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Seasonal activity and reproductive biology of the ground beetle *Carabus dufouri* (Coleoptera: Carabidae)

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Abstract. This paper concerns the life-cycle of *Carabus dufouri* Dejean 1829, one of the most representative species of *Carabus* in the south of the Iberian Peninsula. The study is based on data of the annual activity patterns in the natural habitat, on anatomical observations related to the sex and age of the specimens, on the reproductive condition of females and, finally, on the results of laboratory rearing experiments carried out to study the oviposition patterns and the course of development of immature stages. The results indicate that *C. dufouri* shows the annual rhythm of autumn breeders. However, the rhythm may also be related to the winter-breeder type of North Africa.

INTRODUCTION

Organisms in their habitats are confronted with seasonal fluctuations of physical and biotic factors. Consequently, in order to survive, their development, reproduction period, and population dynamics have to be adapted to these environmental fluctuations. Adaptation of species life cycle to the local environment involves a series of physiological and behavioural features, including growth rate, annual number of generations, dormancy, adult longevity and synchronization between the reproduction period and environmental conditions, fecundity, optional polymorphism and population dynamics (Neumann, 1986).

Carabid beetles are a group of insects sufficiently well-known as to allow the study of their life-cycles in relation to environmental factors. The copious literature published on this subject in the past few years (i.e., Kurka, 1972; Hůrka, 1973, 1986; Thiele, 1977; Paarmann, 1979a, b, 1990, 1994; Den Boer & Den Boer-Daanje, 1990), indicates that the biology of carabid species respond on one hand to their habitat peculiarities, and on the other to adaptations evolved in their evolutionary history.

It is generally accepted that in the Temperate zones the life cycles of ground beetles are governed by annual oscillations in climatic conditions. Also, phylogenetically closely related species show basically the same developmental type, and in the different evolutionary trends a similar spectrum of reproductive rhythms can be found, suggesting a process of convergent evolution (Paarmann, 1979a). Thus, the conditions in each environment can result in the existence of a given developmental cycle, rather than affecting its evolution (Hůrka, 1986; Cárdenas et al., 1996).

Most studies of this kind have been done in the Temperate zone of Central Europe and some also in North Africa (Paarmann, 1975), but in transitional zones, such as the Iberian Peninsula, they are scant (de los Santos et al., 1985). Therefore, we considered that a research programme designed to study the predominant annual life cycles in meridional Europe was necessary to understand the evolution and relationships between the different reproductive rhythms of carabids. In order to fill in this lack of information we started to work on the life-cycle of Iberian carabid species (Cárdenas & Bach, 1992a, b; Cárdenas, 1994; Cárdenas & Hidalgo, 1995; Cárdenas et al., 1996); we followed the criteria provided by Paarmann (1975), Thiele (1977) and Makarov (1994).

This paper investigates seasonal activity, age structure, duration and survival of immature stages of *Carabus dufouri* Dejean 1829.

Most Central European *Carabus* species are “autumn-breeders” (Thiele, 1977), while the North African Carabini studied are mostly “winter-breeders”, showing a temperature-photoperiodic influence on the gonad dormancy (Paarmann, 1979b). The cycles of “autumn-breeders” and “winter-breeders” represent, respectively, the northern and southern variants of a type of annual rhythm characteristic of the Temperate zone, which should find their optimal display in the Mediterranean ecosystems. Therefore, a series of studies have been started on reproductive biology of the *Carabus* species whose distribution area also includes the south of the Iberian Peninsula.

MATERIAL AND METHODS

Species

According to Deuve (1994), *Carabus dufouri* is part of the *Mesocarabus* Thomson, 1875 subgenus which constituted a Tyrrhenian line widely distributed in Central and South Europe, reaching the north of Africa (Morocco), and having its greatest representation in the Iberian Peninsula with 3 species and 42 subspecies (sensu Forel & Leplat, 1998). In spite of this diversification, only *C. dufouri* has colonized the southern Iberian region to the south of the Guadalquivir River and it may be considered as a replacement species of *C. lusitanicus* of which different subspecies occupy the rest of the Peninsular area (Toulgoet & Lassalle, 1983).

