LIFE CYCLES OF RIPARIAN GROUND BEETLES (COLEOPTERA CARABIDAE): STRATEGIES FOR REPRODUCTION IN THE BANK OF A TEMPORARY STREAM IN THE SOUTHERN IBERIAN PENINSULA

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LIFE-CYCLE
RIPARIAN
GROUND BEETLES
COLEOPTERA CARABIDAE
IBERIAN PENINSULA

ABSTRACT. – The life cycles of riparian ground beetles at the bank of the Arenosillo Stream (southern Iberian Peninsula) have been examined in order to elucidate their life strategies for surviving in this type of unstable environment. The study is based on data of annual activity patterns of species in the natural habitat, and on anatomical observations related to the age of specimens and the reproductive condition of females. The carabid community from the Arenosillo stream is representative of the ripicolous communities inhabiting the riverbanks of the southern Iberian Peninsula. Three different life-strategies are shown to be feasible for reproducing in the area. The most representative ripicolous species display a spring-breeder reproductive cycle, although species displaying autumn-breeder reproduction rhythms and unstable annual cycles are also present.

CYCLE BIOLOGIQUE
MILIEU RIPICOLE
COLÉOPTÈRES
CARABIDAE
PÉNINSULE IBÉRIQUE

RÉSUMÉ. – Les cycles biologiques des Coléoptères Carabiques qui colonisent les zones ripicoles de l'Arenosillo, affluent du Guadalquivir (au sud de la Péninsule Ibérique) ont été étudiés afin d'élucider les stratégies de survie dans ces milieux instables. L'échantillonnage sur le terrain permet d'étudier les rythmes d'activité annuelle, et les études anatomiques permettent d'apprécier l´état de développement des ovaires et le degré de détérioration des mandibules et des soies des adultes. Les résultats montrent que la communauté de l'Arenosillo est assez représentative des communautés de Carabiques qui habitent les rivières du sud de la Péninsule Ibérique. D'autre part, trois stratégies différentes se sont montrées viables dans cette zone: la plupart des espèces se reproduisent au printemps, mais il existe des espèces qui se reproduisent en automne et d'autres, qui ont un cycle biologique fluctuant en fonction des conditions de l'environnement.

INTRODUCTION

The present paper is part of a study that examines the adaptive strategies of riparian ground beetles (Coleoptera Carabidae) for surviving under unstable environmental conditions, such as those of the temporal courses of water in the Mediterranean area. One of the main problems for organisms living in riverbank habitats arise from the seasonal fluctuations of physical and biotic factors brought about by periodical rainfall and dryness. To survive under these conditions, their life cycles must adapt to these environmental fluctuations. Ground beetles are a sufficiently well known group of insects so as to study their life cycles in relation to environmental factors. They represent one of the most sensitive groups with many highly specialised taxa and are therefore much more affected by changes in alluvial ecosystems than other invertebrates (Sustek 1994). As a rule, the wet areas lodge a rich fauna of carabid beetles owing to the hygrophilous character of these insects, resulting in the existence of peculiar riparian communities occasionally enriched with the presence of generalist species which seek refuge during the dry period (Rueda & Montes 1987).

Since the appearance of the first paper on the life cycle of carabids (Larsson 1939), numerous studies have been carried out in Central Europe and North America. Thiele (1977) gave a summary of all the research done in this field in temperate zones, distinguishing at least five types of annual rhythms. Later, Paarmann (1979) extended the types of annual reproduction rhythms to include the tropics, subtropics and temperate zones, demonstrating the distinct ability of the carabid to adapt to greatly varying seasonal differences in environmental factors. Paarmann (*op. cit.*) established relationships between the different types of annual rhythms in Carabidae and drew conclusions about the possible evolution of these types. Research has also been carried out into the life cycles of riparian carabids in arctic and alpine zones (Andersen 1970, 1983). However, none of the above mentioned studies has examined the riparian species living in transitional zones such as the Mediterranean area.

On the other hand, much information is available concerning other aspects of the biology of riparian carabid beetles (Darlington 1971, Thiele 1977, Plachter 1986, Siepe 1989, Hering & Plachter 1997). More recently, Boscani *et al.* (2000) used the carabid beetles as a tool for quality assessment in river ecotones.

When summarising the available literature, it could be suggested that the different life cycles displayed by the riparian carabids in temperate zones are governed by annual oscillations in climatic conditions and involve a series of morphological, physiological and behavioural adaptations, including optional polymorphism, growth rate, number of generations, dormancy, fecundity, and synchronisation between the reproduction period and suitable environmental conditions. In the Iberian Peninsula, faunistic research has been carried out in ripicolous and marshy environments by Vives & Vives (1978, 1981), Serrano (1982), Zaballos (1986), Rueda & Montes (1987), Ortiz *et al.* (1989), Serrano *et al.* (1990), Cárdenas & Bach (1992 a, 1992b). Nevertheless, biological and ecological studies in this type of environment are also necessary.

