

Life cycle and population ecology of the cave cricket *Dolichopoda geniculata* (Costa) from Valmarino cave (Central Italy)

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SUMMARY

A *D. geniculata* population inhabiting a natural cave at low altitude near seashore was followed during two years. The population size, distribution in three age classes, spatial distribution, feeding habits were recorded. The life-cycle was found semivoltine, with overlaps between next cohorts in each age class. A comparison to other *Dolichopoda* showed that the population of Valmarino cave is one of the best adapted to cave life, and this may be related with both historical and present geographical and ecological conditions of the cave.

INTRODUCTION

In Italy *Dolichopoda* cave crickets inhabit both natural caves, and newly opened artificial cavities. Populations from most of the species belonging to this genus can be found in either type of cave, even though natural and artificial caves differ in several ecological factors and in the age of the colonization events (Capolongo, 1966; Baccetti & Capra, 1970; Baccetti, 1982).

Previous studies on the genetic structure of several *Dolichopoda* species have stressed the relatively high genetic divergence existing even between geographically close conspecific populations (Allegrucci et al., 1987). It is therefore expected that physiological and morphological adaptations to either natural or artificial caves could be established and maintained particularly in isolated populations.

The aim of this study is to analyse in detail several ecological, phenological and demographic characteristics of a *D. geniculata*

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population from a natural cave, in order to compare them with similar data from artificial cave populations and to highlight possible alternative adaptive strategies.

MATERIALS AND METHODS

Valmarino Cave is a natural cavity located 15 m above sea level on the Tyrrhenian coast near Terracina (Latium). The cave consists of a series of horizontal galleries in calcareous sandstone. The galleries are smooth with almost no fissures and speleothems. These physical features together with the small dimensions of the cave make the by-eye observation of the cave community much easier than in other limestone caves. A detailed topographic, lithological and climatological description of the cave, with a list of the actual fauna can be found in Carchini et al. (1982a). Using topographical methods, the Valmarino cave has been completely mapped and its inner surfaces calculated; the floor surface was 464 square meters and the wall and ceiling surface was 1244 square meters. On the basis of the physical features of the galleries, the cave has been divided in seven sectors (Fig. 1).

The «density plot» method (Seber, 1973) was employed to assess the absolute number of individuals (N) in the population. Permanent counting sites have been assigned in all cave sectors, but only on the cave walls and ceilings, since the cave crickets are rarely found on the floor. The Valmarino cave population was followed for two years. During the first year (May 1973 - April 1974) the population was sampled 9 times over a 341 square meters area. During the second year (May 1974 - April 1975) ten samplings were carried out over a 623 square meters area. The cave crickets were counted at the same time by 3 observers, proceeding from the entrance to the end of the cave. According to Seber (1973) the population size N was calculated by: $N = N^o/p$, where N^o is the total number of the counted crickets, p is the ratio between observed surface and total surface of wall and ceilings.

On the same dates of density plot samples the Valmarino population was estimated also by mark-recapture method. Crickets to be marked were captured wherever found in the cave. After capture was completed, a small spot was painted on each individual on the prothorax. Recapture was undertaken 48 hours later. Population

