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RESEARCH

Annual Activity Density of groundbeetles (Coleoptera: Carabidae) of a *Celtis ehrenbergiana* (Rosales: Celtidaceae) Forest of Buenos Aires Province, Argentina

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ABSTRACT. The aim of this study was to describe the annual activity cycle, the sex ratio, and the relationship between the weather variables and activity density of the 16 most abundant carabid species of a typical southeastern region of Pampasia, Argentina. The study focused on the southernmost *Celtis ehrenbergiana* (Klotzsch) Liebmann (= *C. tala* Guillies ex Planch) native forest of the region, from March 2008 to March 2009, a period during which there was a marked draught associated with the La Niña phenomenon. Forty-five pitfall traps were emptied once every 2 wk, and the occurrence of larvae, tenerals, and subtenerals was recorded. Photoperiod, temperature, and precipitations explained 35% of the total variation in the catch. Total carabid activity was high in early autumn and late spring. Eight species reached their maximum activity in spring, five in winter, two in summer, and one in autumn. Possible reproductive strategies, the influence of different variables involved in the life cycles of the species, and the sex ratio and their limitations are discussed.

RESUMEN. El objetivo de este trabajo fue describir la proporción de sexos, el ciclo de actividad annual, la relación entre las variables meteorológicas y la actividad de las 16 especies más frecuentes de carábidos de una región típica del sudeste de la Pampasia, Argentina. El trabajo se enfocó en el talar, *C. ehrenbergiana* (Klotzsch) Liebmann (= *C. tala* Guillies ex Planch), más austral de la región, durante marzo 2008-marzo 2009, período marcado por una sequía asociada con el fenómeno La Niña. Se utilizaron 45 trampas "pitfall" recambiadas quincenalmente. Se registró la presencia de larvas, tenerales y subtenerales. El fotoperíodo, la temperatura y las precipitaciones explicaron el 35% de la variación en el número de total de individuos. La actividad total de los carábidos fue alta en otoño temprano y primavera tardía. Ocho especies alcanzaron el pico de máxima actividad en primavera; cinco en invierno; dos en verano y una en otoño. Se discuten posibles estrategias reproductivas, la influencia de las variables involucradas en los ciclos de vida de las especies y la proporción de sexos y sus limitaciones.

Key Words: Ground beetles, phenology, sex ratio, life cycle, South America

Terrestrial animals grow and reproduce when conditions are favorable; hence, they develop strategies to optimize and synchronize their life cycle with seasonal changes of the environment (Danks 2002, Kotze et al. 2011). Insects from temperate climatic zones can use environmental cues (photoperiod, temperature, moisture, and food abundance) to respond timely to seasonal challenges at different times or stages (Danks 1987). Responses can vary from slight adjustments in the rate of growth to prolonged and intense developmental arrests. These arrests can be reactions to seasonal drought or heat (estivation) and cold (overwintering) and therefore promote survival, coincidence with food supplies, synchrony of adult emergence, avoidance of competition, etc. (Danks 1987, Delinger 2002, Kotze et al. 2011). Moreover, microclimatic requirements of species are important in determining habitat affinity and daily and annual rhythms of activity (Thiele 1979).

The most reliable cue is usually photoperiod. The short day lengths of late summer signal the advent of winter to temperate zone species, allowing them to store additional energy reserves and seek a protected site for overwintering before the onset of low temperatures (Delinger 2002). Day length may also influence the females by means of their hormonal systems. For example, the change from short-day to long-day causes the juvenile hormone to induce previtellogenesis in females of *Pterostichus nigrita* (Paykull 1790) (Thiele 1979). Unlike photoperiod, seasonal patterns of temperature are more variable. In general, a rise in temperature increases the foraging activity of carabids (Honěk 1997, Saska et al. 2013). Some species, as *Paranortes cordicollis* (Dejean 1828), tolerate low temperatures (subtropical temperature ranges), and experience suitable high relative humidities (Diefenbach and Becker 1997). Soil humidity is affected by rainfall and temperature, and it is critical because eggs absorb water from their surroundings to complete embryonic development and because larvae are sensitive to desiccation (Kotze et al. 2011).

Weather conditions change throughout an annual cycle and thus are ideal for development and reproduction only part of the year. Then, coincidence of the feeding and reproductive stages with the favorable season and other adaptations are necessary features that define the seasonal patterns. For example, estivation is a behavior that serves to delay and so synchronize the life cycle (Danks 2002). A phenomenon is seasonal if it predictably occurs in the same time of the year (Wolda 1988).

Insects are not only one of the most successful groups in abundance and diversity, but also have a wide range of seasonal patterns (McGavin 1997). Among them, ground beetles (Coleoptera: Carabidae) comprise ~38,600 of the species described in the world (Kotze et al. 2011). In Argentina, there are at least 679 species of carabids (Roig-Juñent 1998), 352 of which are found in Buenos Aires province (Cicchino et al. 2010). Carabids are valued for their high diversity, abundance, ecological indication, and therefore for their functional importance in natural and modified ecosystems (Marasas et al. 2001, 2010, Sorensen 2006, Turienzo 2006, Lietti et al. 2008, Paleologos et al. 2008, Canepuccia et al. 2009).

Carabids of temperate zones generally have univoltine reproduction, i.e., only one of the series of generations reproduces each year and a single reproductive period occurs during the year (Thiele 1977, Brandmayr et al. 2005). Larsson (1939) proposed two different reproductive strategies: (1) spring breeders, which reproduce during the spring and hibernate as adults only and (2) autumn breeders, which reproduce during the autumn and hibernate mainly as larvae. However, there are species which are known to breed in a continuous gradient from spring to autumn (and even in winter), some spring breeders whose adults do not hibernate, or even species which require 2 yr to complete their life cycle (Brandmayr et al. 2005, Kotze et al. 2011). Den Boer and Den Boer-Daanje (1990) proposed a new classification based on species with winter larvae (autumn or winter breeders, with larval dormancy), species with summer larvae (spring or summer breeders, without larval dormancy), and species with long development larvae (larvae whose development period exceeds 12 mo).

Studies on the activity density (AD) of carabid species in Argentina are still at their beginning. Previous works that described seasonal activity of species from Buenos Aires province have been carried out in agroecosystems (Cicchino et al. 2005, Sorensen 2006, Turienzo 2006, Paleologos 2012), in an urban garden (Cicchino 2010) and in native forests (Cicchino 2006) and shrublands (Cicchino and Farina 2007, 2010). Seasonal activity was recorded for all species and many of them were more active during spring and summer, e.g., *Scarites anthracinus* (Dejean 1831), *Selenophorus anceps* (Dejean 1831), *Anisostichus posticus* (Dejean 1829), while others reached their activity peak in autumn and winter, e.g., *Argutoridius bonariensis* (Dejean 1831), and *P. cordicollis*, *Incagonum discosulcatum* (Dejean 1828).