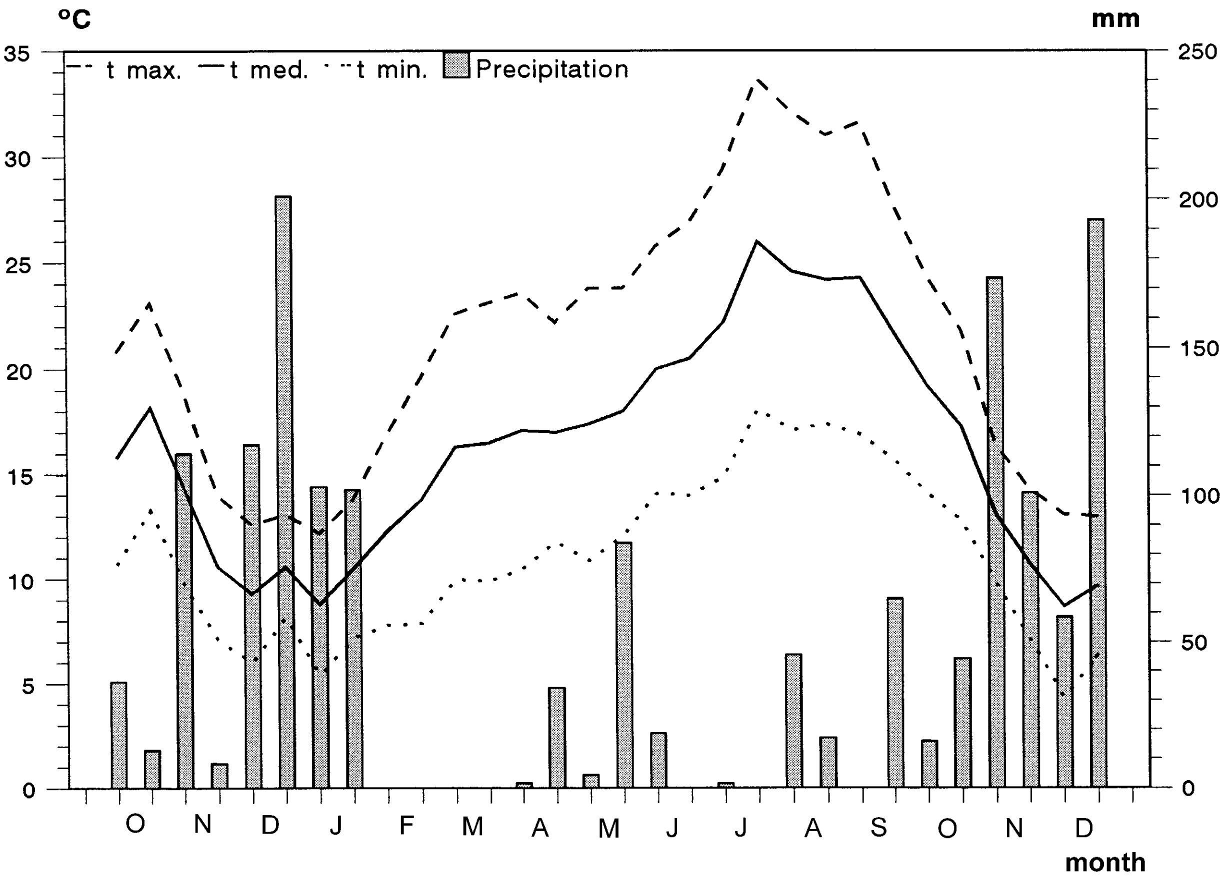

Fig. 1. Climatogram of the research area for the sampling period (October 1996 to December 1997).

C. dufouri may be found at very different altitudes (from low altitude to 2,500 m) in open areas or in forests so it can be considered to be an eurytopic species.

The study area

The sampling was done in the Subbéticas Mountains Natural Park, which is integrated into the Bética Chain of mountains which shape the South of the Iberian Peninsula and are a group of massifs of middle altitude (1,000–1,200 m as middle term) of a calcarean nature that form a karstic landscape of great ecological interest. They are surrounded by cultivated lowland (olive groves). The dominant vegetation is typical of a Mediterranean thick mixed forest, the *Paeonio coriaceae-Quercetum rotundifoliae* association, with a high level of degradation where bushes and pastures prevail. The climate is of the Mediterranean type, but with a clear Continental influence, belonging to a Mesomediterranean bioclimatic belt but, in the highest altitudes it may be considered as a Supramediterranean belt (Rivas-Martínez, 1987) (Fig. 1).

Study methods

Annual activity pattern

The annual activity pattern of *C. dufouri* was recorded in a typical mediterranean mixed forest (La Nava, Subbéticas Mountains Natural Park, 30S UG 81 49 U.T.M. coordinates, 1,000 m altitude) from October 1996 until the end of 1997, using twenty permanent pitfall traps each consisting of two concentric cylindric plastic pots (1,000 cc volume and 8 cm ∅), using the outside of them as a container and the inside one as a recipient. Pitfall traps were mid-filled with a mixed solution of acetic acid as bait and ethanol (70°) as preservative, buried up to the top end, partially covered to avoid inundation and randomly distributed in the area considered. Systematic sampling was carried out at fortnightly intervals.

Anatomical observations related to the sex and age and to the reproductive condition of the females

Age was determined by testing the softness of the integument and the extent of mandible wear, of the cephalic and thoracic bristles, and of the tibial spines and tarsal claws. Adults were placed in the following age classes: callows (or immature, with a very soft integument and unworn structures), young imagoes (with a hard integument but scarcely worn structures) and old imagoes (hard integument, and fairly worn structures, so that they were probably over one year old). In the case of females, the gonadal stage and potential fecundity were also checked. Using the same criteria as Cárdenas (1994), after dissecting the females, they were classified as:

- Teneral females (T), callow beetles, which ovaries are not yet developed.
- Immature females (IF), young beetles, ovarioles not differentiated.
- Pre-reproductive females (PRF), maturing females, with oocytes clearly diferentiated but without mature ova or corpora lutea.
- Gravid females (G), beetles with mature ova but without corpora lutea.
- Females ending reproduction (FER), imagoes with mature ova and corpora lutea.
- Spent females (S), imagoes with regressed ovaria, without mature ova, but with corpora lutea.

The reproductive biology of *C. dufouri*

Laboratory rearing experiments were carried out in culture rooms, under different conditions of temperature, humidity and

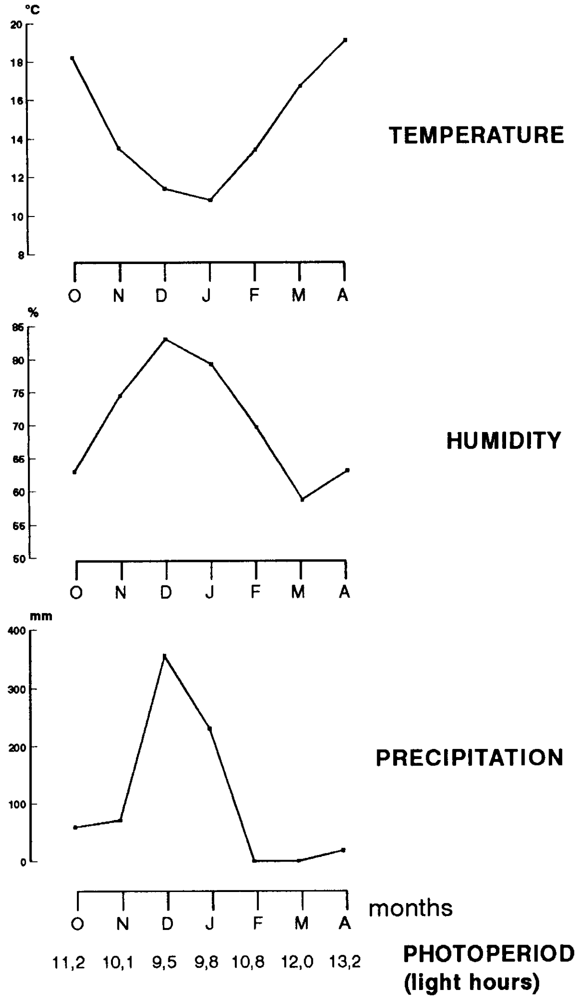

Fig. 2. Monthly data of mean temperature, mean relative humidity, precipitation and photoperiod for the outdoor culture.

photoperiod in order to study their effect on the reproductive biology, oviposition patterns and developmental details of *C. dufouri*.