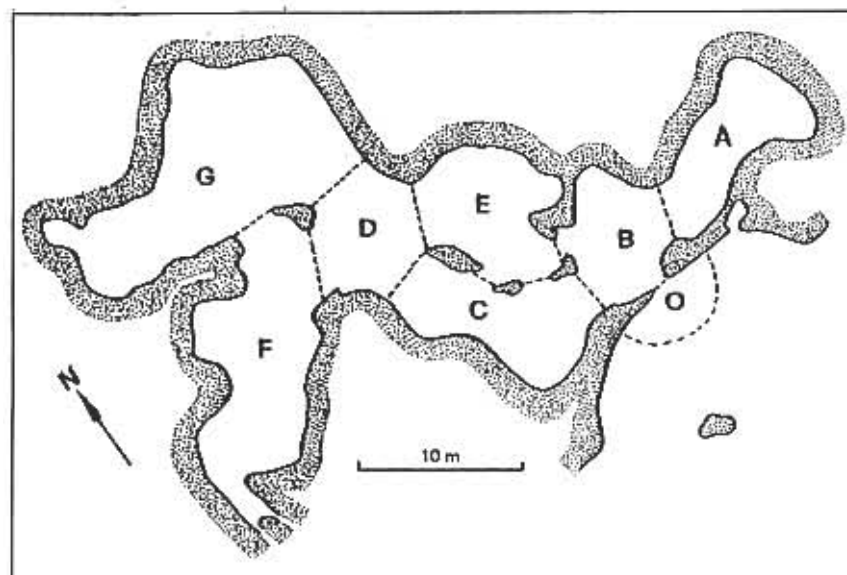


Fig. 1 — Map of Valmarino cave. A to G, inner sector; O outside sector.

size N was calculated according to Bailey (1951) by $N = M(T+1)/(R+1)$ where M is the number of marked individuals, T is the number of individuals caught on the second day and R is the number of individuals marked the first day and recaptured on the second day.

The population size (N) estimates obtained by the density-plot method were very similar to the one obtained by the mark-recapture method. Because mark-recapture estimates have larger confidence intervals than the density-plot ones, in the following we will chiefly consider the latter. Further details of both estimates of N are reported in Carchini et al. (1982b).

At sampling each individual was assigned to one of three age classes based on mature-sex features and size. These classes included the adults (A), nymphs of determinable sex, usually longer than 7 mm (excluding appendages), called sub-adults (SA) and smaller nymphs of indeterminable sex, called young (Y). It was impossible from field observations to exactly determine the instar of nymphs. However, from laboratory data on post-embryonic development of

other *Dolichopoda* populations it could be argue that the Y class include the first four instars, and the SA class the remaining five, being the whole nymphal development characterized by nine instars (Di Russo et al., 1987). The absolute number of individuals included in each age class was estimated using the density plot method. The mobile mean (of order 3) was employed to study the seasonal variation in number of each age class and population size. To measure the degree of age heterogeneity the Evenness Index J' was used, being $J' = H'/H \text{ max}$, where H' is the well known Shannon diversity index $H' = -\sum p_i \log p_i$ and $H \text{ max}$ is the same index, calculated for an equal division of specimens into the three age classes.

Information on the time span of each age class was obtained from mark-recapture data. Since the mark is lost at next moult, the time between the marking date and the last observation of that marked individual is an estimate of the time between two following nymphal moults. Conversely, for the adults that span is an estimate of the adult longevity. Because this method can only provide underestimates, we considered as instar spans or adult longevity the longest observed times.

In order to study the spatial distribution of cave crickets in relation to their distance from the cave entrance, the number of individuals found in a near entrance area (A + B sectors, sampling surface 135 square meters) was compared with that of those in a inner topographically similar area (F sector, sampling surface 105 square meters).

A faecal pellet analysis in *D. geniculata* Valmarino population was carried out from periodical samples accounting for one yearly period (June 1979 - June 1980). The faecal pellets were obtained by individuals caught and isolated in the cave. The pellets were fixed in 70% alcohol and then opened and prepared for microscopic analysis.

Information on mating behaviour, diet and predatory habits was gathered by direct observation during samples between May 1973 and April 1975, and also from scattered observations carried out from January 1973 to May 1973 and from April 1975 to November 1980.

RESULTS AND DISCUSSION

Population size

Table 1 lists numbers of *D. geniculata* cave crickets observed and estimated in Valmarino cave between May 1973 and April 1975. The number of individuals in each age class (A, SA and Y) and the population size (N), all estimated by density plot method, together with H' values are also reported. Fig. 2 shows the monthly mobile means of N, A, SA and Y.