The study of the activity of these beetles is of interest for several reasons. Carabids are often used in biological control and phenological information is needed to predict seasonal activity of beneficial species to understand their co-ocurrence with pest species, so that control measures could be instituted (Danks 1987, Werner and Raffa 2003) and poisoning operations could be timed to minimize risk to non-target carabids (Cartellieri and Lövei 2003). Phenological information can also be used to assess potential impacts of exotic fauna on native species (Werner and Raffa 2003) and to guide conservation efforts (Cartellieri and Lövei 2003) as well as to determine the optimal sampling periods to study the biodiversity of these beetles in different habitats (Harry et al. 2011). Finally, these kinds of researches are relevant to improve the knowledge of the biology of carabids by studying patterns of population changes and their interactions with other organisms, considering that they are also source of food for insectivorous vertebrates (Farias 2000, Ghys and Favero 2004, Biondi et al. 2005).

Therefore, our aim was to describe the annual activity cycle, the sex ratio, and the relationship between the activity and weather variables of the most abundant carabid species of a typical region of southeastern Pampasia. The study focused on a *Celtis ehrenbergiana* (= *C. tala* Guillies ex Planch) forest of the region, which is in good conservation status.

Materials and Methods

Study Area. The study area is located in one of the largest and southernmost *C. ehrenbergiana* forest of southern Buenos Aires, with an area of approximately 15 ha. The sampling was carried out in the northeast margin of the Laguna Nahuel Rucá (37° 37′04″ S, 57° 25′16″ W), which is located in a private property where livestock are kept and agricultural activities are carried out. The site belongs to a Provincial Wildlife Refuge, buffer zone of the Biosphere Reserve "Mar Chiquita" and is thus subject to applicable legislation (Maceira et al. 2005). The area belongs to the Pampean region and the climate is temperate with oceanic influence. The minimum mean annual temperature is 12.9°C and the maximum mean annual is 15°C, the mean annual relative humidity is 80%, and the mean annual rainfall is 923.6 mm (Reta et al. 2001). However, the period in which sampling was conducted, from 21 March 2008 to 22 March 2009, was marked by a deficit in the rainfall pattern in much of the humid and semi-humid regions in Argentina. This phenomenon was associated with the presence of a cold phase or La Niña from the El Niño-Southern Oscillation. During the sampling year, the minimum values of precipitation recorded in the weather station of Mar del Plata (the closest city) were among the lowest in the period 1961–2008 (S.M.N—Servicio Meteorológico Nacional—2008, 2009). The weather station recorded 581.9 mm accumulated throughout the year in Mar del Plata, while the pluviometer located in Laguna Nahuel Rucá recorded 658 mm (Fig. 1).

In southern Buenos Aires, the *C. ehrenbergiana* forest (or "talar") is an extra-zonal edaphic community that develops on silt dunes surrounding the freshwater lakes of the elevated plains (Vervoorst 1967, Cabrera 1976). It confirms "forms" or "integrates" monospecific *C. ehrenbergiana* forest and is the southern end of the talar community that develops toward the northeast of Buenos Aires province (Parodi 1940). In this area, the undergrowth is not present and only the herbaceous stratum is developed. This is composed by *Blumenbachia latifolia* Cambess., *Dichondra microcalyx* (Hallier f.) Fabris 1965, and the adventitious species *Lolium multiflorum* Lam. 1779, *Conium maculatum* L. 1753, *Sonchus oleraceus* L. 1753, *Rumex crispus* L. 1753, *Urtica urens* L. 1753, *Euphorbia peplus* L. 1753, *Torilis nodosa* (L.) Gaertn. 1788, *Marrubium vulgare* L. 1753, and *Carduus thoermeri* Winm. 1837 (Stutz 2001). The property where the sampling was carried out is surrounded by patches of humid prairie which are modified by the agricultural activities practiced in the area (Stutz 2001).

Sampling of Carabid Fauna. Pitfall traps were used, which, despite their widely discussed limitations to reflect the natural composition of the community (Topping and Sunderland 1992, Spence and Niemelä 1994, Adis 2002, Gerlach et al. 2009), are an efficient method to sample. In addition, the information provided allows a good approach to variables such as the "activity density" (Baars 1979, Spence and Niemelä 1994, Adis 2002). In order to capture the maximum diversity, three sampling groups were established on the wire edges, because the edges capture species in transit between two adjacent habitats and harbor viable populations of carabids that have the potential to regenerate adjacent disturbed sites (Magura and Tóthmérész 1997, Magura et al. 2001). At the same time, with this arrangement we aimed to reduce the disturbances that could cause loss of traps and entomological material because of the transit of cattle and the husbandry practices. Each sampling group consisted of 15 pitfall traps of continuous capture, spaced at a distance of 5 m one another. Traps were emptied and replaced once every 2 wk, approximately, so that they were operating for approximately 15-d period continuously during 1 yr. The distance between the groups was at least of 40 m. The traps consisted of plastic cups with a capacity of 850 ml and were buried with their opening 1–2 cm below the soil surface. They contained approximately 400 ml of a solution

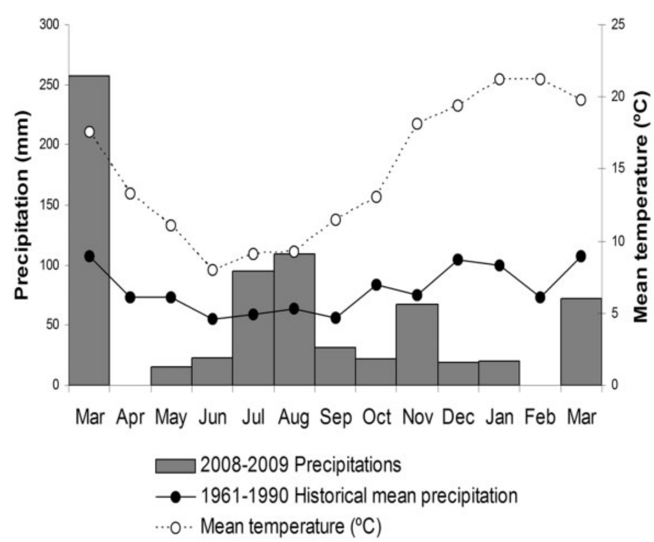

Fig. 1. Monthly precipitations recorded in Laguna Nahuel Rucá (gray bars), mean historical rainfall (1961–1990) (solid line with black circles) and mean monthly temperature (dotted line with white circles) both recorded by weather station of Mar del Plata.

composed of 200 g of sodium sulfite, 200 ml of formalin, and 25 ml of detergent dissolved in 10 liters of water. Traps were covered partially with endogenous elements of the system to reduce the drying by insolation and the falling of rainwater or litter inside them. Carabids were sorted and preserved in a solution of 70/30 v/v of 96° ethylic alcohol and 5% acetic acid; subsequently, the specimens were identified to species level and sexed by Dr. Armando C. Cicchino, using still unpublished keys for local species, as well as reference collection of these beetles inhabiting Buenos Aires province.