We started with ten reproductive groups or parentals (a male and a female in each) sampled in La Nava in October 1996. Previous anatomical studies referring to ovarian state indicated that *C. dufouri* had begun reproduction in this month. Each reproductive group was kept in a cylindrical glass container (12 cm diameter, 14 cm height) with 5 cm thick moistened substrate of peat and a plentiful supply of maggots as food and arranged, in a shaded place adjacent to the laboratory. To indicate environmental conditions we include the monthly temperature mean, relative humidity, monthly precipitation and approximate photoperiod (Fig. 2).

Eggs were kept at 18–20°C and in full-darkness.

For larval rearing we followed the methodology proposed by van Dijk (1973) and Mols et al. (1981). Two groups of larvae were arranged in different conditions to determine the possible effect of temperature on the duration of development, and survival rate of immature stages. The first group was kept outdoors, while the second group was maintained under controlled conditions (20 ± 1°C; ≈ 85% R.H.; 12L : 12D).

The following parameters were recorded:

Potential fecundity. For a specific time period, this was established as the mean number of eggs per fertile dissected female; considering a fertile female to be one which had at least one mature ovum in ovaria.

Realised fecundity. This was defined as the mean number of eggs laid per female in a time period.

Statistics

Finally, for analyzing and comparing the results, the Mann-Whitney non-parametric statistical test was applied (Zar, 1984).

RESULTS

Temporal activity pattern

The temporal activity of adult *C. dufouri* is plotted in Fig. 3, showing two maxima, the first between April–June and the second between October–December. The periods of peak activity are not homogeneous due, probably, to sampling effects. When the activity for males and females are considered in isolation, their respective curves run parallel to those of the summed data, although the males start moving and peak in activity sooner than females. The sex-ratio is favourable for females independently of the time of year. The low activity periods are associated with extreme climatic conditions (winter or summer), but some specimens can be found at these times.

Age-class distribution of *C. dufouri*

Following the criterion previously specified (see Material and Methods section) anatomical studies enabled us to establish three age-classes as represented in Fig. 4. The majority of the members of the population corresponded to individuals belonging to the last generation. At the end of the winter (February– March), the majority of specimens disappear (probably dying) and only a very small fraction of old imagoes survive until the next spring, and are found alongside the new generation. At the beginning of the spring, the first freshly emerged callow imagoes were caught. Emergence peaks in April but is spread out until July. Adults in different states of tegumentary hardening and physiological maturation are found during the main activity period.

Temporal change of female reproductive state

For the course of the reproductive state of females see Fig. 5. The dissected females were teneral, immature, prereproductive, gravid, females ending reproduction or spent females (see definitions in Material and Methods). In the annual cycle there is no repetition of any physiological stage; this is typical for a univoltine species.

After the unfavourable summer, in mid September prereproductive and gravid females were simultaneously found, which indicates that after aestivation the ovaria start differentiation and development. The oviposition period begins at the end of September and continues until the middle of January when the females finishing reproduction disappear, and spent females are present in February and March. Later, most of them probably die and are replaced by teneral and immature females of the new generation.

The course of the oviposition

To estimate the reproductive potential the number of ripe eggs in the ovaria throughout the oviposition period was related to the eggs laid.

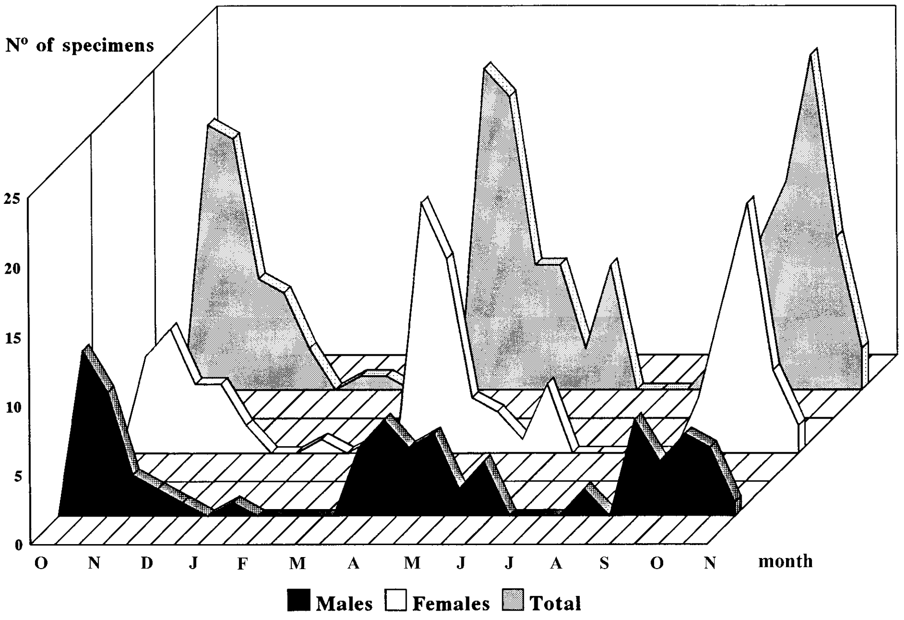

Fig. 3. Field activity pattern of *C. dufouri* in the study area (1996/97).

On the basis of an observation of dissected females and the number of eggs laid in the rearing experiments, it was possible to evaluate temporal change in oviposition during the entire breeding period. The number of ripe eggs in the ovaria was considered to be potential fecundity, while the number of eggs laid expressed realised fecundity.