The average of N for 19 samples in 1973-1975 was estimated 435 by density-plot method and at 427 by mark-recapture method. The seasonal variation in N was noticeable, with a peak in Autumn and a minimum value in the Spring. The variation is obviously due to the cumulative effects of the absolute variations of the three age classes, and mainly from the yearly variation of the Young, linked with the reproduction. However, from the trend of the Adult number in Fig. 2, one could argue for the existence of a longer trend of reduction in number, even if the slope of the regression line of the adult number vs time is not statistically different from 0 (slope = -0.147, $t = 0.637$, $p > 0.25$).

Table 1 — Monthly plot density estimate results. A_0 , SA_0 , Y_0 , number of Adults, Sub-Adults and Young specimens counted within sample surfaces. p, ratio between observed and total areas. A, SA, Y, estimates number of Adult, Sub-Adult and Young specimens. H', Shannon index.

	A_0	SA_0	Y_0	N_0	p	A	SA	Y	N	H'
26.05.73	64	25	56	145	0.274	234	91	204	529	1.03
27.09.73	54	70	90	214	"	197	255	328	781	1.08
28.10.73	29	42	95	166	"	106	153	347	606	0.97
05.12.73	48	17	37	102	"	175	62	135	372	1.02
15.01.74	34	41	29	104	"	124	150	106	379	1.09
05.02.74	46	37	26	109	"	168	135	95	398	1.10
07.03.74	50	34	11	95	"	182	124	40	347	0.96
08.04.74	26	20	8	54	"	95	73	29	197	1.00
27.04.74	37	15	24	76	"	135	55	88	277	1.04
30.05.74	68	56	88	212	0.501	136	112	176	423	1.08
27.06.74	59	42	81	182	"	118	84	162	363	1.06
22.07.74	63	52	138	253	"	126	104	275	505	1.00
29.08.74	33	64	91	188	"	66	128	182	375	1.03
01.10.74	29	67	152	248	"	58	134	303	495	0.91
18.11.74	53	88	102	243	"	106	176	204	485	1.07
17.12.74	56	140	94	290	"	121	279	188	579	1.03
14.01.75	60	132	54	246	"	120	263	108	491	1.01
27.02.75	47	109	22	178	"	94	218	44	355	0.91
08.04.75	44	82	29	155	"	88	164	58	309	1.01