The bycatch was preserved in 70% ethanol for further study. Small vertebrates were well preserved in the pitfall traps on the field; hence, it is unlikely that catches could be altered by the presence of rotting animals during the 15-d period between the visits. The small vertebrates were distributed to other research groups. Forty-seven trap samples were lost out of the 1,080 samples (45 traps by 24 collection dates) because of different disturbances. Some other traps were trampled by cattle but still retained some of its content, so they were considered for counting in the laboratory.

Results about species' richness and carabid assemblage structure have been published previously (Castro et al. 2012). A voucher of the species studied was deposited in the entomological collection MMPE from the Museo Municipal de Ciencias Naturales "Lorenzo Scaglia," Mar del Plata, Argentina.

The sum of the AD from the 63 carabid species recorded was studied and, from these, species whose relative abundance was >1% were chosen for a more detailed study. The 16 species selected for this more detailed study comprised 88% of all the individuals collected (Table 1). The occurrence of larvae, teneral, and subteneral individuals was recorded. To complement the information obtained in this study, we included additional data of tenerals and larvae from another unpublished research of our group as well as from collections carried within the province of Buenos Aires (Table 2). Table 2 specifies the information for each specimen and the collection where it is deposited. In this contribution, larvae belonging to six genera were recorded, and no more than one species per genus in all the cases. Since 1999, five species [*A. bonariensis*, *Loxandrus simplex* (Dejean 1828), *Pachymorphus striatulus* (F. 1792), *S. anthracinus*, and *Bradycellus viduus* (Dejean 1829)] were reared starting from gravid females as a purpose for other unpublished reports. Thus, identification of these species was simple. For the remaining species, *Rhytidognathus* sp., the diagnostic larval features of the tribe (Migadopini) have been summarized by Arndt et al.

Table 1. List of species whose relative abundance was >1% of the whole assemblage

Species	Tribe	Number of individuals	Abbreviations
A. bonariensis (Dejean 1831)	Pterostichini	647	ARBO
P. striatulus (F. 1792)	Pterostichini	571	PAST
M. caudatus (Putzeys 1873)	Pterostichini	154	MECA
Pelmatellus sp. No. 1	Harpalini	124	PEspN°1
B. viduus (Dejean 1829)	Harpalini	118	BDVI
P. vagans (Dejean 1831)	Pterostichini	109	PLVA
L. planicollis (Straneo 1991)	Loxandrini	80	LOPL
N. cupripennis (Germar 1824)	Harpalini	68	NOCU
L. simplex (Dejean 1828)	Loxandrini	63	LOSI
A. posticus (Dejean 1829)	Harpalini	57	ANPO
C. platensis (Berg 1883)	Lebiini	55	CAPL
Rhytidognathus sp.	Migadopini	53	RHsp
P. cordicollis (Dejean 1828)	Pterostichini	53	PACO
S. anthracinus (Dejean 1831)	Scaritini	50	SCAN
Metius circumfusus (Germar 1824)	Pterostichini	47	MECI
S. melanarius (Dejean 1831)	Scaritini	38	SCME

Tribe, number of individuals caught, and abbreviation used in the canonical correspondence analysis are shown. This information was published in Castro et al. (2012).

(2005), being the most relevant: (1) mandibules with subbasal retinacular teeth (in addition a series of prebasal teeth are also present), (2) "caplike glands" present on abdominal hypopleurites I–VIII, and (3) urogomphi relatively short, a little longer than segment X.

Data Analysis.

Analysis of Weather Variables and Ground Beetle Activity. Canonical correspondence analysis (CCA) was used to find relationships between species abundance (as a measure of activity) and meteorological variables (ter Braak 1986). This is a robust method to analyze data from pitfall traps (Palmer 1993). Three variables were included for each 2-wk sampling period: mean temperature (°C), cumulative precipitation (mm), and photoperiod (hours). Temperature data were obtained from the SMN, precipitation from the local pluviometer of the private property, and photoperiod from The Weather Channel database (http://espanol.weather.com/climate/sunRiseSunSet-Buenos-Aires-ARBA0009? month=12). All these variables were obtained first as a daily value and then averaged over the sampling intervals; finally they were standardized (Legendre and Legendre 1998, Zuur et al. 2007). Significances of each axis were analyzed by testing individual canonical eigenvalues for significance using an F ratio (Legendre and Legendre 1998). The analysis was performed with the R software (Bates et al. 2008).

Activity Density. The AD for each species was calculated from the expression proposed by Brandmayr et al. (2005), which indicates the active number of individuals caught per trap in a period of 15 d.

Seasonal activity was described using the quartile method (Fazekas et al. 1997). Based on the the AD curve, the peak of activity was defined as the date when 50% of the total AD was recorded. The beginning and the end of the "main activity period" were defined as the dates when 25 and 75% of the total AD had been recorded, respectively.

The AD recorded in our study was compared with the information published in previous studies conducted in different environments and locations in the province of Buenos Aires (Table 3): a cornfield and its surrounding environments at the Faculty of Agricultural Sciences Experimental Station of La Plata (34° 54′ S, 57° 55′ W) (Cicchino et al. 2005); the *C. ehrenbergiana* forest of Laguna de Los Padres Reserve (37° 56′ S, 57° 45′ W) (Cicchino 2006); *Colletia paradoxa* (Spreng.) Escal. 1946 shrubs of Sierra de los Difuntos highlands (37° 54′ S, 57° 49′ W) (Cicchino and Farina 2007); an urban garden of La Plata city (34° 57′31″ S, 57° 58′15″ W; Cicchino 2010) and vineyards from Berisso (34° 53′ S, 57° 54′ W; Paleologos 2012). All these studies used pitfall traps with 800–900 mm of capacity and formalin as preservative liquid, except Cicchino (2010) sampling, which used saturated saline solution and 2% acetic acid.

Sex Ratio. From the 16 species studied, 14 were readily sexed relying on the characteristics of the structure of the three or four tarsites of the male fore tarsus (expanded tarsites suddenly provided with ventral vestiture of adhesive setae). The remaining two species, belonging to the genus *Scarites*, have unmodified tarsi in male individuals; then, they may be sexed with a ventral features of the head, as proposed by Bänninger (1937), but this approach revealed us as unreliable, mostly because of the high variability in size and body sturdiness of the male individuals, as revealed by genital dissections. The chi-square test was used to analyze whether the sex ratio of 14 species differed from the expected 1:1 (female:male) ratio in each season.