Potential fecundity did not experience great fluctuation (Fig. 6). The last females with mature eggs were found at the end of December but in January the formation and ripening of eggs seem to cease.

In relation to realised fecundity, the fortnightly average values approximate those of potential fecundity and the length of both periods (when egg maturation and egg deposition occurs) is similar; nevertheless, a delay of approximately one month occurs between both processes. The oviposition period was quite long, taking in the whole of the autumn and the first days of winter. The average number of eggs per oviposition for each female ranged from 1.25 to 5.62 (Table 3) and the maximum number of eggs from one oviposition event was 12.

Nevertheless, when the regression between the values of both fecundity estimates is calculated, no significant correlation is found (r = –0.74; P = 0.26). On the other hand, if from the number of ripe eggs found in the ovarian the corresponding number of eggs laid (estimated fecundity) is calculated by the Grüm equation (Grüm, 1984) neither between potential fecundity/estimated fecundity nor realised fecundity/estimated fecundity significant

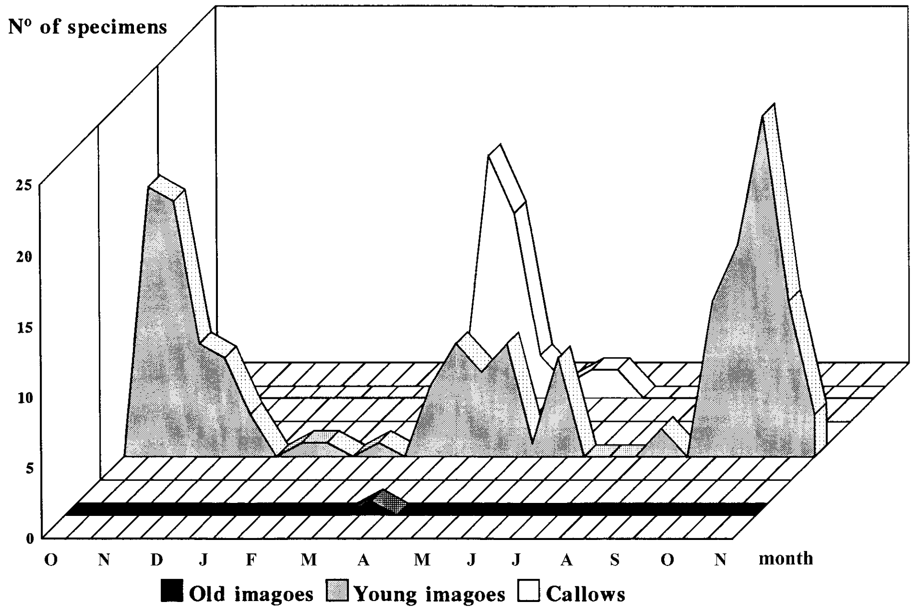

Fig. 4. Age-class distribution of *C. dufouri*.

Table 1. Development of *Carabus dufouri* under controlled (C.C.) and outside (O.C.) conditions.

	C.C.	O.C.
Eggs		
Initial number of eggs	173	
Number of larvae I	119	
Average incubation time (days)	12.13	
Standard deviation	0.80	
Survival rate (%)	68.78	
First instar		
Initial number of L-I	59	60
Number of larvae II	47	49
Mean time for first instar (days)	12.56	19.08
Standard deviation	4.10	3.10
Survival rate (%)	79.66	81.66
Second instar		
Initial number of L-II	47	49
Number of larvae III	40	47
Mean time for second instar (days)	9.25	18.54
Standard deviation	2.84	4.50
Survival rate (%)	85.11	95.92
Third instar		
Initial number of L-III	40	47
Number of pupae	32	40
Mean time for third instar (days)	23.03	50.61
Standard deviation	7.42	9.71
Survival rate (%)	80	85.11
Pupal stage		
Initial number of pupae	32	40
Number of imagoes	10	25
Mean time for preimaginal stage (days)	10.50	16.36
Standard deviation	0.85	1.38
Survival rate (%)	31.25	62.51

corelations are obtained (r = 0.12; P = 0.69 and r = 0.25; P = 0.68, respectively).

There were important differences in the number of eggs laid by individual females (Fig. 7). Most of them had their egg-laying periods between November and December, right in the middle of the oviposition time established for *C. dufouri* in the previous paragraph. The total number of eggs laid per fertile female in the rearing experiment (under outside conditions) ranged from 2 to 67. A low reproductive rate for *C. dufouri* might be expected for a *Carabus* species, compared with other Carabidae (Casale et al., 1982).

Breeding experiments: Biology of immature stages

As happens in most carabids, the development of *C. dufouri* goes through three larval instars and a preimaginal pupal phase. Duration and survival rates of each stage will be analyzed on the basis of environmental conditions (Table 1).

To improve egg-hatching and ensure a suficient number of eggs, the eggs were kept in full-darkness and at constant temperature. For this reason, no available data exist about the incubation time and the survival rate for embryonic period under environmental conditions. Nevertheless, under controlled conditions the mean incubation time was around 12 days and the survival rate reached 69%.