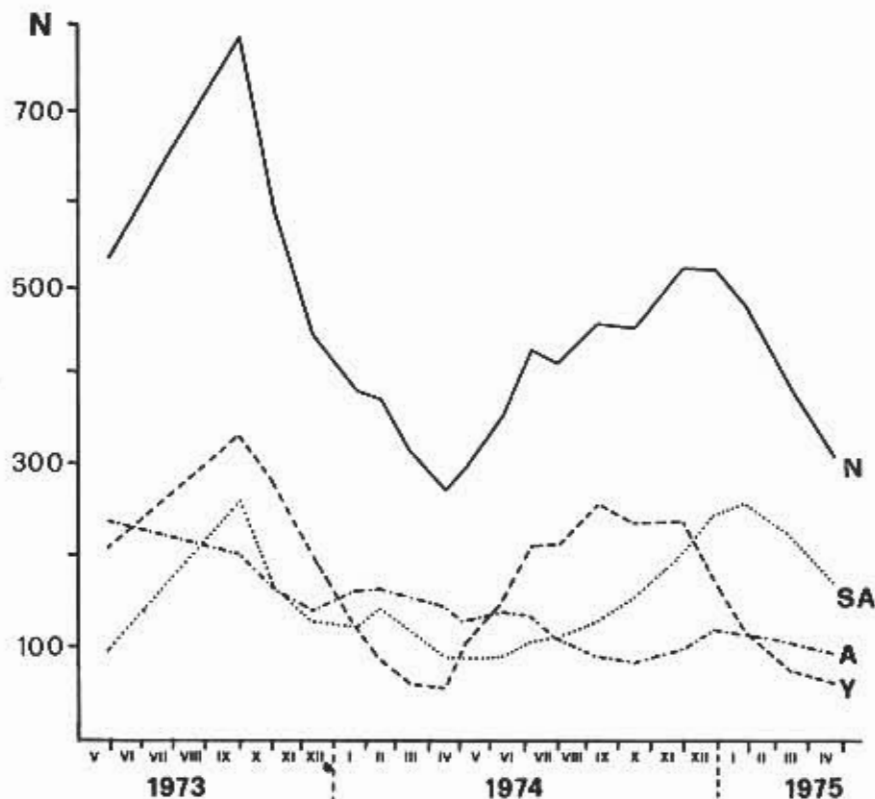


Fig. 2 — Annual trend of the mobile means (of order three) of the number of *Dolichopoda geniculata* in Valmarino cave. N, A, SA, Y: total adult, sub-adult and young specimens respectively. Abscissa, time in months and years. Ordinate, absolute frequencies.

Life cycle and age structure

Mating pairs and egg deposition in the Valmarino population were observed occasionally during the winter, spring and autumn. Laboratory data on other *D. geniculata* populations indicate that egg deposition closely follows mating. No direct information is available on the duration of embryonic growth of the Valmarino population. Fig. 2 shows that the Young increased from April to September 1974 resulting from the hatching of a new generation. Therefore, the egg hatching is lengthened for at least six months.

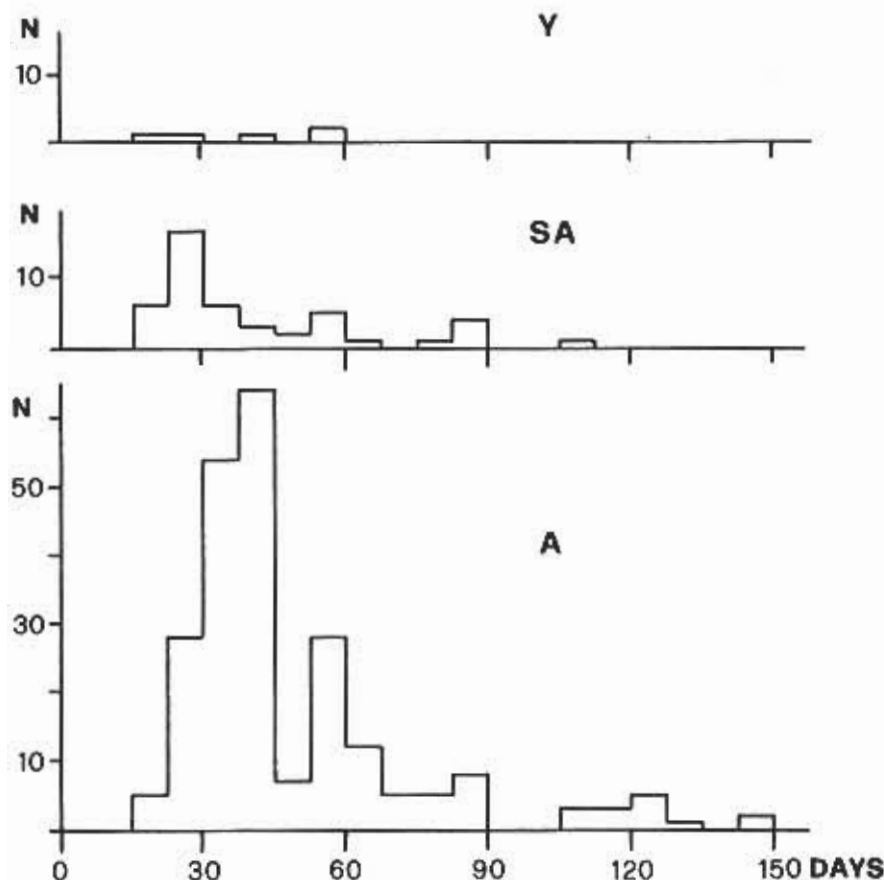


Fig. 3 — Recaptures of marked *Dolichopoda geniculata* specimens in Valmarino cave. A, SA, Y: adult, sub-adult and young specimens respectively. Abscissa, time in days. Ordinate, absolute frequencies.

Fig. 3 reports the frequency of recaptured individuals of the three age classes in relation to the time span since the marking events. From the highest observed values, we infer a duration of nymphal instars of about 2 months for the Young, 3 months for the Sub-Adults, and a longevity of 5 months for the Adults.