Results

Meteorological Variables and Species Activity. The CCA showed strong association of meteorological variables and the seasonal activity of carabid species throughout the year in the talar of the Laguna Nahuel Rucá (Fig. 2). The eigenvalues of the CCA measure the proportion of total variation explained by the abundance of their respective axes (ter Braak 1986). Total inertia is 1.19 and constrained eigenvalues for CCA axes 1–3 were 0.270, 0.151, and 0.02, respectively. The first two canonical axes were significant (axis 1: $F = 7.19$, $P < 0.01$; axis 2: $F = 4.01$, $P < 0.01$; axis 3: $F = 0.53$, $P > 0.05$). The cumulative percentage of

Table 2. Teneral (T), subtenerales (ST), and larvae (L) specimens available from other unpublished studies and collections

Species	Degree of maturity	Date	Location	Entomological collection
P. striatulus	1 ST	I-1997	Madariaga	ACC
	1 T	26-X-1980	Balcarce	EEBA
	1 T	17-XII-1966	Balcarce	EEBA
	1 ST	24-IX-1958	Tres Arroyos	EEAB
	1 ST	8-XII-1938	Lobería	MLP
P. cordicollis	1 ST	13-X-1912	Capital Federal	MLP
	1 T	13-VI-1969	Balcarce	EEAB
	1 T	5-II-1969	Gral. Alvarado	EEAB
	1 ST	4-X-1930	Montevideo (Uruguay)	MLP
	1 ST	15-I-1904	Montevideo (Uruguay)	MLP
	1 T	11-X-1905	Montevideo (Uruguay)	MLP
	1 ST	21-X-1906	Montevideo (Uruguay)	MLP
Argutoridius bonariensis	1 ST	VII-2010	Gral. Pueyrredón	DPP
	1 ST	19-VIII a 23-IX-2010	Gral. Pueyrredón	DPP
	1 ST	XII-2010	Gral. Pueyrredón	DPP
	1 ST	V-2011	Gral. Pueyrredón	DPP
	1 ST	XI-2011	Gral. Pueyrredón	DPP
	1 T	XII-2011	Gral. Pueyrredón	DPP
A. posticus	3 T, 3 ST	II-2011	Gral. Pueyrredón	DPP
	1 T, 1 ST	I-2013	Gral. Pueyrredón	DPP
	1 ST	II-2013	Gral. Pueyrredón	DPP
Rhytidognathus sp.	2T, 4ST	25-XI-2004	Mar Chiquita	ACC
	1T	14-IX-2004	Mar Chiquita	ACC
M. caudatus	1T	23-II-2002	Necochea	ACC
	1 ST	III-2001	Villarino	ACC
	1 ST	I-1997	Gral. Madariaga	ACC
	1 T	XII-2010	Gral. Pueyrredón	DPP
M. circunfusus	1 ST	V-2012	Gral. Pueyrredón	DPP
	1 T, 1 ST	XI-2012	Gral. Pueyrredón	DPP
S. anthracinus	1 L	II-2004	Mar Chiquita	ACC
	1 L	II-2004	Balcarce	ACC
	1 L	III-2004	Gral. Pueyrredón	ACC
	1 L	III-2004	Mar Chiquita	ACC

The abbreviations indicate the collection where specimens are deposited: EEAB (Balcarce Agricultural Experimental Station); MLP (La Plata Museum), ACC and DPP are transitory collections from A. C. Cicchino and D. P. Porrini.

variance explained by the first two axes accounted for 35.4% (22.7 and 12.7%, respectively, for axes 1 and 2) of variation in the data and 95.4% (61.2 and 34.2%, respectively, for axes 1 and 2) of species–environment relationships. Figure 2 shows the biplot of weather variables, scores of species, and sampling periods. Species and sampling periods were distributed according to the seasons. The length of the arrows indicates the strength of the correlation between the variables and the CCA axis. The first axis was influenced by both photoperiod and temperature (biplot scores for constraining variables: photoperiod = 0.98, temperature = 0.97, precipitation = −0.08). The second axis was most influenced by precipitation (biplot scores for constraining variables: photoperiod = −0.08, temperature = 0.24, precipitation = −0.47). Most of the species associated with the spring and summer samplings, e.g., *Scarites melanarius*, *S. anthracinus*, *Notiobia cupripennis*, *B. viduus*, *Metius circunfusus*, and *Metius caudatus* showed positive values on axis 1, i.e., associated with relatively high temperatures and long photoperiods. The species associated with the autumn and winter samplings showed negative values on axis 1, such as *P. cordicollis*, *L. simplex*, *Loxandrus planicollis*, *Rhytidognathus* sp., *Plagioplatys vagans*, and *A. bonariensis*. Results show that *Carbonellia platensis*, *A. posticus*, *S. melanarius*, *P. cordicollis*, and *L. planicollis* occurs at high values of precipitation, whereas *P. vagans* and *M. caudatus* occur at low values of it.

Activity Density. The total activity pattern (63 carabid species) was high in early autumn (3.11 individuals per trap in 15 d) and late spring (3.27 individuals per trap in 15 d) (Fig. 3).

One species, *P. vagans* (Fig. 4a), showed a peak of AD in autumn, during the first 2 wk of April (5–18 April); the main activity period was recorded since 21 March to 7 May, and it was short when compared with most species.

Among the species with a winter activity peak, *A. bonariensis* (Fig. 4b) reached it in June; *L. simplex* (Fig. 4c), *P. cordicollis* (Fig. 4d), and *Rhytidognathus* sp. (Fig. 4e) peaked in July, whereas *L. planicollis* (Fig. 4f) peaked in August. The last three species showed more irregular patterns. Activity of *Rhytidognathus* sp. was not recorded since mid-November to April.

In spring, the peak of activity of *C. platensis* (Fig. 5a), *S. melanarius* (Fig. 5b), and *A. posticus* (Fig. 5c) occurred in October; whereas *P. striatulus* (Fig. 5d), *N. cupripennis* (Fig. 5e), *Pelmatellus* sp. No. 1 (Fig. 5f), *M. circumfusus* (Fig. 6a), and *S. anthracinus* (Fig. 6b) peaked in November. Activity of *A. posticus* was not recorded in summer, as well as *S. anthracinus* and *S. melanarius* showed none or minimum activity in autumn and winter.

Finally, in summer, *M. caudatus* (Fig. 6c) had its peak in February, whereas *B. viduus* (Fig. 6d) peaked in January and was not recorded in winter.

No tenerals were recorded for *P. vagans*, *N. cupripenis*, *L. simplex*, and *S. melanarius*. Tenerals of *A. bonariensis* were recorded in all seasons (Fig. 4b). Activity of tenerals of most species occurred mainly in spring and summer, with some records in late-autumn (e.g., *Pelmatellus* sp. No. 1, *B. viduus*, *A. posticus*, *M. circumfusus*, and *P. cordicollis*). Finally, tenerals of *Rhytidognatus* sp. (Fig. 4e) occurred in winter and spring.