The main objective of our study was to examine the activity patterns and reproductive biology of the most abundant riparian carabids colonising the margins of the Arenosillo Stream, a tributary of the Guadalquivir River (southern Iberian Peninsula), in order to elucidate their life strategies.

THE STUDY AREA

The study was carried out in a section of the Arenosillo Stream (U.T.M. Coordinates X=37774, Y=421484; 220 m in altitude), a tributary of the Guadalquivir River (southern Iberian Peninsula). The stony bed of the stream has developed over red soils and reddish-grey lands with sandy margins as a consequence of the degradation of sandstone, limestone and sediments. The soil characterisation is given in Table IA.

Although the Arenosillo is a temporary course water, in the sections where the flow results interrupted, the stream bed remains humid even throughout the summer.

The climate of the area has been characterised from average monthly precipitation and temperature data (Fig. 1) and from a summary of the hydrological cycle recorded at the Montoro Meteorological Centre located near the study area (Table I B) (CEBAC 1971). The climate is typified as sub-continental and sub-humid with temperate-cold winters and hot-dry summers. Average annual temperature and precipitation values are close to 18 °C and 660 mm, respectively.

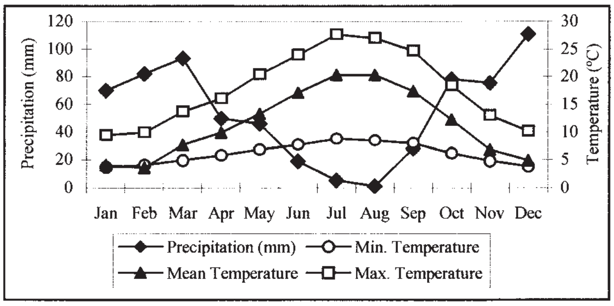

Fig. 1. – Monthly data of mean, maximum and minimum temperatures and precipitation. Data source: Montoro Meteorological Centre.

The vegetation of the section of the stream under study corresponds to the *Oleo-Ceratonion* Alliance, represented in the area by the *Asparago-Rhamnetum* Association. Olive trees, vineyards, residual forest and wooded and open pasture lands are present as well as indicatory species such as *Smilax aspera*, *Phlomis purpurea* or *Clematix flammula, Juncus* sp., *Typha* sp., *Scirpus* sp. and *Nerium oleander*.

METHODOLOGY

Sampling methods: In order to identify the faunistic composition of the Caraboidea that colonise the surrounding area of the Arenosillo stream and to record their temporal activity patterns, systematic samplings were carried out at weekly intervals between March 1997 and June 1998. For each sampling, 20 pitfall-traps were placed at regular intervals in the margins of a section of the Arenosillo Stream. Each trap consisted of two concentric cylindrical plastic pots (11 cm Ø and 1.000 cc volume). The outer portion of the pots was used as a container and the inside as a recipient. Pitfall traps were mid-filled with 250 cc of a mixed solution of acetic acid as bait and ethanol (70%) as preservative. The pots were buried up to the top end, partially covered to avoid inundation and randomly distributed in the study area. Moreover, in specific microhabitats (i.e. under stones or at the foot of sub-aquatic plants) direct collection was made and soil samples (≈5 dm^3) were taken for processing in the laboratory by the Berlese technique. Some samples taken during the rainy period were not effective due to variations in the water level, which inundated them.

Anatomical studies: Anatomical studies to determine the sex and age of the specimens and the reproductive condition of the females were carried out. Age was determined by testing the softness of the integument and the extent of wear in mandibles, cephalic and thoracic bristles, tibial spines and tarsal claws. Adults were classified by age as follows: **tenerals** or immature with a very soft integument and unworn structures; **young imagoes** belonging to the last generation with a hard integument but scarcely worn structures; and **old imagoes** with hard integument and fairly worn structures which were probably over one year old. The gonadal stage of female specimens was also examined and classified following the same criteria as in Cárdenas (1994).

The following concept has been defined in order to describe the results: **Potential fecundity**: Mean number of eggs per fertile dissected female for a given period of time. A female was considered to be fertile when at least one mature *ovum* was found in the ovary. This parameter allowed us to determine the time and course of oviposition.

The systematic criteria of Zaballos & Jeanne (1994) was followed to classify the species.

Statistical methods: $\mathbf{R_1}$ (Margalef) Richness and **H'** (Shannon) Diversity indices and Rarefraction (Hurlbert) curves were calculated (Ludwing & Reynolds 1988) to characterise and compare the carabid community from the Arenosillo stream.

RESULTS

The riparian community of ground beetles in the Arenosillo stream was made up of a total of 50 species (see appendix) and was characterised by the above mentioned Richness and Diversity Indices (Table I). The values obtained for these indices were expectable for this kind of riparian environments in our latitude: they are close to those of other riparian and known communities (Cárdenas & Bach 1992a and 1992b) used as references and located near the research area: the Guadiato River and the Bejarano Stream (at distance of approximately 60 and 40 km, respectively).

