) body size, and (4) parasitization. Females and males of both species were most active/dense in spring and autumn; females of both species were especially active/dense, relative to males, in late summer-early autumn; few females of both species bore post-vitellogenic eggs in summer; and males of *P. subsulcatus* produced mature sperm in spring and autumn. It was concluded that mating occurs in spring and autumn for both species, and oviposition in summer-early autumn. Our data suggest that relatively high percentages of both female and male *P. subsulcatus* trapped in late summer-early autumn were relatively large. In most months, females of *P. subsulcatus* were, on average, larger than males, but the two sexes of *P. strenuus* were similar in size. About 1.4% of *P. subsulcatus* and 3.3% of *P. strenuus* were parasitized by tachinid flies. Parasitization of both species peaked in late summer-autumn, and there was no evidence that paratization was influenced by sex, size, or female gravidity, with one exception. Small individuals of *P. subsulcatus* were parasitized more often than one would expect from their representation among captured individuals.

Key Words: Carabidae, Florida, ground beetles, reproduction, parasitization, mating.

RESUMEN

Se estudió la ecología poblacional de *Pasimachus subsulcatus* Say y de *P. strenuus* LeConte con escarabajos capturados en trampas de suelo. Buscamos patrones en (1) actividad/densidad, (2) reproducción, (3) tamaño del cuerpo, y (4) parasitización. Las hembras y los machos de ambas especies fueron mas activos/densos durante la primavera y el otoño; las hembras de ambas especies fueron especialmente activas/densas, al compararse a los machos, en los fines del verano y los principios del otoño; pocas hembras de ambas especies cargaban huevos post-vitelogenéticos en el verano; y los machos de *P. subsulcatus* produjeron esperma madura en la primavera e el otoño. Se concluyeron que parear ocurre en la primavera y el otoño para ambas especies, y la oviposición ocurre en el verano y los principios de otoño. Nuestros datos sugieren que porcentajes relativamente altos de hembras y machos de *P. subsulcatus* atrapadas en los fines del verano y los principios del otoño fueron de relativamente grandes tamaños. En la mayoría de meses, las hembras de *P. subsulcatus* tenían tamaños más grandes, por el promedio, que los machos, pero los dos sexos de *P. strenuus* fueron semejantes en tamaño. Cerca de 1.4% de *P. subsulcatus* y 3.3% de *P. strenuus* fueron parasitados por moscas tachinidas. El apogeo de parasitización de ambas especies fue en los fines de verano y en el otoño, y no hubo evidencia que la parasitización fue influido ni por el sexo, el tamaño, o la gravidad de las hembras, con una excepción. Los inviduos pequeños de *P. subsulcatus* fueron parasitados más frequentemente que se hubiera esperado basado en su representación entre individuos capturados.

The ground beetle genus *Pasimachus* includes about 25 large, flightless, xerophilic species, all restricted to North America (see Nichols 1988). The most thoroughly-studied species is *P. elongatus* LeConte (e.g., Cress & Lawson 1971, Calkins & Kirk 1974), probably because it is a predator of false wireworms and other agricultural pests (Barney & Armbrust 1980, Wise 1985). Another species, *P. punctulatus* Haldemann, also has been studied in detail (Nelson 1969, 1970). In Florida, several species of *Pasimachus* are common in xeric upland habitats, such as scrub and sandhill, but very little is known about them.

In this paper, we address the population ecology of *P. subsulcatus* Say and of *P. strenuus* LeConte. Trapping data were used to search for patterns of activity/density. Similar activity/density studies of *P. punctulatus* in Texas (Nelson 1970) and of three species of *Evarthrus* (Coleoptera: Carabidae) in Florida (Harris & Whitcomb 1971) indicated peaks in both spring and autumn. The activity/density of *P. elongatus* in more northern locations, Arkansas (Allen & Thompson 1977) and South Dakota (Calkins & Kirk 1974), peaks only in summer. These observations, and others (see Thiele 1977), led us to predict that the activity/density of the two species of *Pasimachus* that we studied would peak in either spring or autumn, or in both seasons.

We used measurements of large numbers of individuals to search for patterns of body size, because the body size of many ground beetle species vary over time, as ecological conditions change (Thiele 1977). We predicted, therefore, that the body sizes of the two species of *Pasimachus* that we studied would vary, and that this variation would be attributable to an environmental cause. We also predicted that females would be larger than males of the same species, simply because this is the case for most animals (Cockburn 1991). However, males might be similar in size to, or larger than, females, particularly if they competed for access to females (Alcock & Gwynne 1991).