Table 3. Seasons in which carabid activity peaks were recorded in different environments and localities of Buenos Aires province in previous works

Species	Activity peak	Habitat	Location	Reference
A. bonariensis	Autumn	Cornfield and surroundings environments	La Plata	Cicchino et al. 2005
	Autumn	*C. ehrenbergiana* forest	Laguna de Los Padres	Cicchino 2006
	Autumn	*C. paradoxa* shrubland	Sierra de los Difuntos	Cicchino and Farina 2007, 2010
	Winter	Urban garden	La Plata	Cicchino 2010
	Autumn	Vineyards	Berisso	Paleologos 2012
P. striatulus	Autumn	Cornfield and surroundings environments	La Plata	Cicchino et al. 2005
	Autumn	Vineyards	Berisso	Paleologos 2012
	Singleton in summer	*C. ehrenbergiana* forest	Laguna de Los Padres	Cicchino 2006
M. caudatus	Autumn	*C. paradoxa* shrubland	Sierra de los Difuntos	Cicchino and Farina 2007, 2010
Pelmatellus sp. No. 1	Singleton in spring	*C. ehrenbergiana* forest	Laguna de Los Padres	Cicchino 2006
B. viduus	–	–	–	–
P. vagans	Autumn	*C. paradoxa* shrubland	Sierra de los Difuntos	Cicchino and Farina 2007, 2010
L. planicollis	–	–	–	–
N. cupripennis	Summer	*C. ehrenbergiana* forest	Laguna de Los Padres	Cicchino 2006
L. simplex	Singleton in summer	*C. ehrenbergiana* forest	Laguna de Los Padres	Cicchino 2006
A. posticus	Spring	*C. ehrenbergiana* forest	Laguna de Los Padres	Cicchino 2006
	Spring or summer	*C. paradoxa* shrubland	Sierra de los Difuntos	Cicchino and Farina 2007, 2010
C. platensis	–	–	–	–
Rhytidognathus sp.	–	–	–	–
P. cordicollis	Winter	Cornfield and surroundings environments	La Plata	Cicchino et al. 2005
	Autumn	Urban garden	La Plata	Cicchino 2010
	Autumn and winter	Vineyards	Berisso	Paleologos 2012
S. anthracinus	Spring	Cornfield and surroundings environments	La Plata	Cicchino et al. 2005
	Spring and summer	Vineyards	Berisso	Paleologos 2012
	Singleton in summer	*C. ehrenbergiana* forest	Laguna de Los Padres	Cicchino 2006
M. circumfusus	Singleton in autumn	*C. ehrenbergiana* forest	Laguna de Los Padres	Cicchino 2006
S. melanarius	–	–	–	–

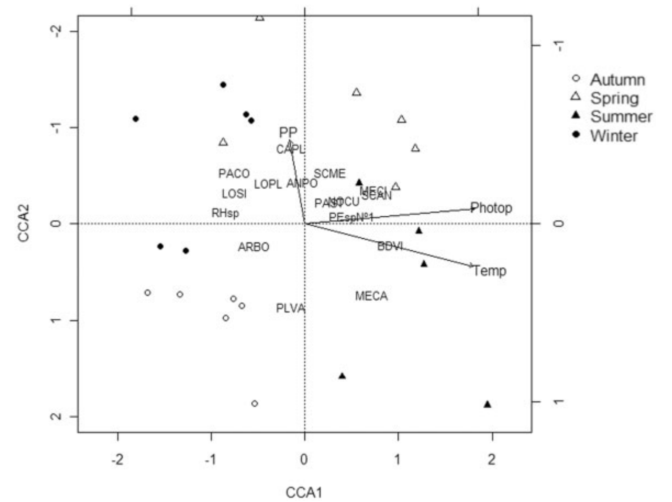

Fig. 2. Biplot of carabid abundance and weather variables from CCA. The abbreviations of the name of the species were plotted, complete names are listed in Table 1. Environmental variables are represented by arrows and dots correspond to the sampling periods.

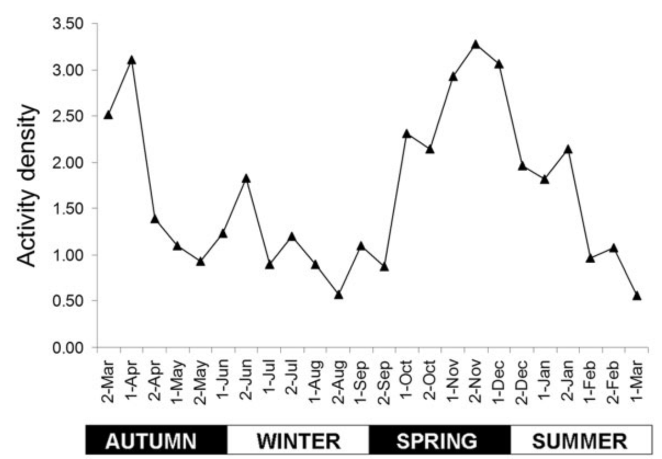

Fig. 3. Total AD (of 63 carabid species) recorded in the talar during the annual cycle March 2008 to March 2009. On the x-axis, the digit before each month indicates that the sampling date corresponds to the first (1) or second (2) 2-wk period of the month.

Sex Ratio. Eight of the species studied (*M. caudatus*, *Pelmatellus* sp. No. 1, *L. planicollis*, *L. simplex*, *N. cupripennis*, *C. platensis*, *Rhytidognathus* sp., and *P. cordicollis*) did not show significantly different activities between the sexes ($P > 0.05$) in the seasons in which the number of individuals captured was enough to perform the analysis. *A. bonariensis* showed a female-biased sex ratio in autumn ($\chi^2_{0.05;1} = 12.04$; $n = 309$; $P < 0.01$), winter ($\chi^2_{0.05;\ 1} = 8.10$; $n = 160$; $P < 0.01$), and spring ($\chi^2_{0.05;\ 1} = 5.26$; $n = 92$; $P < 0.05$), whereas the sex ratio of *P. striatulus* was male-biased in autumn ($\chi^2_{0.05;\ 1} = 4.56$; $n = 137$; $P < 0.05$), winter ($\chi^2_{0.05;\ 1} = 7.91$; $n = 79$; $P < 0.01$), and summer ($\chi^2_{0.05;\ 1} = 6.25$; $n = 108$; $P < 0.05$). The sex ratio was female-biased in autumn for *P. vagans* ($\chi^2_{0.05;\ 1} = 10.89$; $n = 94$; $P < 0.01$), in winter for *A. posticus* ($\chi^2_{0.05;\ 1} = 6.25$; $n = 16$; $P < 0.05$) and in spring for *M. circunfusus* ($\chi^2_{0.05;\ 1} = 5.16$; $n = 38$; $P < 0.05$); *B. viduus* showed a male-biased sex ratio in autumn ($\chi^2_{0.05;\ 1} = 4.45$; $n = 11$; $P < 0.05$).

