Oviposition patterns in *Steropus globosus* (Fabricius, 1792) (Coleoptera, Carabidae)

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Oviposition patterns in Steropus globosus *(Fabricius, 1792) (Coleoptera, Carabidae).*— Oviposition types observed in *Steropus globosus* Fab. (Coleoptera, Carabidae) are reported. Relationships between the oviposition pattern and the survival rates during the embryonic period and the first larval instar are analysed. As environmental variables may determine the oviposition pattern, the egg viability and the duration of the developmental states, oviposition and survival tests were made under environmental and controlled conditions. The oviposition rate varies individually and also during the egg-laying period. Significant differences between the oviposition patterns could be established when the egg morphology and their viability were analysed. Fluctuations in the amount of reproductive females are more connected with their physiological state than with the different reproductive strategies.

Key words: Oviposition, *Steropus globosus*, Coleoptera, Carabidae.

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Introduction

Several studies on the dynamics of Carabid populations are directed towards quantifying the influence of the variations in oviposition and survival rates on the total members of a population and their stability through time (BAARS & VAN DIJK, 1984; NELEMANS, 1987; AUKEMA, 1991). Others focus their analysis on the circumstances conditioning a potential breeder of a species, such as environmental factors or food availability (HEESSEN, 1981; DEN BOER, 1981; LENSKI, 1984; VAN DIJK, 1994; ZANGGER et al., 1994).

To determine some of these aspects for Iberian fauna, a series of studies was carried out to assess and interpret the oviposition strategies of *Steropus globosus* Fab., one of the most common carabid beetles in southern Spain. The activity patterns, the duration of the egg-laying period and the establishment of the life-cycle of the species is known from previous research (CÁRDENAS & BACH, 1988a, 1988b, 1992a, 1992b). The frequency and rate of oviposition did not remain constant throughout the period, suggesting that *S. globosus* present different reproductive strategies.

In this paper the quantification, distribution and viability of the egg output of *Steropus globosus* Fab. (Coleoptera, Carabidae) and their possible relation with the survival rate during the first stages of development is studied and discussed. The influence of environmental variables on the oviposition pattern as well as on the viability and duration of the first stages of development was evaluated by oviposition and survival tests under different conditions, in order to determine the extent to which the potential breeders of the species can be affected.

Material and methods

The study period lasted from October, 1995 to April, 1996.

Cultures of *Steropus globosus* Fab. were made in which pairs (1♂, 1♀) of the species were kept in cylindrical glass containers (6.5 cm diameter, 8 cm height) with a 5 cm thick moistened substrate of peat and plentiful supply of maggots as food. A group of 20 pairs was kept under outside conditions while a similar group was placed in a culture room at controlled temperature, humidity and photoperiod (the conditions of both cultures are shown in fig. 1 and table 1). The substrate from each container was renewed and the eggs found were removed three times per week. Each egg was kept isolated in a petri-dish with moist carbon filter paper and under similar conditions to those of the imagoes in order to determine the rate and time of hatching.

For each experimental group, the number of fertile females (those which laid eggs) was 16.

To characterize the egg output, the following criterion was applied: oviposition was considered massive if $n > 25$, numerous if $10 \leq n \leq 25$ and sparse if $n < 10$; n is the number of eggs of one oviposition, that is the number of egg laid per one female and sampled at each moment that they were removed.

The total number of each type of oviposition (sparse, numerous and massive) for the whole sampling period is recorded in table 2.

In order to detect the morphometric variations between eggs for each type of oviposition, the length and width of a number of randomly chosen eggs were measured. The number of eggs measured was 31, 17 and 20 for samples originating from sparse, numerous and massive ovipositions, respectively. The sample size of these eggs was determined by the availability of them in each case. With these morphometric data, corresponding statistical parameters were determined and subsequently compared using the non-parametric statistic Z, corresponding to the Wilcoxon-Mann-Whitney test (STEEL & TORRIE, 1992).

From the larvae hatched in each culture, a sample was taken from which n is shown in table 5 as initial number of larvae in stage one. Each larva was kept in a separate petridish, under conditions similar to those of the imagoes during the monitoring of the development.