The number of Youngs decreases from September to April. The decrease is due both to mortality and to recruitment of individuals into the next age class. The time span of the Young age class should sum up to 8 months, because the Young age class includes 4 instars,

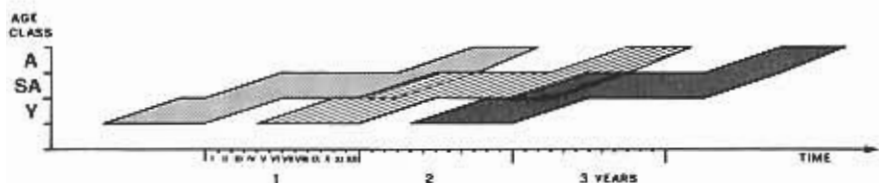


Fig. 4 — A model of *Dolichopoda geniculata* life cycle in Valmarino cave. Only three subsequent yearly generations are showed. Note that three cohorts are often present in the cave at same time. Abscissa, years in Arabian and months in Roman numerals. Ordinate, age classes. For age class limits see text.

and each instar lasts about 2 months. Since the sum of the Young time span with hatching period reaches 14 months, yearly generations of Youngs overlap each other. Accordingly, the number of Youngs observed in the Valmarino cave never drops to zero, even if it shows clear yearly fluctuations.

The Sub-Adult time span is much longer than the Young's one because the Sub-Adult age class includes 5 instars and each lasts about 3 months, so the total duration should be about 15 months, with an overlap of 3 months between subsequent generations. Moreover the overlap increases because of the long hatching period. Consequently, the yearly generations overlap each other for several months. Accordingly, the Sub-Adults always occur in the cave, their number doesn't fluctuate as the number of Youngs and their periodicity is clearly not annual.

The Adult age class shows a time span of about 5 months. So, we should expect a lack of adults during some months. Nevertheless, the long hatching period reduces the theoretical time of the Adults absence to 1 month. Actually, the Adults are always present in the Valmarino population, and only a little yearly fluctuation with a minimum in October - November is detectable. The constant presence of Adults in the Valmarino population must be caused by the overlapping of following generations probably due to both different hatching dates and different growth rates among individuals of the same yearly generation. In fact, we observe that some Sub-Adults grow slowly (see Fig. 4), reducing the gap between the subsequent Adult generations.

From laboratory data, the Adults start to reproduce one month after the last moult and continue until their death, so the mating period lasts 4 months. Because of the above mentioned overlap, it may

be possible that mating occurs between individuals from distinct cohorts, i.e. between individuals from the subsequent generations.

To sum up, the Valmarino cave *D. geniculata* life cycle should take on average 23 months for the larval stage and 5 for the imaginal one. In other Rhaphidophoridae cave crickets, the egg duration is 4-12 months long (Sbordoni et al., 1987) and in other *D. geniculata* populations the embryonic development lasted, on average, 200 \pm 21 days (Di Russo et al., 1987). So we could infer that in Valmarino population the egg stage requires several months. In any case, the life cycle is semivoltine, it requires about 3 years and the growth of the individuals of the same generation is not synchronous. A hypothetical model of the Valmarino cave *D. geniculata* life cycle is shown in the Fig. 4. The considerable time span of the egg hatching, and the length of time span of Y, SA and A age classes, cause the overlap between the next generations, for every age class. Consequently, the evenness value (J'), does not fluctuate like the absolute number of the individuals. It shows only small aperiodic oscillations and an overall constant trend in time (Fig. 5, regression line slope = 0.00009).

Spatial distribution

Crickets are found throughout the cave and, although their density varies in different sectors, it is very rare to observe individuals in contact as well as aggregates. Fig. 6 shows the seasonal variations of the density of individuals in the inner (F) and outer (A+B) sectors of the cave. The inner sector is always more densely occupied than the outer, and the difference between the average value of density is statistically significant (t test: $p < 0.003$). Moreover, the outer sectors are more thickly populated during the colder months of the year. The contrary occurs in the inner sector, where a marked increase in number of individuals is noticeable during the summer.