Finally, we used internal examinations of individual beetles to search for patterns of reproduction and parasitization. It was predicted that peaks in reproduction would coincide with peaks in activity/density, because ground beetle behaviors often are interdependent and triggered by similar environmental cues (Thiele 1979). We also predicted that rates of parasitization would be low, because parasites and parasitoids are thought to play only minor roles in governing the density and distribution of ground beetle populations (Thiele 1977). Predators, on the other hand, are thought to play a major governing role (Thiele 1977, Murdoch 1966, Parmenter & MacMahon 1988); so much so that conspicuous anti-predator adaptations have been induced (Thiele 1977). We cite, for example, the defensive secretions of some species of *Pasimachus* (Nelson 1970, Davidson et al. 1989, Witz & Mushinsky 1989).

Materials and Methods

Totals of 2280 individual *P. subsulcatus* and 545 individual *P. strenuus* were captured in pitfall traps located in The University of South Florida's Ecological Research Area. The traps were open from November 1982 to May 1984 (see McCoy 1987). The site had been divided into approximately 1 ha plots for the purpose of studying the effects of burning on resident organisms. Because burning regimes differ among plots, the sandhill habitat (see Myers 1990) at this site varies from virtually open wiregrass, to wiregrass-turkey oak woodland, to near xeric oak woodland. More detailed information about the site is available in Mushinsky (1985), McCoy (1987), and Mushinsky & Gibson (1991).

The traps were 60 5-gal buckets arranged in pairs connected by an aluminum drift fence 7.5 m long and 0.5 m high. Ten traps each were distributed among six plots, four of which were sampled for the entire 19 months, one for 16 months from February, 1983 to May, 1984, and one for 14 months from April, 1983 to May, 1984. Within a plot, traps were overdispersed (mean distance between traps = 30 m), to minimize the possibility that traps would sample overlapping areas of habitat. We checked all traps at least twice weekly, but combined individuals captured in the same month for analysis.

We recognize that data can be mis-interpreted when using pitfall trapping to monitor ground-dwelling arthropods (e.g., Mitchell 1963, Greenslade 1964). To minimize mis-interpretation in this study, we neither made comparisons between species (cf. Halsall & Wratten 1988) nor computed estimates of absolute numbers (cf. Baars 1979). We also recognize that removal trapping may affect population structure and we assumed that the low density of traps reduced the possibility that any patterns we detected were caused by method of sampling.

Beetles collected from the traps were frozen immediately upon return to the laboratory and then stored in 70% isopropanol. Each individual was dissected to determine its sex, its gravidity (presence of post-vitellogenic eggs; cf. Mitchell 1963, Dawson 1965), the number of eggs, and the occurrence of parasites. The numbers and identities of parasites were recorded. The size of each individual beetle was measured, using interocular distance (transverse distance across the dorsum of the head, between the compound eyes at their longitudinal midpoints). Measurements were made with an ocular micrometer installed in a dissecting microscope (120X). Interocular distances were measured precisely, and were highly correlated with other measures of size, such as length of elytron.

We collected 64 males of *P. subsulcatus* in November-December 1988, January 1989, and July 1989, and examined them for sperm production (see Witz 1990). These males were collected in pitfall traps, as described above. In the laboratory, the abdominal cavities of decapitated individuals were flooded immediately with a 1.5% glutaraldehyde, 2.0% tannic acid fixative solution in 0.05M sodium cacodylate buffer (Seagull & Heath 1979). The reproductive tracts were removed while still emersed in fixative. The testes were separated and placed individually in vials of fixative solution for two hours. Post-fixation was in cold 1.5% osmium tetroxide, 2.5% potassium ferrocyanide solution for one hour (Russell & Burguet 1977). We dehydrated the testes in a graded alcohol series, embedded them in Spurr's plastic (Spurr 1969), sectioned them on a Sorvall MT-2 ultramicrotome, and double-stained sections with uranyl acetate and lead citrate (Venable & Coggeshall 1965), prior to examining them with an Hitachi H500 transmission electron microscope. Insufficient *P. strenuus* males were collected to examine sperm production.