The hatching times of the eggs and their viability (percentages of hatched eggs) were compared, as were the duration and survival rate of the first larval stage obtained in each culture. The differences between these data were also quantified by the non-parametric statistic Z.

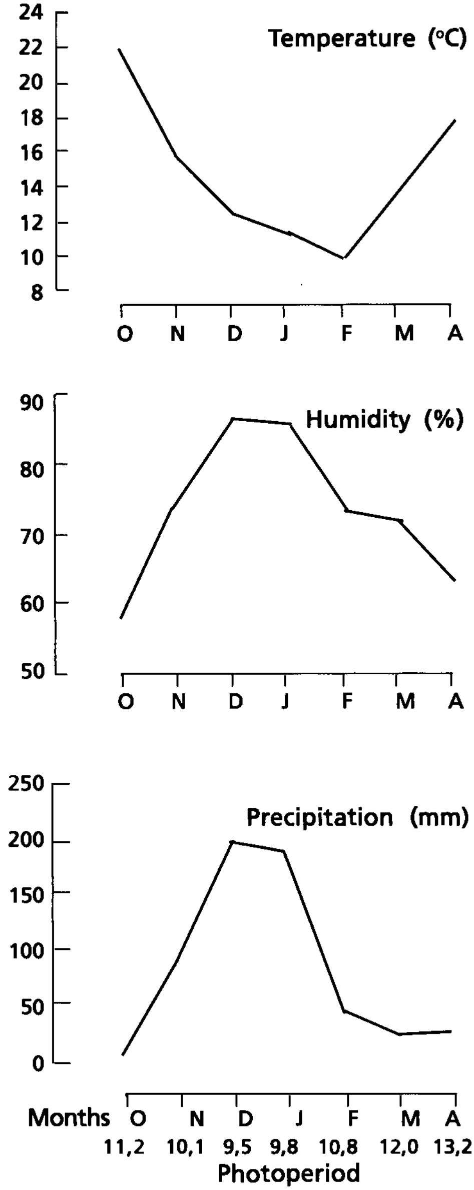


Fig. 1. Monthly data of mean temperature, relative humidity, precipitation and photoperiod for the culture in environmental conditions (1995/96).

Datos mensuales de temperatura media, humedad relativa, precipitación y fotoperiodo correspondientes al cultivo sometido a condiciones ambientales (1995/96).

Only the egg stage period and the first larval stage were considered since the next developmental stages (second, third and pupal stages) are influenced by several factors inherent in the form of culturing (handling, monoalimentary diet, viruses and other pathologies, parasitation,...) and have, therefore, no relation with the viability of the eggs. This could adversely affect the interpretation of the results.

Results

Quantification and characterization of the ovipositions

Figure 2 shows the duration of the reproductive period and the distribution of ovipositions for each female integrated in the experimental groups. The information contained in these graphs is interpreted as follows:

- The period of the potential fecundity (ovaries containing mature eggs) of *S. globosus* is long, both with regard to individuals and the population as a whole. It lasts from November to March but centres on the winter months. Furthermore, oviposition is substantially prolonged under controlled conditions of temperature, humidity and photoperiod.

- The oviposition pattern (length of the total oviposition period, the moment when

Table 1. Temperature (T), relative humidity (H) and photoperiod (Ph) for cultures in controlled conditions.

Temperarura (T), humedad relativa (H) y fotoperíodo (Ph) correspondientes a los cultivos sometidos a condiciones controladas.

	Oct 95-Nov 95		Dec 95-Apr 96	
	Day	Night	Day	Night
T	20±1°C	15±1°C	17±1°C	12±1°C
H	80-90%	80-90%	80-90%	80-90%
Ph	12h	12h	10h	14h

Table 2. Analysis of ovipositions, under controlled and environmental conditions: ♀ Number of fertile females; O. Number of ovipositions; E. Number of eggs; $\bar{O}$. Average numer of eggs per oviposition; $\bar{F}$. Average numer of eggs per fertile female; %O. Percentage of ovipositions; %E. Percentage of eggs; %H_o. Percentage of hatched-eggs in each oviposition type.