Feeding habits

Faecal pellets of 230 individuals of different age classes were analysed to study their diet habits. 20 individuals showed a predominance of vegetables (not green) remains; 25 individuals had unidentified remains and the remaining individuals showed a large prevalence of arthropod parts. The identifiable remains of arthropods were mostly Lepidoptera scales (into 62 faecal pellets) and bits of

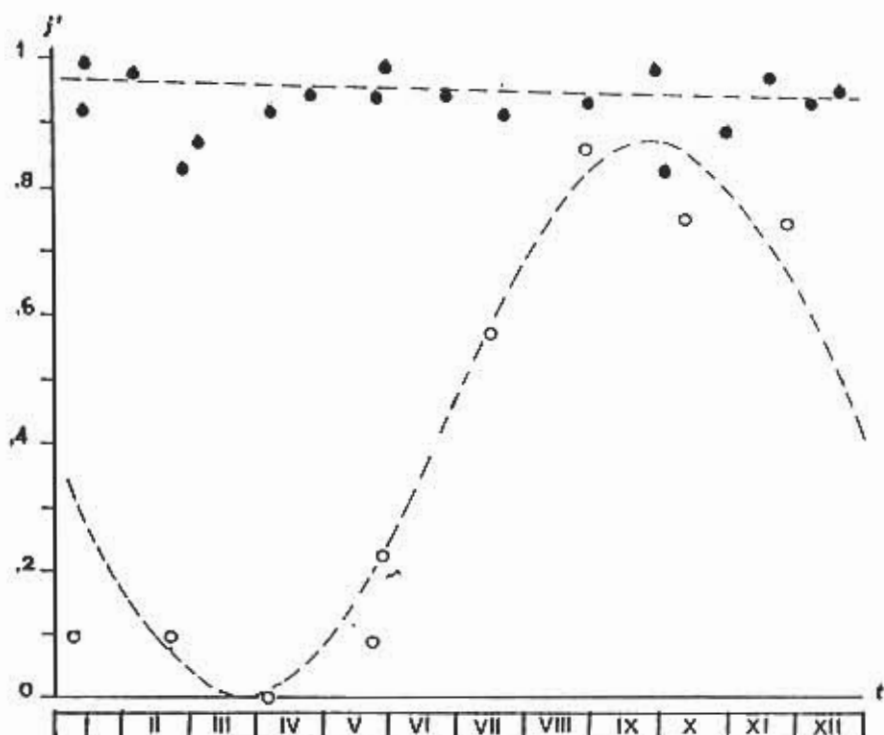


Fig. 5 — Comparison between annual trends in the Evenness (J') of age classes in Valmarino and Villa Ada cave *Dolichopoda geniculata* populations. Solid circles, Valmarino cave values. Empty circles, Villa Ada cave values. Abscissa, time in months. Ordinate, Evenness values. Dotted straight and sinusoid lines were obtained by minimum square method.

spider cuticle (into 30 faecal pellets), with less numerous Diptera and Coleoptera remains. Bat hairs are also very frequent. Overall faecal pellets seem very similar in appearance to the bat guano found in the cave, when prepared and examined by the same technique.

Information on the feeding habits of *D. geniculata* of the Valmarino cave were also derived from direct observation: there are several reports of individuals feeding on spider exuviae or dead moths, moreover Sub-Adult and Young were mainly found where bat guano was accumulated. So the diet of *D. geniculata* in the Valmarino cave appears to be mostly a saprophagous diet based on food found inside the cave.