Bearing in mind that the possible differences in sample size could affect the results of these indices, the Rarefraction curves – a most suitable statistical method in this situation – were also calculated (Fig. 2). The graph allows to get the same result since the three localities appear rather proximate. So, the Arenosillo community is

Table I. – Top, A, Soil analysis results for the Arenosillo Stream. B, Summarised hydrological cycle for the research area. Data source: Montoro Meteorological Centre (CEBAC, 1971). Bottom, N° sp, Richness and Diversity Indices calculated for the Arenosillo, Guadiato and Bejarano localities.

A	
PARAMETERS	
Thick elements	5,8
Sand %	70,8
Slime%	23,8
Clay %	5,4
PH (H_2O) 1:2,5	6,91
PH (ClK) 1:2,5	5,99
% Oxidised Organic Matter	0,96
% Organic Nitrogen (N)	0,06
Phosphate ppm (P)	14,7
Potassium ppm (K)	608,6
Carbonates (%)	0,0
B	
PARAMETERS	
Annual Precipitation (mm)	659,6
Annual Average Temperature (°C)	17,9
Potential Evapotranspiration (mm)	941,5
Excess Water (winter) (mm)	225,8
Water Deficiency (summer) (mm)	507,7
Aridity Index	53,9
Humidity Index	-8,3
Climatic Type	Dry-Subhumid
Symbology	$C_1B'_3s_2b'_4$

INDICES	ARENOSILLO	GUADIATO	BEJARANO
N° sp.	50	46	38
R_1	6,09	7,32	4,34
H'	2,06	2,69	2,29

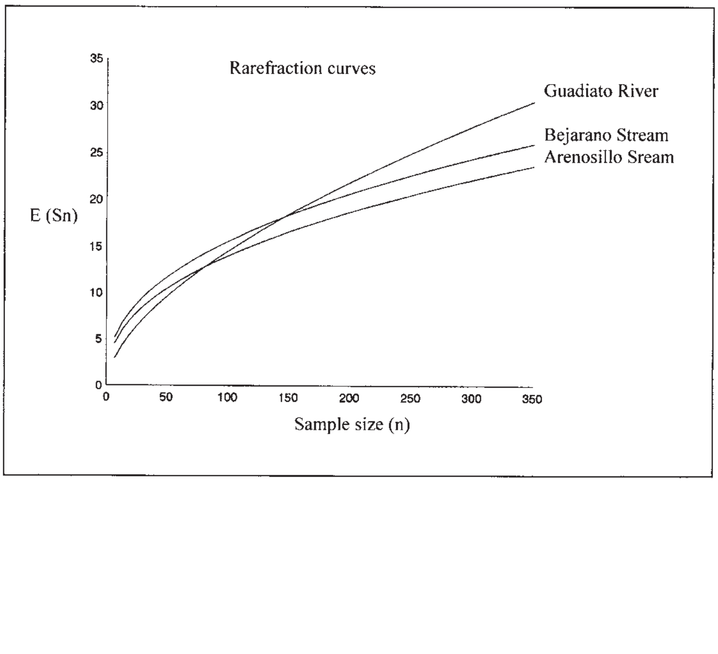

Fig. 2. – Rarefraction curves for the Arenosillo, Guadiato and Bejarano localities, showing the expected number of species as a function of sample size.

enough representative as to study the surviving strategies of the species inhabitant this kind of environments.

Sufficient data (total abundance ≥ 100 specimens and number of dissected females ≥ 50) was available to establish the respective life cycles of only nine of the collected species.

The activity patterns in field and the potential fecundity obtained for these nine species are described as follows:

Paranchus albipes (Fabricius, 1792)

Fig. 3A shows the activity curve for *P. albipes* in the Arenosillo stream obtained from the number of imagoes caught in pitfall traps. As shown, this species is active during an extended period of the year (from November to June) and remains inactive in summer (from July to September). Nevertheless, the activity graph is not uniform, since the curve drops in winter when temperatures are unfavourable.

Based upon anatomical studies of the females, we have investigated the development of potential fecundity for *P. albipes* as shown in Fig. 3B. The course of this parameter indicates that at any given time during adult activity, some females are also active from a reproductive point of view, with gonads in development or mature ova in the ovary. Notwithstanding, the most significant values of potential fecundity for this species are reached in spring, with maximal values observed in April. Thus this species can be classified as a spring-breeder.