Análisis de la oviposición en condiciones controladas y en condiciones ambientales: ♀ Número de hembras fértiles; O. Número de puestas; E. Número de huevos; $\bar{O}$. Número medio de huevos por puesta; $\bar{F}$. Número medio de huevos por hembra fértil; %O. Porcentaje de puestas; %E. Porcentaje de huevos; %H_o. Porcentaje de huevos que eclosionan en cada tipo de puesta.

	♀	O	E	$\bar{O}$	$\bar{F}$	%O	%E	%H_o
Controlled conditions								
Sparse	14	117	220	1.9	15.7	95.1	36.4	0
Numerous	2	2	25	12.5	12.5	1.6	4.1	0
Massive	3	4	359	89.7	119.7	3.2	59.4	67.8
Environmental conditions								
Sparse	16	76	137	1.8	8.6	93.8	37.6	2.2
Numerous	1	2	30	15	30	2.5	8.2	0
Massive	3	3	197	65.7	65.7	3.7	54.1	57.2

it begins and the number of eggs for each oviposition) varied between individuals. Throughout the reproductive phase, several oviposition types can be distinguished according to the number of eggs (see methodology for ascertaining the classification criteria of ovipositions).

- In the majority of cases, the amplitude of the oviposition period was determined by the sparse ovipositions since this type prevail.

- No strict association between each female and one oviposition type or between one oviposition type and the phase of the reproductive period was observed, although on closer consideration of each case, the largest ovipositions tended to appear at the beginning of the oviposition period.

Morphometry of the eggs

Table 3 shows values of length and width of eggs for each type of oviposition. Few differences in the width were observed. The comparison of lengths is given in table 4. Contrary to expectations, the number of eggs in each oviposition did not limit length and the eggs from the massive ovipositions were clearly the largest ones.

Analysis of the oviposition

Oviposition was analysed under controlled and environmental conditions (table 2). Results led to the following conclusions:

- While the culture conditions did not appear to affect the proportion of females with respect to the oviposition type, the total fecundity in each reproductive group (expressed as the total number of ovipositions, total number of laid eggs, average number of eggs per oviposition or average number of eggs per female) appeared to be higher under controlled temperature and photoperiod conditions.