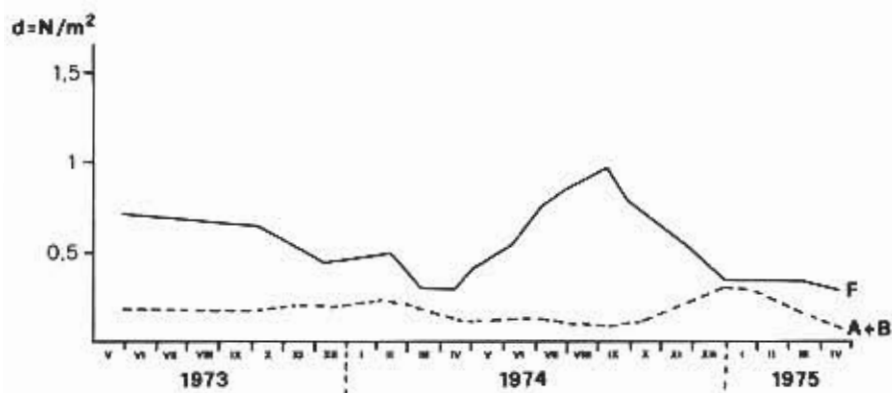


Fig. 6 — Comparison between specimens density of Valmarino cave *Dolichopoda geniculata* in a deep area (sector F) and a near entrance area (sum of A and B sectors). Abscissa, time in months. Ordinate, density values.

COMPARISON WITH OTHER POPULATIONS

Even if several studies have been devoted to population ecology and genetics of *Dolichopoda* few populations have been investigated to some detail as Valmarino population. However, a comparison with a population of *D. geniculata* from the artificial cave of Villa Ada is of a special interest since physical features of these two caves are similar and seasonal data on population size, age class structure, spatial distribution and feeding habits were seasonally recorded for two years (Rampini et al., 1983). Table 2 shows the comparison between physical features of the two caves and table 3 some comparable data of *D. geniculata* populations.

Population size

The average population size of Valmarino population was surprisingly low for an Insect population. In particular it was about ten times lower than recorded in Villa Ada cave, which shows similar physical features (see Tabs. 2 and 3). This findings supports the general trend of artificial caves populations which are bigger than population from natural caves, even when the ratio between

population size and cave dimension is considered (Carchini et al., 1983).

Life cycle and age structure

Data on egg, nymph and adult time span, here inferred by mark-recapture data, were also studied in samples reared in the laboratory. The life cycle observed in samples from artificial caves shows shorter growth times and Adult longevity: 15 months for the larval stage, and 3-4 months for the Adult life span. Therefore the overlap between the next generations in each age class is smaller than in natural cave populations. Consequently, the presence of two separate cohorts is clearly observed in artificial populations, while natural cave populations do not show the separation between the cohorts (Di Russo et al., 1987).

In agreement with the above mentioned features of life cycle, the age structure is more constant in the Valmarino population than in the other studied populations, as displayed by J' values, summarizing the age class composition. A comparison between the two populations from Valmarino cave and Villa Ada cave is shown in Fig. 5. It can be observed that the Valmarino J' values are almost constantly near the maximum, while the Villa Ada values strongly fluctuate seasonally and are rarely near the maximum. This means that the Valmarino population is always equally divided into the three age classes and, conversely, the Villa Ada population is often unequally divided. In fact, in some seasons the Villa Ada population completely lacks of one age class (e.g. the Adults in winter) (Rampini et al., 1983). This particular character was subsequently investigated in 35 natural and 32 artificial cave populations. The natural cave population J' values were significantly ($P < 0.001$) higher than artificial ones at a Mann-Whitney "U" test (Carchini et al., 1989).

Spatial distribution

As reported in the results, cave crickets in the Valmarino cave do not form aggregates and only rarely can individuals be found close to each other. On the contrary, it is always possible to find aggregates of hundreds of individuals in close contact in the Villa Ada cave, even though the size of the cave allows large inter-individual distances. Furthermore, in the Villa Ada cave the outer sectors are the

Table 2 — Comparison between some physical and environmental parameters of the Valmarino and Villa Ada caves.