Discussion

Few studies on annual AD of carabidae have been carried out in agroecosystems and native environments from Argentina (Cicchino et al. 2005, Cicchino 2006, Sorensen 2006, Turienzo 2006, Castro and Porrini 2010, Cicchino and Farina 2007, 2010, Paleologos 2012). This article provides original information about the activity of carabids under atypical weather conditions as the severe draught associated with La Niña phenomenon, in a native environment of Buenos Aires, Argentina (S.M.N 2008, 2009).

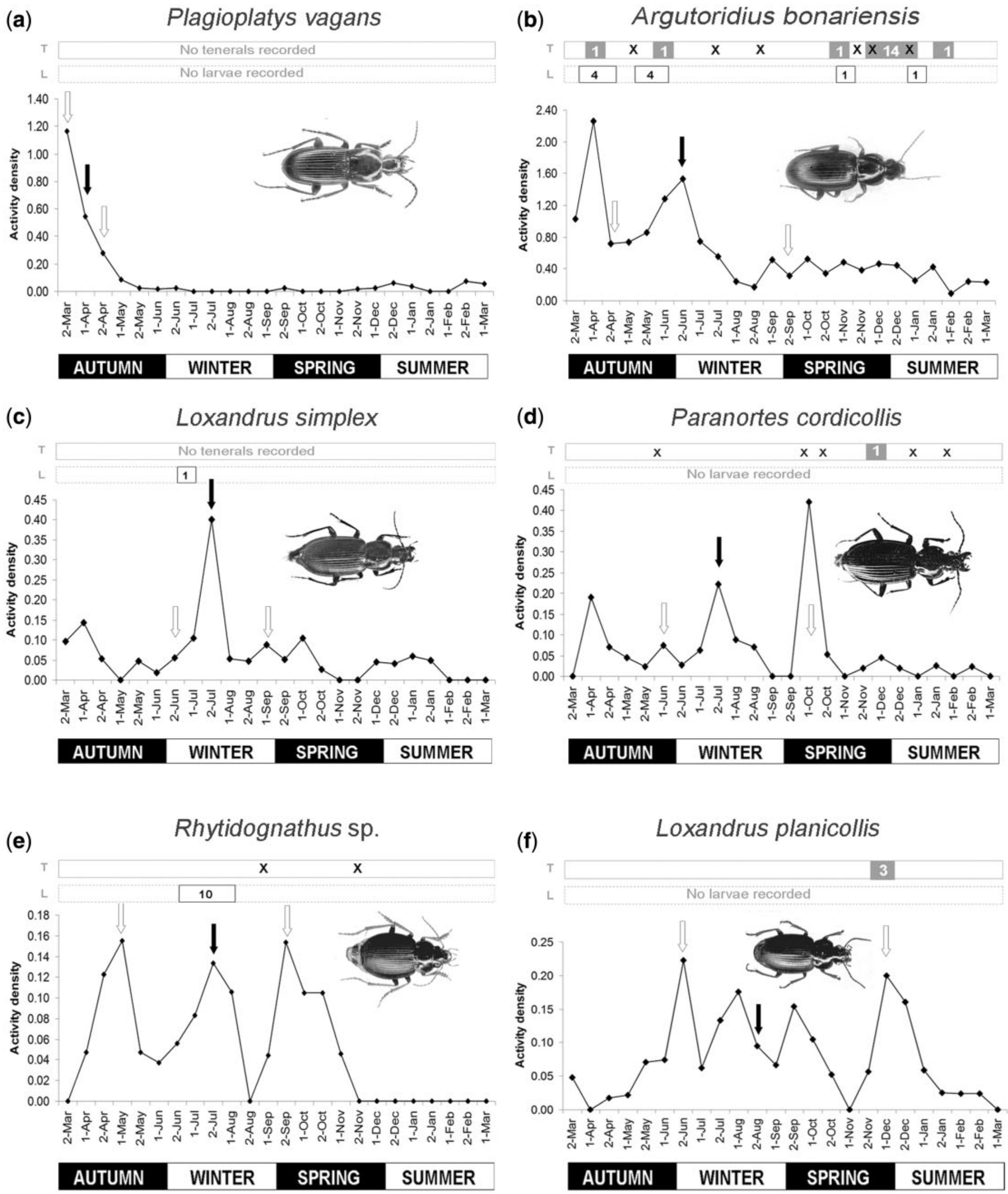

Fig. 4. Activity Density of adult carabid species recorded in the talar during the annual cycle March 2008 to March 2009. Sampling dates and seasons are indicated on x-axis. The digit before each month indicates that the sampling date corresponds to the first (1) or second (2) 2-wk period of the month. The two upper bars indicate the number of tenerals (T) and larvae (L) recorded in the corresponding sampling period. The X indicates data supplied by other collects as denoted in Table 2. Arrows indicate the main activity period (white arrows) and the activity peak (black arrow).

The species studied here showed a clear seasonality in the activity pattern, which agreed with previous works, except for a few species. The activity of *P. vagans*, *N. cupripennis*, and *A. posticus* is usually high in summer (Cicchino 2006, Cicchino and Farina 2007, 2010); however, our results showed that the activity remained very low throughout that season. Only *M. caudatus* reached a peak of activity in summer. These behaviors may be associated with the drastic deficit of rainfall occurred in the summer (S.M.N 2009). Many species of beetles acquire the ability to survive during drier periods of "La Niña" by the marked reduction of their populations, in which the adults take refuge in galleries, crevices, or cavities underground, feeding on the resources that remain available (Larrain et al. 2001).

Climatic conditions are determinants of the variation in assemblages (Irmler 2003), but despite the fluctuations that may exist in abundance through the years, seasonal patterns of activity remain similar in a site (Niemelä et al. 1989). Life history of temperate-region ground beetles