- The proportions of ovipositions and eggs

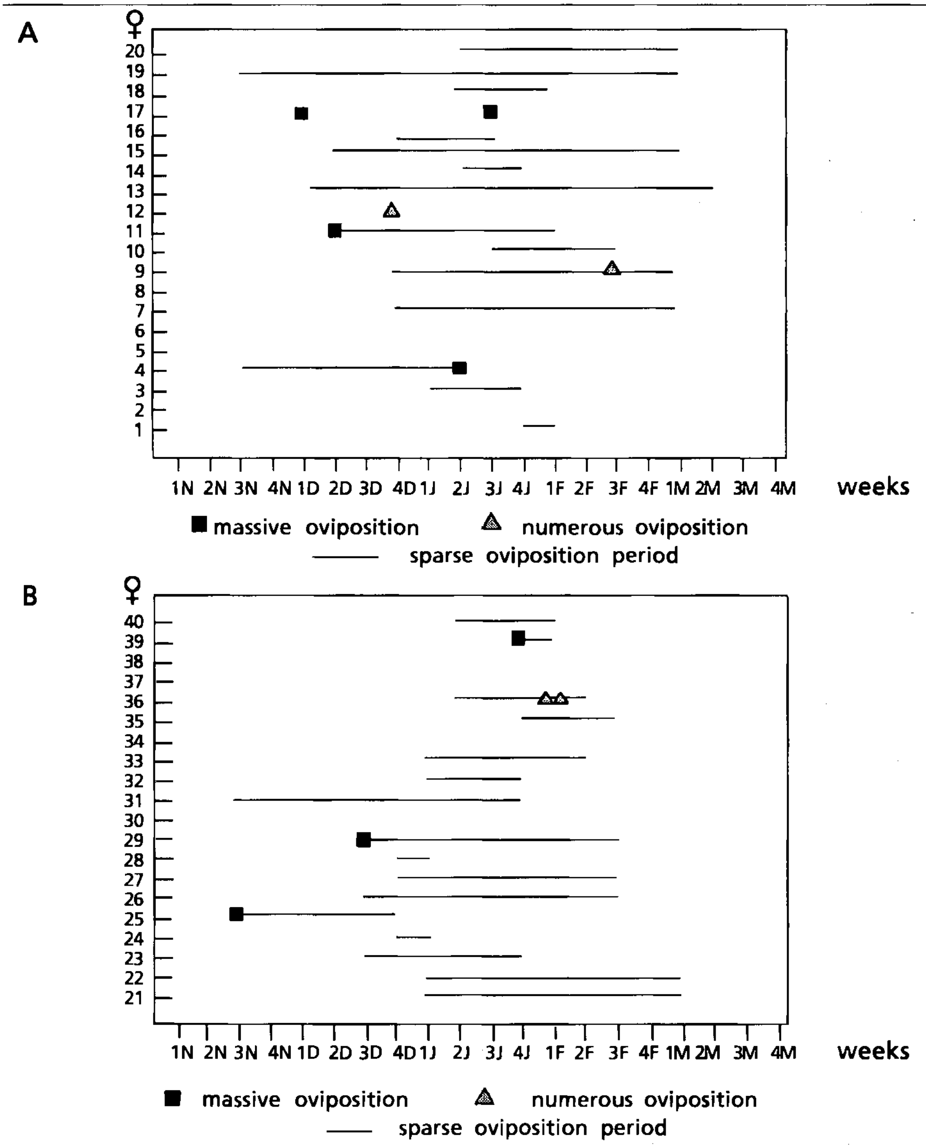


Fig. 2. Size and pattern of oviposition of each female in the experimental group kept under controlled conditions (A) and environmental conditions (B) in 1995/96. Continuous line indicates the time between the first and the last sparse ovipositions, and the symbols indicate the moment when a massive or numerous oviposition occurred. (Number of fertile females in each case 16.)

Amplitud y patrón de puesta de cada hembra del grupo experimental correspondiente a 1995/96 sometido a condiciones controladas (A) y a condiciones ambientales (B). La línea contínua indica el período comprendido entre la primera y la última puesta dispersa, y los símbolos indican el momento en que se produce una puesta masiva o numerosa. (Número de hembras fértiles en cada caso 16.)

Table 3. Morphometrical values for eggs coming from the different oviposition types. (Scale: 1 unit = 0.035 mm.)

Valores morfométricos de los huevos procedentes de los distintos tipos de puesta. (Escala: 1 unidad = 0,035 mm.)

	n	$\bar{x}\pm$s.d.	Min.	Max.
Sparse ovipositions				
Length	31	64.6±3.4	58	71
Width	31	29.2±1.5	26	33
Numerous ovipositions				
Length	17	63.2±2.4	59	67
Width	17	27.9±1.2	26	30
Massive oviposition				
Length	20	68.5±2.8	63	75
Width	20	28.9±1.2	27	31

Table 4. Comparison of the length of eggs coming from the different ovipositions types by the Wilcoxon-Mann-Whitney test (* $P \leq 0.05$).

Comparación de la longitud de huevos procedentes de los distintos tipos de puesta mediante el test de Wilcoxon-Mann-Whitney ($P \leq 0,05$).*

Ovipositions	Z	P
Sparse-numerous	0.99	0.32 (n.s.)
Sparse-massive	-3.84	1.21×10^{-4}(*)
Numerous-massive	-4.43	9.62×10^{-6}(*)

corresponding to each oviposition type remain similar in the two different culture conditions, and the sparse ovipositions always exceeded 90% of the total, whilst neither the numerous nor the massive ovipositions exceeded 5%. However, the highest proportion of eggs corresponded in both cases to massive ovipositions and was between 54 and 60%. The percentages of eggs for numerous and sparse ovipositions ranged from 4.1-8.2 and 36.4-37.6%, respectively.

- The only viable eggs are those from massive ovipositions, with hatching values of around 60%. A minimum percentage (approx. 2%) of eggs from sparse ovipositions were hatched under environmental conditions.