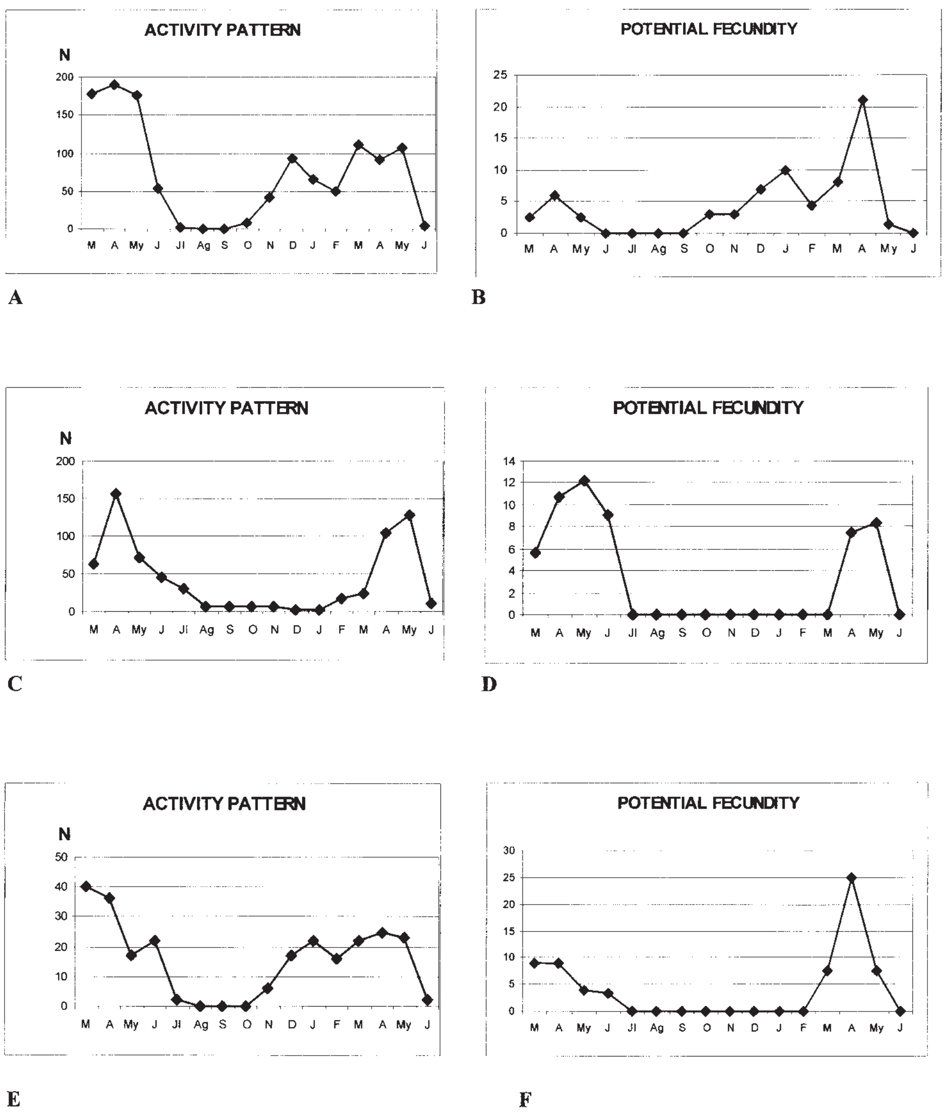

Fig. 3. – A, Field activity pattern and B, Course of potential fecundity for *Paranchus albipes* in the research area (1997/98); C, Field activity pattern and D, Course of potential fecundity for *Chlaenius velutinus* in the research area (1997/98); E, Field activity pattern and F, Course of potential fecundity for *Chlaeniellus vestitus* in the research area (1997/98).

Chlaenius velutinus (Duftschmid, 1812)

The activity pattern in field for *Chlaenius velutinus* is given in Fig. 3C. As shown, the species displays its highest level of activity in spring, aestivates later, and may be slightly active in autumn and even in winter.

From the estimation of potential fecundity shown in Fig. 3D, it may be supposed that reproduction occurs in spring and that *C. velutinus* also belongs to the spring-breeder reproductive type.

Chlaeniellus vestitus (Paykull, 1790)

Given the field activity pattern (Fig. 3E) and the course of potential fecundity for this species (Fig. 3F), it can be concluded that, like the previous species, *Chlaeniellus vestitus* is a spring breeder with a strictly defined reproductive phase.

Astigis salzmanni (Germar, 1824)

The activity cycle of *A. salzmanni* adults is plotted in Fig. 4A. The species is shown to display an extended period of activity with two peaks. The first peak occurs between April and June with a second peak at the end of autumn (November-December). The extreme climatic conditions (low temperatures in winter and dryness in summer) appear to be unfavourable for this species and could determine periods of inactivity that might be interpreted as aestivation and hibernation states. Potential fecundity (Fig. 4B) was also considered in order to elucidate which of the two previously observed peaks was a consequence of reproduction. The results suggest that, in spite of an unsignificant number of females with developing gonads in autumn, the majority of the population starts to reproduce at the beginning of spring, reaching maximum reproduction in April and May, with a sudden drop

