Field- and laboratory observations on the life cycle of *Cœlotes terrestris* and *C. inermis* (Araneae : Agelenidae)

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Introduction

While sampling forest habitats in Central or Western Europe, one of the most commonly captured spider species in many cases turns out to be *Cœlotes terrestris*. In some cases, the congeneric species *C. inermis* may also be found. During a sampling campaign in the Zoniën forest, both species were caught in high numbers. *C. terrestris* even turned out to be the most abundantly caught spider species, especially when the captures of juveniles are taken into account (in total, about 10,000 specimens were caught).

As both species were caught in high numbers and as some remarkable observations on the size distribution of these species were made (see further), we decided to pay special attention to, amongst others, the study of the lify cycle of these two species. In the present contribution, the results of this study are presented and the life cycle of both species is compared. A further comparison is made between our results and those of Tretzel (1961) on the life cycle of *C. terrestris*.

Material and Methods, Study area

Sampling took place in the Zoniën forest, which is situated near Brussels, Belgium. In total, sixteen different forest stands were sampled. Only the results of the sampling in four stands in which *C. terrestris* or *C. inermis* were most abundantly caught will be discussed upon in this contribution.

For this study, a biometrical analysis was also executed on specimens from the Ardennes (*C. inermis* : Moha, Baert & Kekenbosch 1980, both species : Ferrières, Baert & Kekenbosch pers. comm.).

Sampling was done during three subsequent year cycles (1985-1986, 1986-1987 and 1987 - 1988) using seven pitfall - traps per stand. The numbers of specimens captured per period were recalculated for fortnightly or monthly intervals.

The abdomen of the adult females was dissected in order to check on the ovarial development. The following groups are distinguished : "mature" : eggs filling up practically the entire abdomen, "maturing" : egg buds clearly present on the ovaria, "beginning" : small egg buds visible, and "absent" : no sign of ovarial development visible.

The width of the cephalothorax of all specimens, with a maximum of fifty per period, (adults and juveniles) was measured. The resulting frequency distribution was analysed following the method proposed by Bhattacharya (1967) (Alderweireldt & Maelfait 1988, Segers 1989). The agreement of the sum of the resulting distributions with the empirical distribution was tested using a G - test (Sokal & Rohlf, 1981).

Laboratory observations and breeding experiments were carried out under the following experimental circumstances. Food supply (wingless *Drosophila melanogaster*) was kept *ad libidum* for adult females garding cocoons or offspring and was restricted to four *Drosophila*'s per two days in the breeding experiments. Temperature and light regime were kept constant at 20 C and light:dark 16:8 hours respectively.

Results and Discussion

A) *Cœlotes terrestris*

The phenology of *C. terrestris* is represented in figs. 1, 2 and table 1. The species exhibits one very distinct period of high activity per year. This period is situated in September. Adults of both sexes can however be caught during the whole year, with a secondary small peak of male (and female) activity during Spring. Such a "diplochronous" activity- pattern has been reported by several authors (Tretzel 1954, 1961, Russel-Smith & Swann 1972) although in some cases, the species was not caught the whole year round (Tips 1978, Dumpert & Platen 1985).

Figure 1.
Phenology of both sexes of *C. terrestris* in Station K (1986 - 1987)

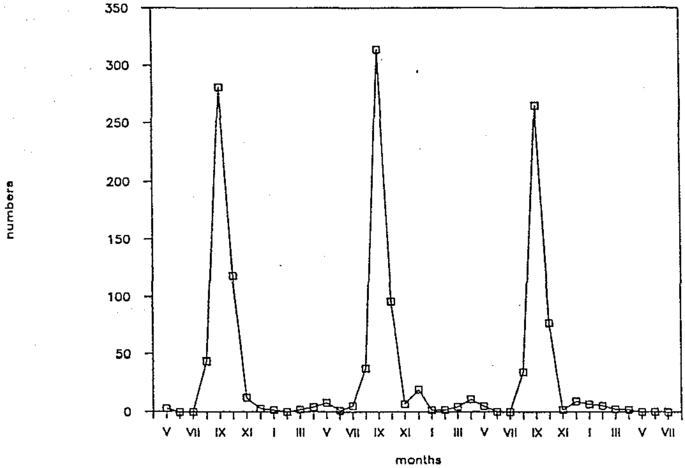
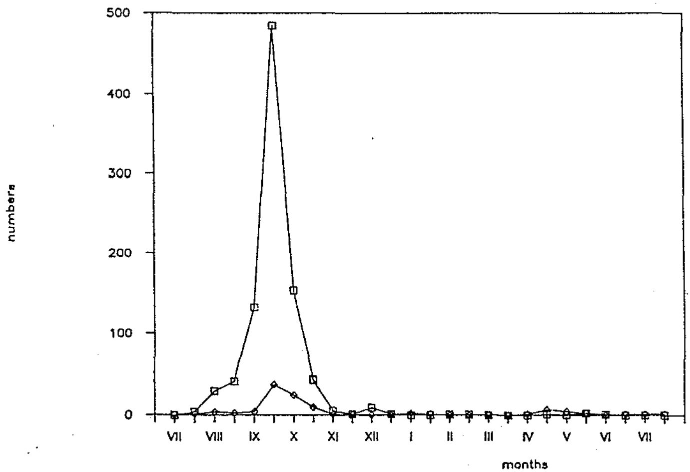