Rearing of larvae under different environmental conditions provided data on the duration and mortality of each stage (Table 1). There was high survival in all stages, especially in the second larval instar, whose survival rate exceeded 95%. The first and third larval instars had sur-

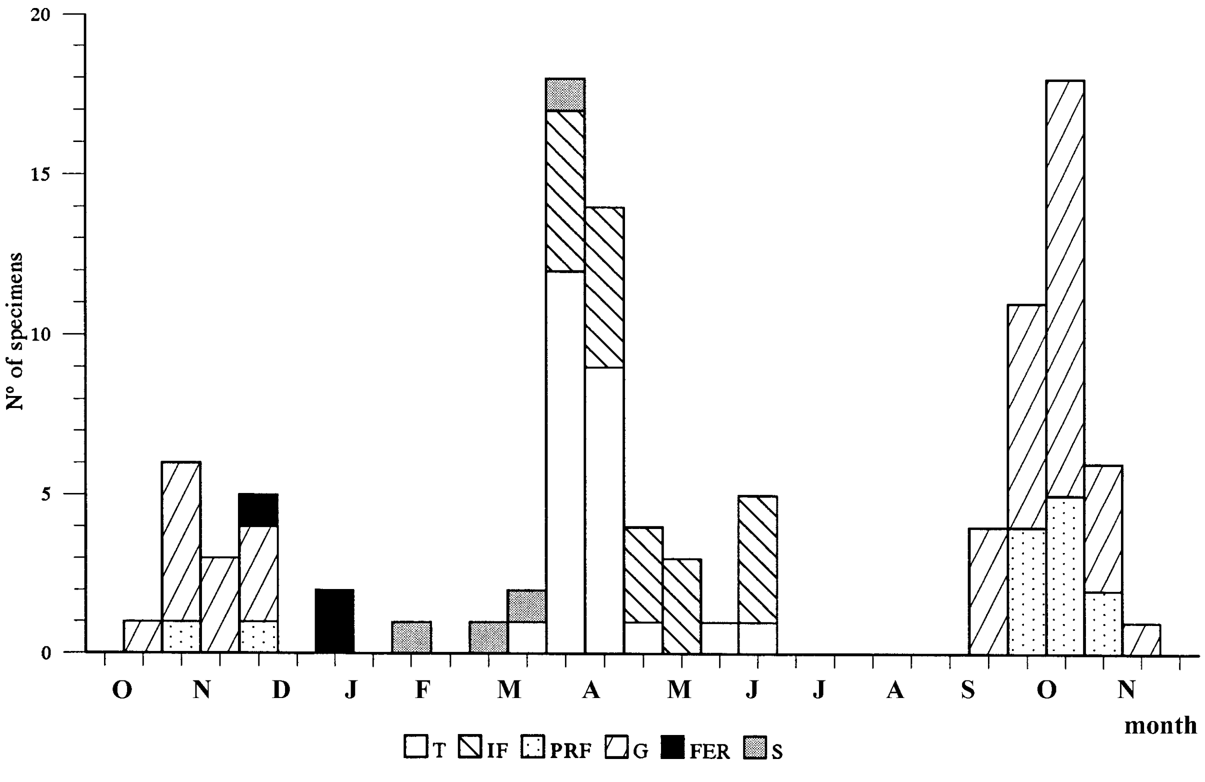

Fig. 5. Temporal change in *C. dufouri* female reproductive state. T – teneral females; IF – immature females; PRF – prereproductive females; G – gravid females; FER – females ending reproduction; S – spent females.

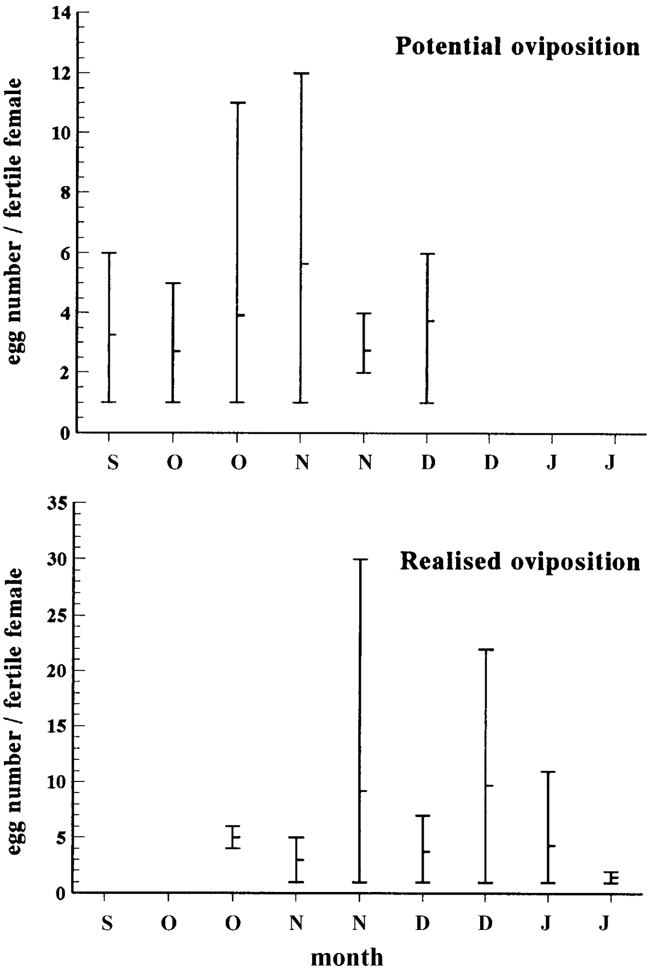

Fig. 6. The course of the oviposition in *C. dufouri*: Potential oviposition (mean, maximum and minimum values of egg number per fertile dissected female). Realised oviposition (mean, maximum and minimum values of laid egg number per fertile female).

vival rates of between 80 and 85%, while the preimaginal stage did not exceed 63%.

With regard to the duration of the different developmental stadia, the first and second larval instars were similar (≈20 days). However, the third larval stage lasted for almost 50 days. The mean time for the preimaginal stage was again shorter lasting approximately 16 days. In summary, mean total developmental time was 104.6 days, and the total survival rate exceeded 40%.

To test the effect of temperature, a parallel culture was kept under controlled conditions (see Fig. 2) starting from a similar number of larvae in first instar, kept in equal substrate conditions and supplied with an equivalent amount of food.

Table 2. The "Z" values of Mann-Whitney-Wilcoxon Test and significance levels for differences in development time in *C. dufouri*.

	Z	Significance (P)
First instar	6.794	$1.092E^{-11}$
Second instar	7.465	$8.348E^{-14}$
Third instar	6.780	$1.206E^{-11}$
Preimaginal stage	4.373	$1.224E^{-5}$

Table 3. Mean, standard deviation, maximum and minimum number of eggs per oviposition for each fertile female from culture.