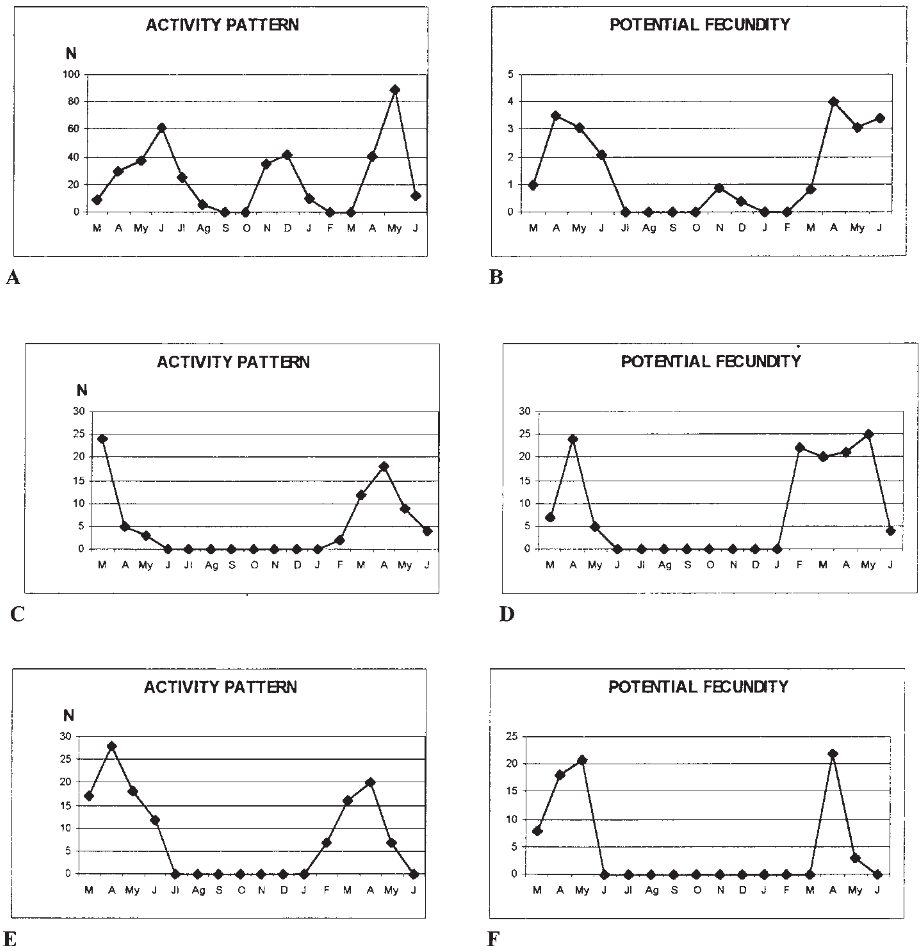

Fig. 4. – A, Field activity pattern and B, Course of potential fecundity for *Astigis salzmanni* in the research area (1997/98); C, Field activity pattern and D, Course of potential fecundity for *Melanius nigrita* in the research area (1997/98); E, Field activity pattern and F, Course of potential fecundity for *Pterostichus aterrimus* in the research area (1997/98).

after June. Thus this species may also be classified as a spring-breeder.

Melanius nigrita (Paykull, 1790)

Melanius nigrita is a silvicolous and ripicolous species whose adults display activity for only a short period of time from February to June (Fig. 4C). The potential fecundity graph for this species (Fig. 4D) runs quite parallel to the field activity pattern. It may thus be deduced that the total activity observed is due to their reproductive behaviour and that this species is also a spring-breeder.

Pterostichus aterrimus (Herbst, 1784)

The field activity pattern (Fig. 4E) and the evolution of potential fecundity (Fig. 4F) for *P. aterrimus* is quite similar to that of *M. nigrita*, with both species sharing the same reproductive strategy.

Steropus globosus (Fabricius, 1792)

The activity pattern of *S. globosus* adults in the research area peaks twice (Fig. 5A). The first peak is observed from May-June, while the second peak occurs between October and November. A morphological examination of the specimens captured in the field showed that the spring peak corresponds to the emergence (new generation) and to old imagoes (which were in gonad dormancy). The second peak is the result of reproductive activity (*i.e.* searching, mating and, particularly, oviposition behaviours). The highest potential fecundity value (Fig. 5B) was recorded at the very beginning of autumn, suggesting that this species is an autumn-breeder.

Rhabdotocarabus melancholicus (Fabricius, 1798)

A uniform trend in the field activity of *R. melancholicus* adults (Fig. 5C) was not observed, although the curve peaks twice in spring and autumn depending on the year. The anatomical studies demonstrated that this species is able to reproduce at different times of the year: females starting reproduction and gravid females bearing mature *ova* were found in spring as well as in autumn (Table II), and young beetles (tenerals and reproductive females) can be found at any time during the imaginal activity period (Fig. 5D).