Results and Discussion

Activity/Density

Individuals of both species were captured most frequently in spring from April to May and in autumn from September to October (Fig. 1). The frequency of capture of females was correlated positively with the frequency of capture of males of the same species (Spearman's Rank Correlation; $r = 0.89$, $p < 0.05$, $n = 19$ (*P. subsulcatus*); $r = 0.88$, $p < 0.05$, $n = 16$ (*P. strenuus*)). The sex ratios of both species varied over time (G Test of Independence; $G = 28.47$, $p < 0.10$, $df = 18$ (*P. subsulcatus*); $G = 16.32$, $p < 0.10$, $df = 9$ (*P. strenuus*)), indicating that the magnitude of the changes in activity/density between months were not similar for the two sexes. In most months, the numbers of males captured exceeded the numbers of females; some late summer-early autumn months were the only important exceptions (Table 1).

Reproduction

Gravid females usually bore a single post-vitellogenic egg (72% of *P. subsulcatus* with one egg, 25% with two eggs, and 3% with three eggs; 50% of *P. strenuus* with one egg, 31% with two eggs, 13% with three eggs, and 3% each with four and five eggs).

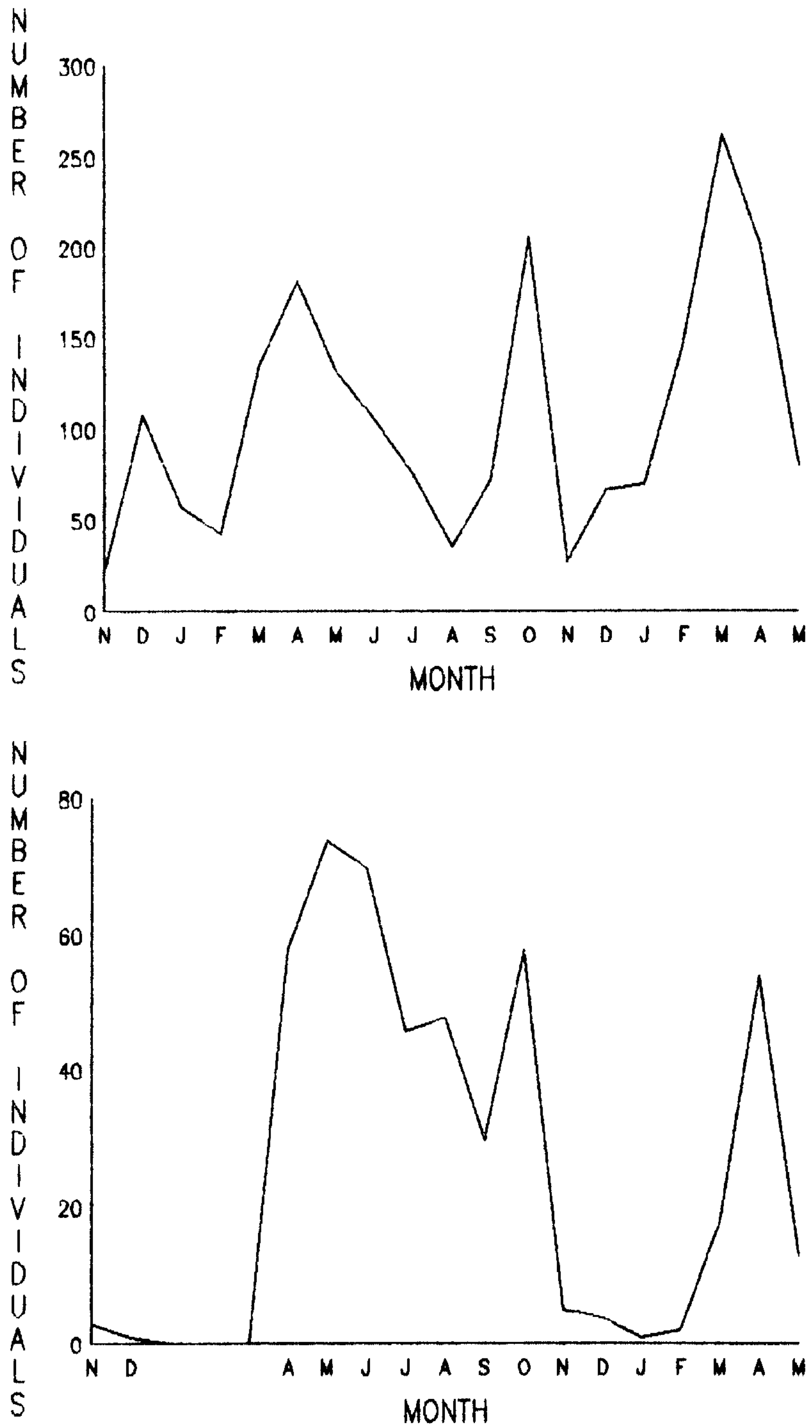

Fig. 1. Number of individual *Pasimachus subsulcatus* (upper) and *P. strenuus* (lower) captured in each of the 19 months of sampling.

There was no apparent seasonal pattern in the tendency of gravid females to bear more than one egg. We also saw no apparent tendency for females bearing more than one egg to be especially large.

TABLE 1. DATA DERIVED FROM BEETLES CAPTURED DURING A 19-MONTH STUDY. FIRST ENTRY IS *PASIMACHUS SUBSULCATUS* AND THE SECOND IS *P. STRENUUS*. PERCENTAGES ARE REPORTED ONLY FOR N = 10 OR GREATER.

Month	No. of Females	No. of Males	Gravid (%)	Parasitized (%)
Nov.	7/ 2	15/ 1	-/ -	0/ -
Dec.	38/1	70/ 0	63/ -	0/ -
Jan., 1983	20/ 0	38/ 0	65/ -	0/ -
Feb.	13/ 0	30/ 0	61/ -	0/ -
Mar.	37/ 0	98/ 0	65/ -	3/ -
Apr.	49/25	133/33	53/48	3/ 0
May	49/28	84/46	57/43	2/ 0
Jun.	41/26	65/44	46/46	0/ 1
Jul.	30/22	46/24	67/14	1/ 2
Aug.	20/23	16/25	25/30	14/12
Sep.	41/27	32/35	49/52	5/ 6
Oct.	86/39	120/19	58/69	7/ 9