Female no.	$\overline{X}$	σ	Max.	Min.
1	3.35	2.41	9	1
2	2.75	1.70	5	1
3	2.66	1.52	4	1
4	3.20	2.04	5	1
5	1.25	0.50	2	1
6*	2	–	–	–
7	2.66	1.52	4	1
8	2.16	1.94	6	1
9	5.62	4.27	12	1

* Only one oviposition.

Substantial differences can be observed in relation to the duration and the survival rates of each instar (Table 1). In all stages the development was shortened and survival reduced (mean total developmental time: 55.34 days, total survival rate: 16.95%). To evaluate the significance of the differences observed between the two experimental groups the Mann-Whitney-Wilcoxon test was applied. The Z values and the respective significance levels are recorded in Table 2. Very significant statistical differences occur when the mean values of developmental time of each stage are compared, strongly suggesting that temperature influences development rate.

Also, an additional fact is gleaned from the laboratory study when the duration of the developmental stages is related to the breeding period. In Fig. 8 (A and B) the course of the experiment (days) is related to the larval development time (from LI–LIII) and duration of the prepupal stage (L–III to Pupa). In both graphs a shortening at the end of the breeding period can be observed even when culture conditions are kept constant. This fact is shown if the regression of the duration of the different stadia is calculated over time ($r = -0.43$, $P = 0.006$ and $r = -0.56$, $P = 0.001$ respectively).

The same situation was recorded for outdoors (Fig. 8 C and D), but a better regression and a higher slope are obtained when the temperature also affects the duration of the developmental instars ($r = -0.56$, $P < 0.0001$ and $r = -0.89$, $P < 0.0001$ respectively).

DISCUSSION

In Temperate Zones the life-cycle of ground beetles is firstly determined by annual fluctuations in environmental (climatic) conditions and, consequently, they are likely to be univoltines. Our results show that *C. dufouri* has a single generation each year and that its life-cycle belongs to autumn-breeders (sensu Thiele, 1977). The species shows a marked rhythm in activity and requires enough humidity and relatively low temperatures for oviposition and development. In the South of the Iberian Peninsula, the summer is an unfavourable season for *C. dufouri* when it shows the lowest surface activity, adapting itself to climatic conditions by taking refuge under trunks and stones

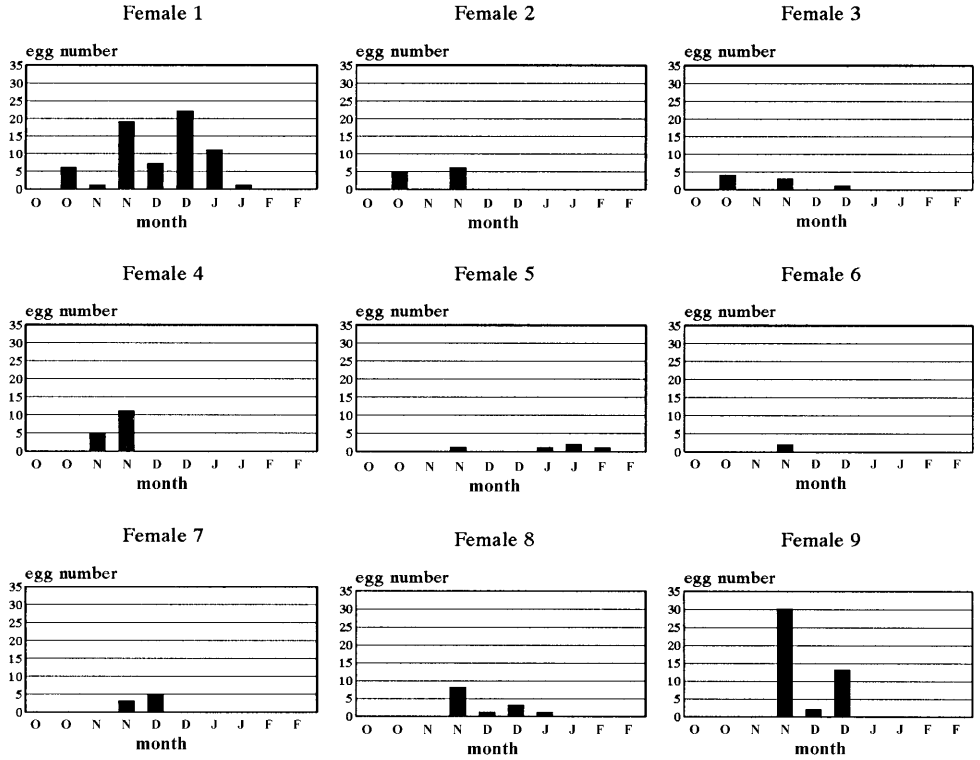

Fig. 7. Oviposition course of each female from culture expressed as laid egg number for fortnightly periods.

probably in a state of gonadal dormancy (aestival parapause, Thiele, 1969). It is known that for species showing this developmental form, dormancy is terminated by changes in photoperiod from long day to short day. Thus, at the beginning of September the imagoes renew their activity, the males approximately two weeks earlier than the females. This delay is predictable when reproduction starts since the searching-activity anticipates oviposition. Whenever the activity of both sexes coincides, the sex ratio is female biased. This last fact may be associated with the effect of the pitfall-traps on the aggregation of individuals (different for males than for females), but it may also be interpreted as a manifestation of a real numerical difference that tends to compensate for scant dispersal ability (due to the absence of wings) and the low reproductive rate of this species, as will be commented on in the next paragraphs.

To evaluate the reproductive potential of *C. dufouri,* the average number of laid eggs/female in the reproductive period has been estimated and compared with those of other *Carabus* species available in the literature: Scherney (1959) estimates for *C. ullrichii* Germar, 22 eggs/♀/season, for *C. granulatus* Linné, 41 eggs/♀/season, for *C. cancellatus* Illiger, 45 eggs/♀/season; Zetto-Brandmayr (1981) indicates an average value of 30–40 eggs/♀/season – maximum 82 – for *C. creutzeri* F.