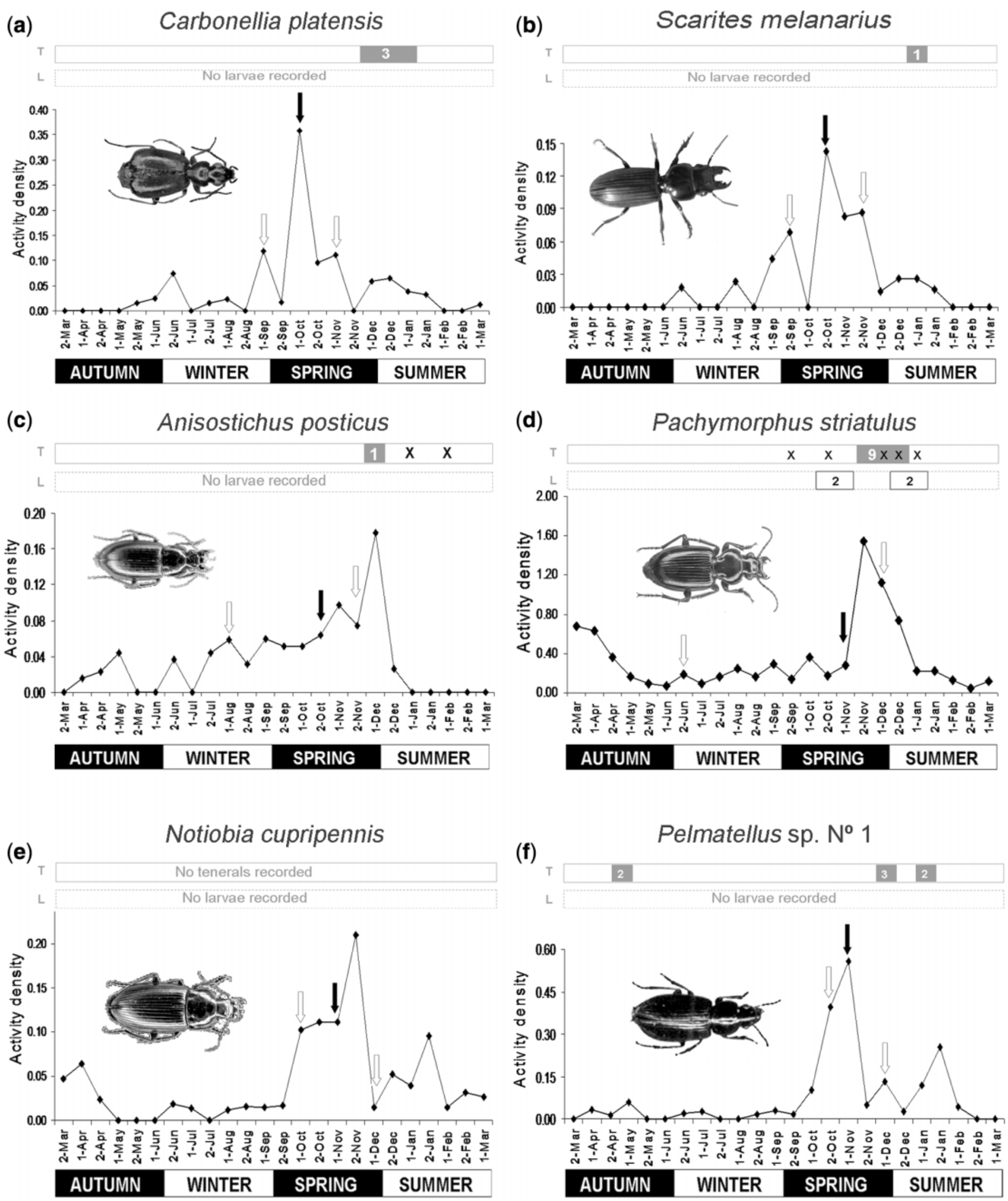

Fig. 5. Activity Density of adult carabid species recorded in the talar during the annual cycle March 2008 to March 2009. The x-axis indicates sampling periods and seasons, upper bars and arrows denote maturity degree and activity dates, respectively, as in Fig. 4.

involves dormant periods during winter or summer (Lövei and Sunderland 1996). The most important factors influencing seasonal rhythms on carabids are photoperiod and temperature (Thiele 1977). For example, a positive association between *S. anthracinus*, *M. circunfusus*, *B. viduus*, and *M. caudatus* with temperature and photoperiod was found. The first three species seem to overwinter since no catches were recorded in the cold season. On the other hand, *Rhytidognathus* sp. probably undergoes a period of estivation from mid-November to early April.

Negative correlation between activity and temperature might express a dependence on high relative humidities, since in lower temperatures the relative humidity tends to be higher (Diefenbach and Becker 1997). In this regard, some of the species that peaked in winter, as *P. cordicollis*, *L. simplex*, and *L. planicollis*, showed a strong positive association with precipitation. Similarly, *C. platensis*, *S. melanarius*, and *A. posticus*, which peaked in spring and whose main activity period started from late-winter, showed a positive association with precipitation. In contrast to these results, Cicchino and Farina (2007) describe *C.*