Nov.	12/ 3	16/ 2	42/ -	4/ -
Dec.	25/ 1	42/ 3	64/ -	1/ -
Jan., 1984	23/ 0	48/ 1	56/ -	1/ -
Feb.	49/ 1	97/ 1	82/ -	1/ -
Mar.	86/10	177/ 8	76/30	0/
Apr.	75/25	127/29	68/28	1/ 0
May	31/ 7	50/ 6	52/ -	0/ 0

The percentage of females with post-vitellogenic eggs for both species appeared to decrease early in the year to a low in summer and then to increase later (Table 1). To test this apparent relationship, we separated the data by plot to expose between-plot variation and correlated the percentages of females with post-vitellogenic eggs with the rank-order of months. For *P. subsulcatus*, correlations were performed separately for the months of January to August, 1983 (apparent decrease) and August to December, 1983 (apparent increase). For *P. strenuus*, correlations were performed separately for the months of April to July, 1983 (apparent decrease) and July to October, 1983 (apparent increase). The apparent decrease was confirmed (Spearman's Rank Correlation, $r = -0.54$, $p < 0.05$, $n = 44$) for *P. subsulcatus*, but the apparent increase could not be confirmed (Spearman's Rank Correlation, $r = 0.27$, $p > 0.10$, $n = 27$). On the other hand, both the apparent decrease (Spearman's Rank Correlation, $r = -0.43$, $p < 0.10$, $n = 20$) and the apparent increase (Spearman's Rank Correlation, $r = 0.64$, $p < 0.05$, $n = 22$) were confirmed for *P. strenuus*. For either species, pooling data among plots to avoid possible pseudoreplication did not alter the results.

Spermatocytes and spermatids were present, and mature sperm were absent, in all *Pasimachus subsulcatus* males ($n = 31$) collected in January 1989; mature sperm were present, and spermatocytes and spermatids were absent, in all males ($n = 24$) collected in November and December, 1988. Spermatogonia were present, and spermatids and mature sperm were absent, in all males ($n = 9$) collected in July 1989. Although these results must be viewed cautiously, they suggest that a first cycle of spermatogenesis is initiated early in the year and culminates by mid-year. It is then followed immediately by a second cycle that culminates late in the year.