Our results for *C. dufouri* give values of 19.44 eggs/♀/season and 6 ovipositions/♀/season (σ = 21.84 and σ = 5.61 respectively), the average number of eggs/oviposition being 3.06 (σ = 2.33). These data together with those mentioned in the previous sections and included in Table 3 confirm that the species has a low reproductive rate but a high probability of developmental success (nearly 70% of the eggs hatched and, under outside conditions, 50% of them completed development). If the reproductive potential is estimated following the Grüm (1984) method based on the ripe-eggs found in the ovaria between November–December (when centred on the oviposition, since not enough data are available for the total egg-laying period), it gave a similar value (18.04 eggs/♀) although those deposited at the beginning or at the end of the reproductive season (October, January respectively) are not considered and in any case they would have little influence on the outcome.

The lack of a linear correlation between the values of the potential oviposition, the real oviposition and those calculated from Grüm's equation is explicable because the value of n (number of ripe-eggs found or the number of eggs laid by the culture females) are insufficient in all cases; so it is not possible to obtain definitive conclusions in this regard.

The establishment of the age classes led us to affirm that the majority of the specimens active in autumn had emerged the previous spring and belonged to the new generation. The oviposition activity peaks in mid-autumn, when females in maturation state and gravid females are the only components of the female population. In December gravid females and females ending reproduction are found together in pitfall-traps and the first spent females are trapped in January. The progressive substitution of the different kinds of reproductive females shows the evolution of the oviposition phases. The surface activity ceases sooner in males than in females; in December, few or no males are caught in traps.

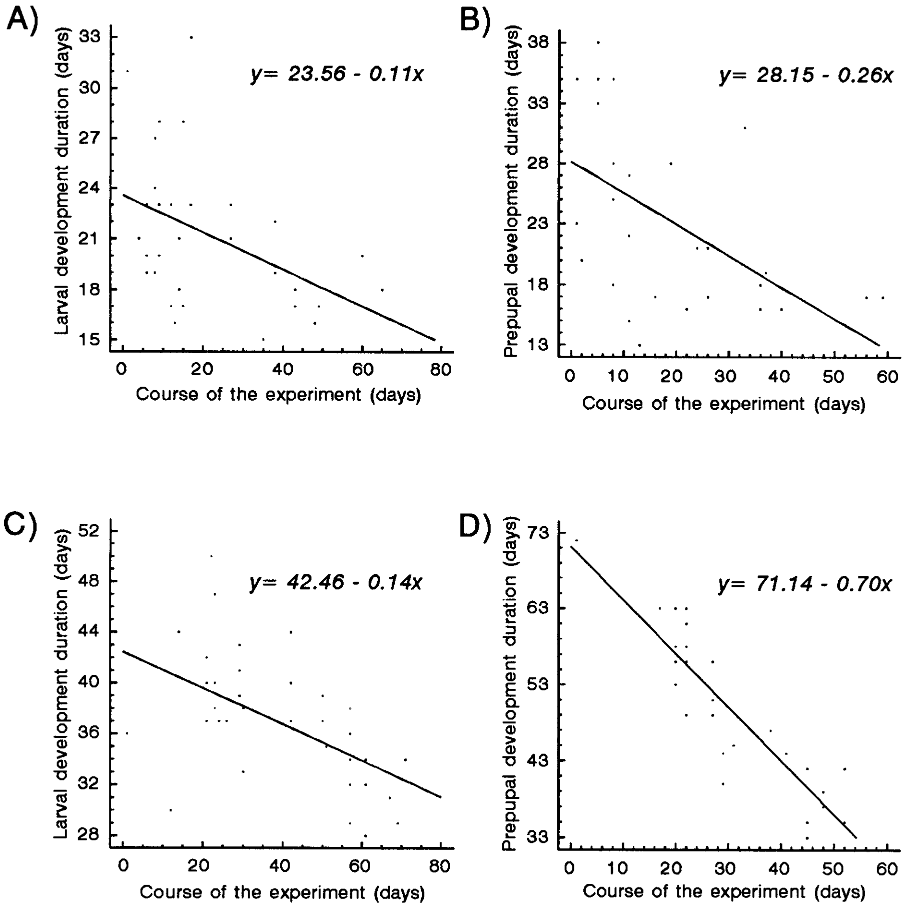

Fig. 8. Linear regression of the duration of the developmental stages over the course of the breeding experiments: A) For the two first larval stages kept under controlled conditions. B) For prepupal stage kept under controlled conditions. C) For the two first larval stages kept under outside conditions. D) For prepupal stage kept under outside conditions.

The new generation emerges in mid-spring, without going through an obligate diapause in any of the immature stages, as has been demonstrated by the cultures carried out under different experimental conditions. In both cultures, full development was possible, but at constant temperature the development rate was faster than in the outdoor culture, completing all the stadia in approximately half the time (55 days). The literature data indicate that humidity and temperature are the most limiting factors for carabid larval development. As the relative humidity was similar in both cultures (70–80%) it seems clear that the temperature was the principal factor. On the other hand, temperature also exercised a negative influence, since in the laboratory the mortality rate was doubled (41.66% of the first larval instar reached the imaginal stage under outside conditions, while only 16.95% did the same at constant temperature). Nevertheless, survival was similar for larval instars (66.67% outdoors and 54.25% under controlled conditions), the pupal stage being clearly affected by temperature (62.5% as compared to 31.25%). High humidity and temperature in culture favoured the proliferation of acari that attacked the pupae, as the immobile stage is particularly vulnerable. Later it was verified that for pupae taken off the substrate and isolated in an aseptic medium (sterile sand) their probability of reaching the adult stage increased and was similar to those pupae kept outdoors. In conclusion, temperature accelerates development, but does not decrease the viability of individuals.

In the field, the duration of the preimaginal stages (approx. 100 days) is confined to the winter period in which the adults show scarce or no surface activity. In spring, the new generation emerges and is only coincident with a few specimens of over one year of age. Later, as the season passes, and depending on the local or climatic particularities, the imagoes will go into a state of inactivity, ending the life-cycle of *C. dufouri*, as is recorded in Fig. 9. Our experiments do not indicate which environmental factor induces this developmental pattern; a subsequent paper will be devoted to this topic.