Temporal course of the oviposition

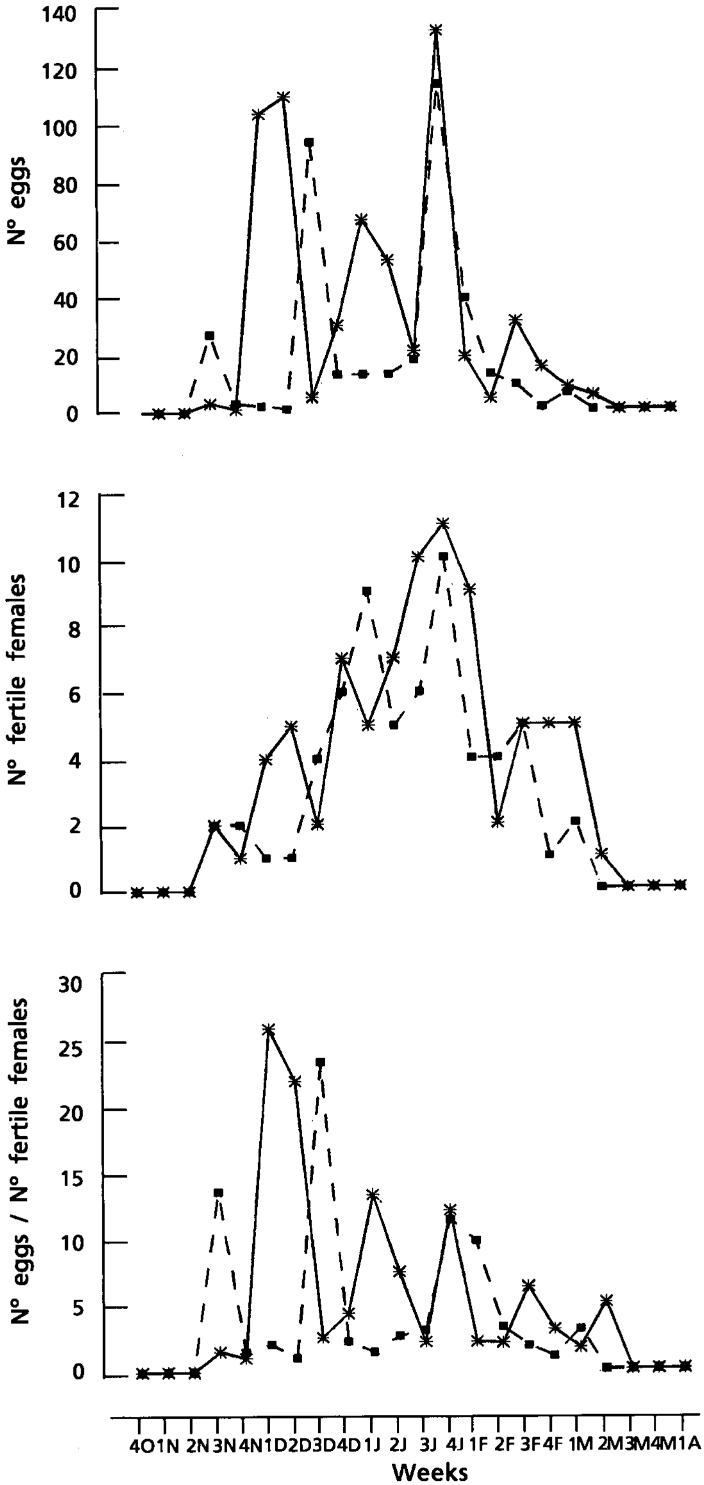
In order to analyse the temporal course of oviposition under the different study conditions, the following were considered: the weekly fluctuation of the number of eggs, the number of fertile females and the relation between both parameters as a measurement of the oviposition rate (fig. 3). It was concluded that:

- During the oviposition period, the number of eggs oscillated considerably between consecutive weeks. Maximum levels were occasionally reached, but values were mostly relatively low. This trend occurred under both environmental and controlled conditions, although it was more apparent in the latter.