Our data suggest that at least parts of the reproductive phenologies of the two species are apparent. Four conclusions are particularly relevant: (1) both sexes were most active/dense in spring and autumn (both species), (2) females were especially active/dense, relative to males, in late summer-early autumn (both species), (3) few females bore post-vitellogenic eggs in summer (both species), and (4) males produced mature sperm in spring and autumn (*P. subsulcatus*). Taken together, these conclusions indicate for both species that matings occur in spring and autumn, and oviposition in summer-early autumn.

Body Size

The median size (interocular distance) of females of *P. subsulcatus* appeared to be larger than the median size of males in every month and was significantly larger (Wilcoxon Rank Sum Test, $W^* = 2.0\text{-}9.1$, $p < 0.05$, $m = 13\text{-}80$, $n = 30\text{-}174$) in every month, except occasionally between August and January (Fig. 2). The median size of males of *P. strenuus* appeared to be larger than the median size of females in seven of eight months, but was significantly larger only in May 1983 (Wilcoxon Rank Sum Test, $W^* = 5.1$, $p < 0.05$, $m = 26$, $n = 46$).

No seasonal pattern in body size was obvious to us. Both the mean and median sizes of males of *P. subsulcatus* declined over the entire 19-month sampling period (Spearman's Rank Correlation; $r = -0.65$, $p < 0.05$, $n = 19$ (mean); $r = -0.70$, $p < 0.05$, $n = 19$ (median)), as did the mean size of females (Spearman's Rank Correlation, $r = -0.51$, $p < 0.05$, $n = 18$). The median size of females also appeared to decline over the sampling period, but we could not confirm this tendency (Spearman's Rank Correlation, $r = -0.35$, $p > 0.10$, $n = 18$). We did not attempt similar analysis with *P. strenuus*, because large numbers of beetles of both sexes were captured in only a few months.

Although females of *P. subsulcatus* tended to be larger than males during most of the year, this size distinction was conspicuously reduced in late summer-early autumn (Fig. 2). Furthermore, although the median size of females of *P. subsulcatus* usually appeared to exceed the mean size, the disparity was greatest in late summer-early autumn (Fig. 2). We concluded from these observations that relatively high percentages of the females and males of *P. subsulcatus* trapped at this time were large individuals. Data from additional years would be needed to test this conclusion.

Parasitization

Only two types of internal parasites were found. The first was an unidentified species of nematode which we removed from a single female of *P. subsulcatus* captured in February 1983. The second was a species of Tachinidae (Diptera), which we have tentatively identified as *Sitophaga* sp. (Arnaud 1978 and included references). Immature stages of this parasitoid were removed from both species. About 1.4% of individual *P. subsulcatus* and 3.3% of individual *P. strenuus* were parasitized. The mean number of parasitoids per host was 1.4 (SD = 0.7) for *P. subsulcatus*, and 3.4 (SD = 3.9) for *P. strenuus*.

We found no evidence, for either species, that one sex was parasitized disproportionately. For *P. subsulcatus*, the expected number of parasitized females, based on the percentage of females, was 13.3, and the observed number was 14; for *P. strenuus*, the expected and observed numbers were 7.4 and 7, respectively. We also found no evidence that certain sizes of *P. subsulcatus* were parasitized disproportionately (Kolmogorov-Smirnov Test, $D = 0.07$, $p > 0.10$, $n = 23$). *P. strenuus* with an interocular distance of 8.8 mm or less were parasitized more heavily than individuals of other sizes (Kolmogorov-Smirnov Test, $D = 0.37$, $p < 0.10$, $n = 12$): Beetles of this small size were expected to comprise only about 46% of parasitized individuals, but actually comprised about 83%. Finally, we found no evidence, for either species, that gravid females were parasitized more frequently. For *P. subsulcatus*, the expected number of parasitized gravid females, based on the percentage of gravid females, was 8.6, and the observed number was 6; for *P. strenuus*, the expected and observed numbers were 3.1 and 3, respectively.