In any case, these results are in contrast to what Hůrka (1986) found for the Temperate zone autumn breeders, i.e. that it was obligatory to go through a temperature controlled larval dormancy in winter to complete their development. According to the same author, habitat and its microclimatic factors limit the occurrence of certain types of annual reproduction rhythms but do not cause their evolution. Nevertheless, according to the findings of Paarmann (1979a, b) it is possible to establish clear evolutionary relationships between certain types of annual

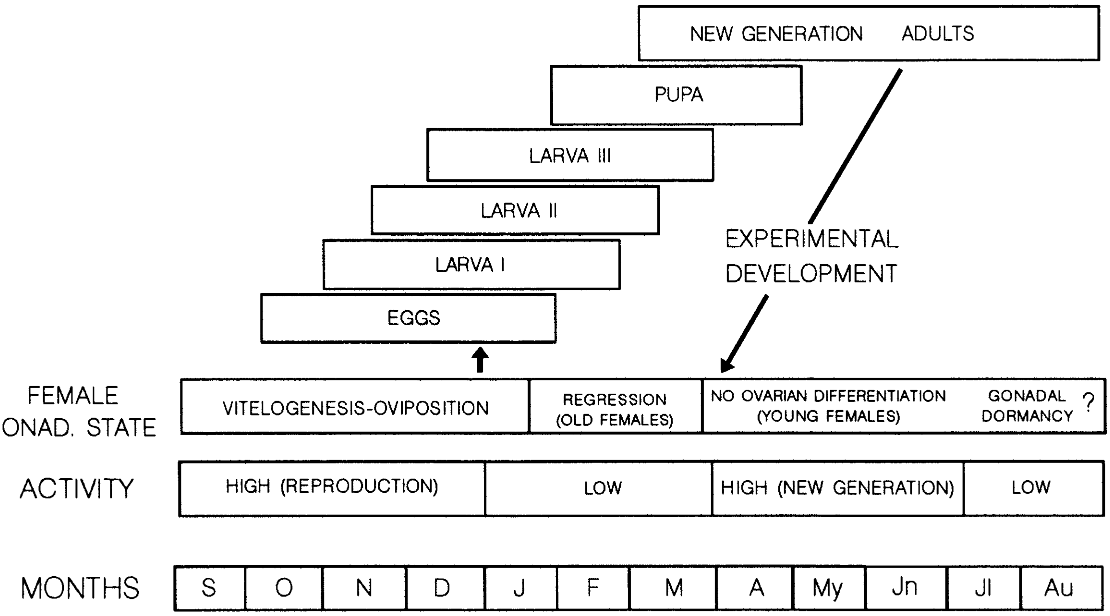

Fig. 9. Life cycle of *C. dufouri*.

cycle-life. It seems to have been well demonstrated that the annual rhythm of autumn-breeders (with gonad dormancy during aestivation and temperature controlled larval dormancy in winter, Paarmann, 1979a) is in some way connected to that of the winter breeders of the north of Africa (with gonad dormancy during aestivation and first indication of a temperature controlled larval dormancy in winter), and these cycles are the extreme (northern-most and southern-most) variants of one type of annual reproduction rhythm which perhaps finds its optimal expression in the Mediterranean region. In effect, the detailed study of the activity, in the different stadia, of *C. dufouri* shows an intermediate life-cycle type supporting Paarmann's assertions, because it basically corresponds to the type 4 of autumn breeders, but is also related to that of the winter-breeders due to the temporal delay in the period of maximum surface activity of adults and the larval development free of obligatory interruptions.

Besides the cited temporal delay and the extent of the reproductive period, the results indicate that a shortening of the duration of developmental stages at the end of the breeding time is independent of the rearing conditions. This fact may be interpreted as a synchronization in the emergence of the new generation because the particular climatic conditions in the studied area (in late spring) hasten the completion of the life-cycle. In this sense, Paarmann (1979b) verified that the shortening, even the suppression of developmental stages is one of adaptative strategies acquired by carabid beetles to survive in dry habitats and extreme aridity.

Finally, when the developmental cycle of *C. dufouri* is compared with those of other species closely related taxonomically, also belonging to the *Mesocarabus* subgenus, where the annual periodicity has been reported, i.e. *C. lusitanicus* and *C. problematicus*, differences are seen. The life cycle of *C. lusitanicus*, also in the South of the Iberian Peninsula (Cárdenas & Hidalgo, 1995), is similar to that of *C. dufouri*, but a slight temporal delay in oviposition time is observed in *C. lusitanicus* in respect to *C. dufouri*, as well as some asynchronisms in the duration of the preimaginal stages and, also, in the extent of the emergence time of the new generation. These phenomenon may be adaptative responses to the particular microclimatic conditions inherent to the altitudinal differences between the respective natural areas of origin (Sierra Morena and Subbéticas Mountains).

The developmental cycle of *C. problematicus* in northern England (Houston, 1981) is different from that of *C. dufouri* in southern Spain. Even though both species are autumn breeders (Larsson, 1939), the activity pattern in the field varies, with *C. problematicus* inactive in winter and *C. dufouri* in summer, probably as a consequence of the geographical location of their distribution areas. As a result, *C. problematicus* behaves as a larval hibernator while the adults of *C. dufouri* go through an aestivation period. Moreover, *C. problematicus* has a biennial life cycle, but the majority of *C. dufouri* individuals live for a year in our research area.

On the other hand, in Holland (van der Drift, 1951) and in the south of England (Greenslade, 1965), adults of *C. problematicus* emerge in the spring, aestivate during the summer and breed in the autumn. This is similar to the cycle observed for *C. dufouri* in the Iberian Peninsula.

In summary, the data referred above support the statement that carabids living in the Temperate zone show climatic adaptations which affect the duration and the strategy of each developmental stage and alter their life cycles independently of phylogenetic relationships.

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