	Villa Ada Cave	Valmarino Cave
Length, m	350	124
Altitude, m asl	50	15
Temperature max - min, in °C	10 - 16	13 - 19
Relative humidity max - min %	94 - 99	80 - 99
Age, year	2,000	200,000
Vegetation near entrance	<i>Laurus</i> Wood	<i>Olea</i> , <i>Cupressus</i> Bush
Number of species	15	31
Guano presence	no	yes

most densely populated, especially during the warm months. On the contrary, in the Valmarino cave the inner sectors host the majority of the population, while a shift towards the outer sectors occurs only in the cold months. Preliminary unpublished studies on several populations show that the two opposite spatial distribution patterns, observed at the Valmarino and Villa Ada caves, are linked with the cave type (natural or artificial), as for the above mentioned characters.

Table 3 — Comparison between the Valmarino cave and the Villa Ada cave *Dolichopoda geniculata* (Costa) populations. N, population size. L, cave length. H', Shannon index calculated from age class composition. V_N , coefficient of variation of population size. $V_{H'}$, coefficient of variation of the Shannon index.

	Valmarino Cave	Villa Ada Cave
N, mean	435	4516
N mean/L	3.51	12.9
V_N %	30.7	7.9
H', mean	1.02	0.47
$V_{H'}$ %	7.0	34.5

Feeding habits

Even though data on faecal pellets of the Villa Ada cave crickets are very limited, the collected data contrast with data of the Valmarino population. Faecal pellets from 14 individuals showed vegetable remains in 8 individuals (2 were green tissues), unidentifiable fragments in 5 and fragments from arthropods cuticle in one individual only. These findings indicate a diet based on foraging outside the cave, in clear contrast with the diet observed in the Valmarino population. Other studies on feeding habits of several, even conspecific, *Dolichopoda* populations confirm these differences between those inhabiting artificial and those inhabiting natural caves (Di Russo et al., 1991).

CONCLUSIONS

The *D. geniculata* population of the Valmarino cave showed marked differences compared to the conspecific population of the Villa Ada cave. Similar differences were also highlighted from a broad comparison based on several artificial and natural cave populations (Carchini et al., 1991). To sum up, the overall life cycle features assessed in these *Dolichopoda* populations agree with two opposite life cycle patterns: a seasonal one and an aseasonal one. The first is characterized by a limited reproductive period, and a conspicuous seasonality both in age structure and nymphal diapause. The second is characterized by continuous reproduction and absence of both seasonality in the age structure and nymphal diapause. These two different patterns are related to differences in feeding habits, the seasonal populations having a diet mainly based on green vegetables and other epigeal food sources, and the aseasonal ones a diet mainly based on animal remains, occurring in the cave itself such as bat guano. Moreover, differences in egg number, egg size, fertility and population size were pointed out, all related to the ecological features of the caves, rather than to genetic or geographic distances between populations. As a whole, the differences observed between natural-artificial-cave populations seem to match the "K" and "r" adaptive strategies, the "K" pattern being a result of an adaptation to the life in the caves (Carchini et al., 1991; Di Russo et al., 1994). The Valmarino cave population, compared to Villa Ada and the re-

maintaining studied populations from artificial caves, showed the typical traits of the aseasonal life cycle. In a sense, this allows us to consider the Valmarino cave population as one of the best cave-adapted populations studied so far.

Although the life cycle traits are not related to the genetic structure of population (Sbordoni et al., 1991), the reduction of the gene flow between neighbouring populations may have encouraged the establishment of an aseasonal life cycle. Gene flow was found particularly low between populations at low elevation near the seashore (Sbordoni et al., 1985). In fact, several marine transgressions, in the last 1.000.000 years, isolated some coastal areas (Bigazzi et al., 1973) and, added to this, present xerothermic climate does not allow long distance migration outside the cave for the *Dolichopoda* cave crickets which inhabit coastal zones. The Valmarino cave open at the base of the Ausoni mountains, circumstance that created a confinement when the sea level was higher than now. Furthermore, the cave entrance is at present on the boundary between a cultivated coastal plane and an arid mountain slope facing South, with grass and a few *Cupressus* trees, often burnt on summer. Therefore, historical factors and present climatic condition limited and limit the gene flow between the Valmarino cave population and the surrounding ones, protecting its adaptation to cave life.

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