Penetretus rufipennis (Dejean, 1828)

P. rufipennis is a typical species found in ripicolous environments of the SW Iberian Peninsula with a bimodal curve of annual activity (Fig. 5E). Hence, activity can be observed in autumn (October-December) and in spring (April-May) and the species remains inactive in summer and winter. Anatomical studies in females showed that reproduction occurs between November and December, with optimal reproduction in November (Fig. 5F). Our anatomical observations indicate that a large percentage (83%) of the spring population is made up of teneral and young beetles with undeveloped gonads (females). Thus of all the strictly ripicolous species recorded in the Arenosillo Stream, this is the only one displaying an autumn-breeder reproduction strategy.

Table II. – Top, Monthly reproductive state of females of *R. melancholicus*. Below, Monthly reproductive state of females of *C. velutinus* (from Cárdenas *et al.* 1999).

FEMALE STATE	M	A	My	J	Jl	Au	S	O	N	D	J	F	M	A	My	J
Young gravid	0	1	0	0	0	0	0	0	4	4	0	0	0	0	4	0
Old gravid	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Starting reproduction	0	9	12	3	8	0	0	4	0	0	0	0	0	2	10	4
Spent	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Teneral	1	3	0	0	0	0	0	0	0	0	0	0	0	6	0	0
Total	2	15	14	3	8	0	0	4	4	4	0	0	0	8	14	4

FEMALE STATE	M	A	My	J	Jl	Au	S	O	N	D	J	F	M	A	My	J
Young gravid	9	47	16	3	0	0	0	0	0	0	0	0	0	5	36	0
Old gravid	7	18	11	8	0	0	0	0	0	0	0	0	1	7	2	0
Starting reproduction	11	10	2	2	1	0	0	0	0	0	0	4	4	8	14	1
Spent	2	7	9	4	1	1	1	4	2	0	0	1	1	11	2	0
Teneral	0	5	0	8	5	2	2	0	0	0	0	0	0	0	1	1
Total	29	87	38	25	7	3	3	4	2	0	0	5	6	31	55	2

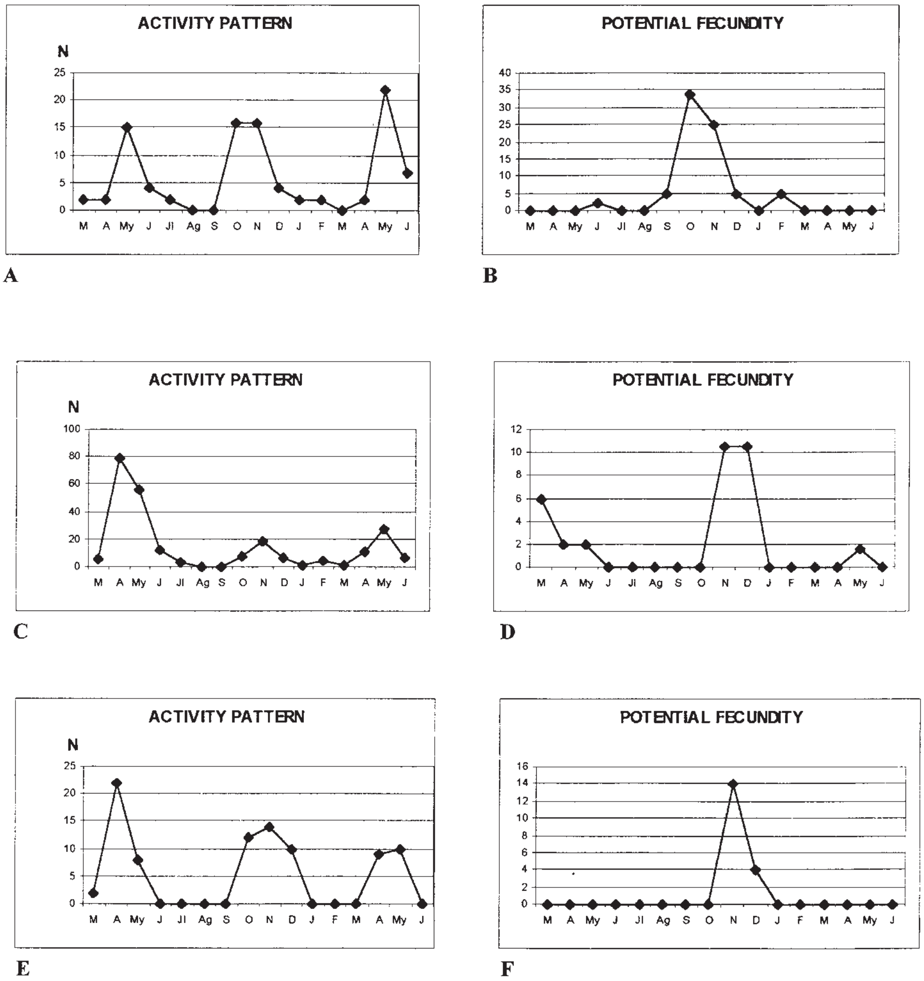

Fig. 5. – A, Field activity pattern and B, Course of potential fecundity for *Steropus globosus* in the research area (1997/98); C, Field activity pattern and D, Course of potential fecundity for *Rhabdotocarabus melancholicus* in the research area (1997/98); E, Field activity pattern; F, Course of potential fecundity for *Penetretus rufipennis* in the research area (1997/98).