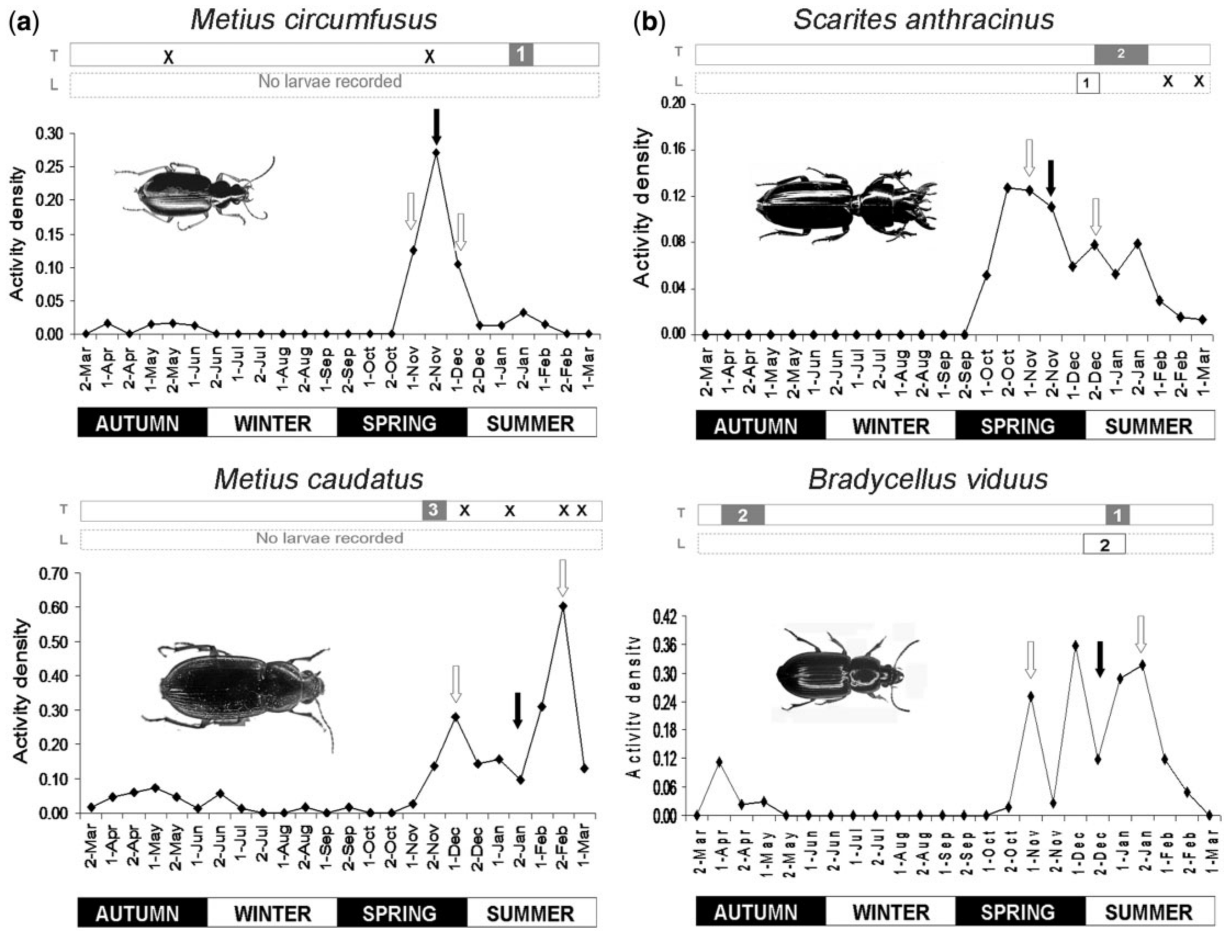

Fig. 6. Activity Density of adult carabid species recorded in the talar during the annual cycle March 2008 to March 2009. The x-axis indicates sampling periods and seasons, upper bars and arrows denote maturity degree and activity dates, respectively, as in Fig. 4.

platensis as a xerophylic species, whose typical habitats are short pastures (Canepuccia et al. 2009) and open grasslands (Cicchino 2003). On the other hand, *M. caudatus* and *P. vagans* showed a negative correlation with precipitation. These results agree with previous studies where both species, typical of open grasslands and highlands, were described as mesophilic and xerophilic, respectively (Cicchino and Farina 2005). It must be noted that the preference of xerophilic habitats by some species do not necessarily implies negative association with precipitations, which may eventually trigger some biological events such as the couple-seeking or reproduction, as in the case of *C. platensis*. All local "populations" of this species from eastern Buenos Aires province (east of 59° W meridian) are micropterous, while those from southwestern localities ranging from western of Bahía Blanca (38° 42′41″ S, 62° 16′01″ W) to central Mendoza province (33° 44′16″ S, 69° 07′04″ W) are wing-dimorphic (Cicchino and Farina 2005), meaning differences in habitat-occupancy as well as in dispersal strategies, probably linked to different precipitation regimes (Hoffmann 1989).

It can be assumed that species would respond more flexibly to other less predictable stimuli than photoperiod or temperature, such as the availability and quality of food and population density (Hodek 2012). There are granivorous carabids whose reproduction depends on the mature seeds that appear at the end of the wet or warm seasons (Kotze et al. 2011), which would also explain the high activity of granivorous species such as the harpalini *N. cupripennis*, *B. viduus*, *Pematellus* sp. No. 1 and *A. posticus* in spring and summer seasons. Lietti et al. (2000) reported that *N. cupripennis* feeds more often on plant seeds that bloom in spring and bear fruit until summer. Similarly, high abundance of prey can increase the activity of predator carabids (Stork and Paarman 1992, Honěk and Jarošík 2000). For example, *S. anthracinus* feeds on slugs and pillbugs which proliferate from October to December (Tulli et al. 2009). In addition, there are changes in the abundance of species that may occur due to demographic processes inherent to populations, strategies of dispersal, and habitat stability (Luff 1996, Honěk 1997). *P. striatulus* and *A. bonariensis* were the most active species; they were recorded all months and peaked in spring and early autumn, respectively. The activity pattern of *P. striatulus* differed from previous results, where this species reached the maximum activity in autumn (Cicchino et al. 2005, Paleologos 2012). *P. striatulus* has been identified as eurytopic, ubiquist, and synanthropic (Cicchino 2003) and therefore, it is likely that its phenology varies between different habitats (Danks 2002) since carabids occupying a wide range of habitats are usually more eurythermic than those with apparently narrow habitat preferences (May 1979).

Reproductive period usually coincides with the peak of activity, although this connection is flexible in many species (Niemelä et al. 1989, Lövei and Sunderland 1996). Then, from seasonal activity patterns and teneral records we hypothesize that the carabid species under consideration can be classified into at least three broad categories according to their reproductive strategies: (1) whole year breeders (*A. bonariensis*), (2) spring to early autumn breeders (*B. viduus*, *M. circunfusus*, *Pelmatellus* sp. No. 1, *A. posticus, S. melanarius*, *S. anthracinus*, *C. platensis*, and *N. cupripennis*), and (3) late autumn to early spring breeders (*L. planicollis*, *L. simplex, P. cordicollis*, and *Rhytidognathus* sp.). There are other species for which we cannot assume reproductive strategies and more studies are needed since no tenerals were recorded, there are differences in seasonal patterns with previous results (*P. striatulus* and *M. caudatus*) and/or the talar is not the most representative habitat of some species, as *P. vagans*, typical of open grassland (Cicchino and Farina 2005).

Regarding the sex ratio, differential locomotor activity of males and females in general is reflected by pitfall traps (Szyszko et al. 2004, Tyler 2012). The sex ratio can vary during the year depending on the species (Tyler 2012) and reproductive status (Levesque and Levesque 1994), but is also influenced by other factors such as food availability (Szyszko et al. 2004) or the ability of each sex to escape the traps (Yamashita et al. 2010). Males are presumed to show higher activity than females (Gerlach et al. 2009), but these trends do not hold for all species (Philip and Burgess 2008). A female-biased sex ratio can suggest high breeding activity, since the activity of the female tends to be increased during the development of eggs (Levesque and Levesque 1994). Because formalin was used as preservative agent in the pitfall traps, sex ratio of catch should be interpreted with caution. Formalin can act as attractant to some species of carabids and this attraction may vary in different periods of the year (Luff 1968). Nevertheless, the results about differential reactions to preservative solutions between the sexes are variable, and it should be noted that the effect of preservatives can also be influenced by many environmental factors; it may occur that during dry weather periods the fluids can have an attracting effect on the animals (Gerlach et al. 2009).

The phenology of the species studied in this article, which was focused on a small rural area subject to the conditions established for the management of a Provincial Wildlife Refuge, buffer zone of the Biosphere Reserve "Mar Chiquita," is representative of what happens in other rural environments of south-east Buenos Aires. More studies on seasonal activity of the regional species in similar and different habitats, following a standardized method as suggested by Fazekas et al. (1997), are needed to compare the seasonal patterns and corroborate whether the trends found here are due to the conditions of La Niña phenomenon. Similarly, dissection of males and females should be performed to determine the developmental stage of gonads and the number of eggs and to improve the knowledge on reproductive behavior.

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