- Concerning the number of fertile females, there is a progressive increase reaching a maximum between January and February. In all cases, the oviposition period is centred in win-

Fig. 3. Temporal course of the oviposition considering the weekly number of eggs, the number of fertile females and the number of eggs/number of fertile females under controlled (✱) and environmental conditions (■).

Evolución temporal de la oviposición según el número semanal de huevos, el número de hembras en oviposición y el número de huevos/número de hembras en oviposición en condiciones controladas (✱) y en condiciones ambientales (■).


140
120
100
80
60
40
20
0
Nº eggs
12
10
8
6
4
2
0
Nº fertile females
30
25
20
15
10
5
0
Nº eggs / Nº fertile females
4O 1N 2N 3N 4N 1D 2D 3D 4D 1J 2J 3J 4J 1F 2F 3F 4F 1M 2M 3M 4M 1A
Weeks

ter, independently of the rearing conditions.

- The ratio of the number of eggs per fertile female fluctuated considerably, with the highest values being reached during the first half of the oviposition period which coincided with the first maximum number of eggs, and tended to normalize towards the second half of the period. The number of eggs per female was nearly always higher under constant photoperiod and temperature cycles.

Effect of culture conditions on development

A quantification has been made of the effect of culture conditions based on the duration and survival rate of the first developmental stages (table 5).

A constant photoperiod and temperature cycle increased oviposition, and also had a significantly accelerating effect ($Z = -9.083$; $P = 5.286 \times 10^{-20}$) on the embryonic development. Thus, the average time of incubation was reduced to almost half of the time and was homogenized (s.d. = 1.25) compared with the data of the experimental group at environmental conditions (s.d. = 6.35). With regard to the survival rate at this stage, hatching percentages were between 30 and 40% in both cases, and were only slightly affected by culture conditions.

With regard to the length of the development time and survival chances of the first larval stage, larvae under laboratory conditions reached the second stage in significantly less time ($Z = -6.208$; $P = 2.686 \times 10^{-20}$) and with a higher percentage of survival (73.33% compared to 54.68%) than those kept at environmental conditions.

Table 5. Duration and survival rate for the first developmental stages in controlled (C) and environmental conditions (E): N. Number of eggs; L1. Initial number of larvae at 1st stage; L2. Number of larvae at 2nd stage; S. Survival rate (%); X(It). $\overline{X}$ incubation time (days); X(t-1I). $\overline{X}$ time 1st intermoult (days);

Duración y tasa de supervivencia de los primeros estadios del desarrollo en condiciones controladas (C) y en condiciones ambientales (E). (Para abreviaturas, ver arriba.)

	Conditions	
	C	E
N	604	364
X(It)±sd	11.86±1.25	21.90±6.35
S	38.7	31.1
L1	60	64
X(t-1I)±sd	17.79±5.45	28.88±6.64
S	73.33	54.68
L2	44	35

Discussion

As in previous reports on the dynamics of populations, it is important to quantify the fluctuations in numbers of individuals. These numbers are determined by rates of mortality, natality, emigration and immigration for each generation, and influenced by biotic (competition, predation, pathologies, ...) and abiotic (temperature, humidity, photoperiod, food, ...) factors which reinforce certain strategies.

Significant fluctuations in the course of fertility, i.e., different sizes of oviposition (number of egg laid) in females of the same generation with similar potential fecundity (number of eggs contained by the ovaries), suggest that the reproductive plasticity of the species enables it to develop different patterns of oviposition as a response to the influences of exogenous factors.

Previous research provided knowledge about the activity pattern, the reproduction period and the reproductive potential, and the establishment of the life cycle of *Steropus globosus* in the southern Iberian peninsula. This species behaves as an "autumn breeder" (THIELE, 1977) needing a high level of humidity and low temperature for its reproduction and development. It adapts to climatic conditions in the temperate zone, with gonadal dormancy during the summer, thus shifting its reproduction period (CÁRDENAS & HIDALGO, 1998). It can thus be considered as a "winter breeder" (PAARMANN, 1973). The present study highlighted a great variability in the oviposition rate, the significance of which is analysed from the perspective of the previous considerations and on the basis of the results shown.