DISCUSSION

According to our results, the carabid community of the Arenosillo Stream is representative of the riparian communities developed in unstable and temporary streams like those of the southern Iberian Peninsula. The Richness and Diversity values approximate other ripicolous communities such as those of the Guadiato River and the Bejarano Stream (Table I). The same assertion can be made from the Rarefraction curves (Fig. 2). So, the strategies developed for surviving in the Arenosillo could be extended to other similar environments in the southern Iberian Peninsula.

Two distinct groups were identified from all of the species recorded (n=50). The first was composed of typically riparian species belonging to the Bembidiinae, Callistinae, Oodinae, Platyninae and Pterostichinae subfamilies, while the second group was made up of somewhat generalist species typically found in forests (i.e. C*alathus granatensis*), meadows or open areas (*i.e. Campalita maderae*, *Steropus globosus*, *Macrothorax rugosus*) and cultivated fields and irrigation channels (*i.e. Pheropsophus hispanicus*), which seek refuge in the borders of the ponds of stagnant water that remain during the dry period in the stream bed.

Most of the species were caught in small number. Consequently, no data were available to establish their respective life cycles. Significant data were available for only nine of the total recorded species. To interpret the results obtained for these nine species we considered the reproduction rhythms established by Paarman (1979) for temperate zones.

Detailed information on the reproductive biology of *C. velutinus* is available from previous research (Cárdenas *et al*. 1999). This species is, moreover, one of the most abundant and representative ripicolous species in the Arenosillo community, which exhibits a spring-breeder strategy. In the prior study we concluded that *C. velutinus* centres its highest activity between April and May, when reproduction and emergence also occur and when environmental conditions are optimal. The emergence of the new generation mainly occurs in late May or June. The oviposition period for this species resulted quite long (Table II) and some females showed several maturation *ova* and egg-laying phases (females had, occasionally, been observed with *corpora lutea* and developing *ovariola* or ripening eggs simultaneously). Nevertheless, only one generation reached maturity per year. These is in agreement with Paarmann's (1979) assertion "in Temperate zones the life cycle of ground beetles is firstly determined by annual fluctuations in environmental (climatic) conditions and the species initially appear to be univoltines".

Previous research (Cárdenas *et al*. *op. cit.)* and our observations for this work indicate that C. *velutinus* is a spring breeder (Larsson 1939) with facultative gonad dormancy (depending on temperature) which is able to complete gonad maturation in both males and females during an ample range of light cycles, but always under long day conditions with favourable temperatures. This type of life strategy approaches that of spring breeders type 2 as described by Paarmann (1979). It is also similar to other ripicolous species belonging to the genera *Bembidion* (Heydemann 1962) and *Elaphrus* (Bauer 1974), which have been studied in the temperate zone.

The information obtained from field surface activity and anatomic observations suggests that the majority of strictly ripicolous species displays the same spring-breeder life strategy for surviving in unstable conditions as *C. velutinus,* with an unimodal (*Pterostichus aterrimus* and *Melanius nigrita*) or a bimodal (*Paranchus albipes*, *Chlaenius velutinus*, *Chlaniellus vestitus* and *Astigis salzmanni*) activity curve. The spring peak for both groups corresponds to the reproductive period and coincides with the maximum in the water level. The water resources ensure the high humidity level that these species requires for ovipositing and larval developing. When a second period of activity is recorded, it is located in autumn, after the first rains, and corresponds to the low surface activity of the adults from the last emergence. Later, the activity of these species decreases or becomes zero when the unfavourable conditions of winter impose hibernation.

Like other typically riparian carabids, *Penetretus rufipennis* displays a surface activity curve that peaks twice: in spring and autumn. However, the reproductive phase does not occur in spring, but in autumn. In spite of the ripicolous condition of this species, it behaves in a similar way to autumn breeders (Larsson 1939). The field and anatomical observations support the idea that they can hibernate as larvae and emerge in spring. Adult activity then decreases in summer (aestivation) and starts up again in autumn as a consequence of mating and oviposition behaviour. According to these assumptions, *P. rufipennis* could display a biological cycle similar to the autumn breeder type 4 described by Paarmann (1979). Previous research on this subject (Cárdenas 1994, Cárdenas & Hidalgo 1998a, 1998b, 2000) regarding woodland species (*Calathus granatensis, Carabus dufouri, Steropus globosus*) has shown that this type of life cycle is common for silvicolous, but not ripicolous species living in the Mediterranean thick mixed forest, common in the southern Iberian Peninsula. The results obtained for *Steropus globosus* in the Arenosillo Stream are in accordance with the above assumptions: even though the species has been captured in the margins of the Arenosillo Stream, it is a coincidental element in the riparian community which seeks refuge when environmental conditions are unfavourable. Thus, from a reproductive point of view, both species, *P. rufipennis* and *S. globosus*, behave as autumn breeders, following the same pattern of ecologically silvicolous and lapidicolous species.