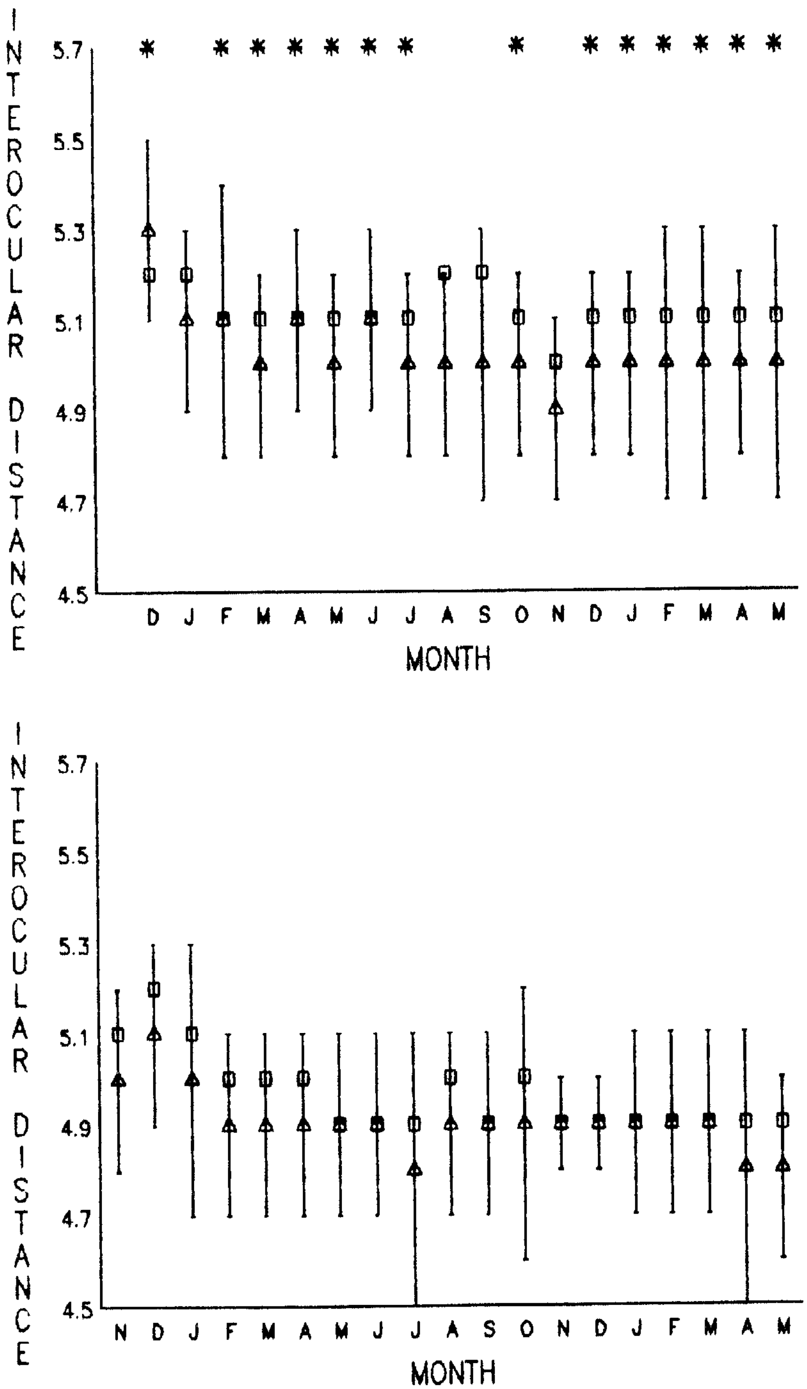

Fig. 2. Mean (triangles) and median (squares) inter-ocular distances of female (upper) and male (lower) *Pasimachus subsulcatus* in each of the 19 months of sampling. Vertical bars are one standard deviation and asterisks at the top of the upper graph designate months of which median sizes of females and males differed significantly ($p < 0.05$). Sizes are compared only for months in which at least ten individuals of each sex were captured.

Parasitization of both species appeared to peak in late summer-autumn (Table 1), but because of the small number of parasitized individuals, this result must be viewed cautiously. It suggests that relatively high levels of parasitization coincided with relatively high levels of activity of both species of *Pasimachus* (see Fig. 1). The number of parasitized individuals was correlated strongly with the total number captured for *P. strenuus* (Spearman's $r = 0.50$, $p < 0.05$, $n = 16$), but not for *P. subsulcatus* (Spearman's $r = 0.29$, $p > 0.10$, $n = 19$). The difference between species may simply reflect a better match of the seasonal activity/density of *P. strenuus* (see Fig. 1) with the life cycle of the parasitoid.

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