If the criteria of GRÜM (1984) are applied, the fecundity of *S. globosus* is relatively low. Together with its apterism (which determines its low dispersal ability) this situates this species close to K strategists (BRANDMAYR, 1983) in spite of its abundance in the study area. However, this general trend towards a moderate or low fecundity is not uniform and there are distinct individual differences in the size of ovipositions and different oviposition patterns throughout the reproductive period even when some of the factors considered as determinants of the fecundity rate, such as temperature (VAN DIJK & DEN BOER, 1992) or kind of food (VAN DIJK, 1986), remain constant.

From the different oviposition patterns observed, a morphometric analysis of eggs from different types of ovipositions indicates that, contrary to what might be expected, the size of the oviposition does not limit the size of the eggs: the largest eggs are present in the massive ovipositions. According to ERNSTING & ISAAKS (1994) "greater length/massive ovipositions" relation suggests that only the massive ovipositions contain viable eggs and that the fertilized eggs are mostly the bigger ones.

When the hatching rates of eggs from the different oviposition types were analysed, the population size of the following generation in *S. globosus* was especially determined by the proportion of massive ovipositions, since only eggs from these ovipositions were significantly viable. This was independent of the culture conditions. The proportion of females which oviposited eggs in each type of oviposition was not affected by the abiotic factors considered in this study since it remained on about the same level in different experimental conditions. However, the duration of the oviposition period, the mean number of eggs per oviposition and the mean number of eggs per female were higher in the group maintained at controlled temperature and photoperiod conditions. This agrees with the results obtained by VAN DIJK & DEN BOER (1992) for *Calathus melanocephalus* L. and *Pterostichus versicolor* Sturm and by AUKEMA (1991) for *Melanocephalus* Group of *Calathus*, in the sense that the length of the oviposition period and the size of egg production were favourably affected by temperature (always within a range). This could be interpreted as an adaptative strategy which compensated for the negative effects on oviposition by certain factors related with increases in temperature such as environmental desiccation.

No oviposition type is characteristic for any particular female and may alternate throughout reproductive activity. Although the sparse ovipositions (low number of eggs) are those which delimit the oviposition period for each female, as they predominate and are more prolonged in time, the real reproductive potential of this species tends to be found at the beginning of the oviposition stage when most massive ovipositions are concentrated.

Survival in the embryonic phase seems to be determined by the oviposition type (sparse, numerous or massive), but this did not affect the incubation time, the percentage of success, or the duration of the first larval stage. The constant cycles of photoperiod and temperature accelerate and increase the development, a finding previously observed in other species of carabids (VAN DIJK, 1983).

Finally, the biological significance of the oviposition patterns observed in *S. globosus* can not be determined from the results. However, the different oviposition models observed may not be the result of different reproduction strategies connected with the fluctuating environmental conditions but rather due to an adequate change in the physiological state of the females (i.e. their fertility) throughout the laying period.

Resumen

Patrones de oviposición en Steropus globosus *(Fabricius, 1792) (Coleoptera, Carabidae)*

Se estudian los patrones de oviposición y la relación de éstos con la tasa de supervivencia durante la fase embrionaria y el primer estadio larvario de *Steropus globosus* Fab. (Coleoptera, Carabidae). Además, considerando que las variables ambientales (fig. 1,

tabla 1) pueden determinar el patrón de puesta así como la viabilidad y duración de los distintos estadios del desarrollo, se han realizado test de oviposición y supervivencia en condiciones ambientales y en condiciones controladas (tabla 5). Los resultados permiten afirmar que la tasa de oviposición varía individualmente y durante el período de puesta (figs. 2, 3), y que existen diferencias significativas entre los tipos de puesta desde un punto de vista morfométrico (tablas 3, 4) y en cuanto a la viabilidad de los huevos (tabla 2). Sin embargo, la interpretación de los resultados lleva a concluir que éstos no responden a diferentes estrategias reproductivas en *S. globosus*, sino más bien a fluctuaciones en la fecundidad que dependen del estado fisiológico de las hembras.

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