Finally, *Rhabdotocarabus melancholicus* is a highly hygrophilous element that colonises different kinds of humid environments such as riverbanks, ponds or marshes and the margins of temporary streams. Our findings regarding surface activity and potential fecundity of *R. melancholicus* in the Arenosillo stream surroundings indicate that the species has an unstable annual rhythm. Initially, it is free of dormancies, being able to remain active at any time, depending on environmental factors such as temperature and, fundamentally, humidity. Nevertheless, the highest levels of activity are recorded in spring and in autumn. In our opinion, the life cycle observed for this species could be chiefly governed by humidity and temperature conditions. No reproduction has been observed in winter or summer. Young and old beetles, as well as reproductive and non-reproductive females, can be found at any time during the imaginal activity period. Gonad maturation seems to be independent of photoperiodic conditions. The life cycle of this species represents a third type of life strategy for surviving in the margins of the Arenosillo stream.

It can therefore be concluded that, at least, three different strategies are feasible for surviving in the unstable and ripicolous environments of the margins of the Arenosillo stream: the strictly ripicolous species (i. e. *C. velutinus*) are mostly spring breeders. Nevertheless, this strategy is not totally applicable by the less common species, because exceptions have been also found: *P. rufipennis* – a typically riparian element – behaves in the same way that other no ripicolous species, displaying an autumn breeder reproductive cycle. Lastly, a species with an unstable reproductive cycle (i.e. *R. melancholicus*) is also able to survive in this kind of unstable habitats.

APPENDIX – Carabid beetle species recorded in the arenosillo stream.

Campalita maderae indigator (Fabricius, 1787)
Rhabdotocarabus melancholicus dehesicola (Garcia-Paris & Paris, 1995)
Macrothorax rugosus pseudoboeticus (Lassalle, 1986)
Hadrocarabus lusitanicus gougeleti (Reiche, 1863)
Nebria (s.str.) *salina* (Rambur, 1837)
Dyschirius sp.
Perileptus areolatus (Creutzer, 1799)
Trechus obtusus Erichson, 1837
Trechus fulvus Dejean, 1831
Tachys (Paratachys) bistriatus (Duftschmid, 1812)
Tachyura parvula (Dejean, 1831)
Tachyura ferroa Kopecký, 2003
Notaphus varius (Olivier, 1795)
Trepanes (s. str.) *bedelianum* (Netolitzky, 1919)
Bembidion quadripustulatum Serville, 1821
Philochtus antoniei Puel, 1935
Princidium (Testedium) laetum (Brullé, 1838)
Princidium (Actedium) paulinoi (Heyden, 1870)
Nepha genei (Kuster, 1847)
Sinechostictus elongatus (Dejean, 1831)
Ocydromus (s. str.) *siculus* (Dejean, 1831)
Ocydromus (Peryphus) tetracolum (Say, 1823)
Metallina (*Neja*) *ambiguum* (Dejean, 1831)
Ocys (s. str.) *harpaloides* (Serville, 1821)
Penetretus rufipennis (Dejean, 1828)
Astigis salzmanni (Germar, 1824)
Poecilus (s. str.) *quadricollis* Dejean, 1828
Angoleus crenatus (Dejean, 1828)
Pterostichus (Melanius) aterrimus nigerrimus (Herbst, 1784)
Melanius (Pseudomaseus) nigrita (Paykull, 1790)
Steropus (Sterocorax) globosus ebenus Quensel, 1806
Paranchus albipes (Fabricius, 1792)
Calathus (Neocalathus) granatensis Vuillefroy, 1866
Amara (s. str.) *aenea* (DeGeer, 1774)
Dixus sphaerocephalus (Olivier, 1795)
Ophonus (Metophonus) parallelus Dejean, 1829
Acupalpus sp.
Acupalpus brunneipes (Sturm, 1825)
Egadroma marginatum (Dejean, 1829)
Stenolophus teutonus (Schrank, 1781)
Chlaenius velutinus (Duftschmid, 1812)
Chlaenites spoliatus (Rossi, 1790)
Chlaeniellus vestitus (Paykull, 1790)
Chlaeniellus olivieri (Crotch, 1870)
Lonchosternus hispanicus (Dejean, 1826)
Singilis alternans Bedel, 1905
Microlestes abeillei Brisout, 1885
Pheropsophus hispanicus (Dejean, 1824)
Brachinus (Brachynidius) sclopeta (Fabricius, 1792)
Brachinus (Brachynolomus) immaculicornis Dejean, 1826

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