Figure 2.
Phenology of males of *C. terrestris* in Station F (May 1985 - September 1988)



As all females collected during winter are able to produce fertilized cocoons, we can assume that copulation must take place during the main activity period in September (Tretzel 1961). The fact that these females produce only one fertilized cocoon (Tretzel 1961, Krafft *et al.* 1986) and the observation that females that had already produced a cocoon in the field, can produce a second fertilized cocoon after taking them to the laboratory, shows that copulation can also take place during spring.

These observations and the results of the dissections of female specimens (table 1), that specimens with mature eggs or maturing eggs are caught from May untill September, indicate that at least two subsequent broods can be produced. The first brood takes place from May onwards. The second brood, wich is produced subsequently or wich replaces a destroyed first brood, can start from the end of July onwards. We can not exclude that late broods were inseminated by males from the following generation, who have just reached adulthood.

After a period of brood-care by the mother, the juveniles begin to lead an independant life after their third moult (Tretzel 1961, Kraft *et al.* 1986). These small juveniles are caught in pitfall-traps from the second half of July onwards (table 1). During their first year, they moult a few times before hibernation takes place. They grow further after the winter till the end of August. Juveniles of *C. terrestris* exhibit un unusually strong activity during summer (Alderweireldt 1988, table 1).

From August onwards, most of the juveniles from the previous year reach the adult instar. In laboratory conditions, this instar is reached after 8, 9 or 10 moults for males and after 7, 8, 9 or 10 moults for females. In field conditions, males seem to reach maturity a bit earlier than females. During the beginning of the main activity period, still large numbers of subadult females are caught (table 1). Reaching maturity in the field seems to be strictly synchronised.

Table 1. : Summary of the observations on <u>Coelotes terrestris</u> in station K. (1986-1987)

Period number:	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
* Number of specimens caught in 7 pitfall traps :																									
adults: MM		1	23	67	132	507	162	5	5	1	9	1		1	1					2		3	1		
FF	1	1	4	4	4	40	30	3		1			4						2	9	3	2		2	2
subadults:MM	76	6	5	1																				42	*
FF	42	11	40	25	3																			8	
juveniles:	44	6	24	19	8		8	1		5	13	5		4		1	1		1	5	7	13	8	53	
* Maturation stage of eggs in ovaria of dissected females :																									
Mature	1		1																	1	2			1	
Maturing			1	1																7		1			
Beginning		1	1	1						1			4						2	1					
Absent					4	40	30	3																	
* Cephalothorax width of juveniles and subadults (in mm.) :																									
3.4 - 3.6			1																						
3.2 - 3.4	1		5	3	1																				
3.0 - 3.2	3	2	11	4																				1	
2.8 - 3.0	14	3	13	9	1																			4	
2.6 - 2.8	42	4	9	2	1																			11	
2.4 - 2.6	43	4	4	4																				23	
2.2 - 2.4	32	4	2	2																		1	1	24	
2.0 - 2.2	15						1														3	4	5	28	
1.8 - 2.0	8	2																		1	4	6		8	
1.6 - 1.8	3						1				2	3		2						2		2	2	5	
1.4 - 1.6	3			1			2			3	5	2		1		1	1			2					
1.2 - 1.4				8	7		2	2		2	5			1					1						
1.0 - 1.2			18	7	1		2				1														
0.8 - 1.0		3	5	3																					

legend : MM : males; FF : females.

Periodnumber : 1/ 2/ 3/ 4/ 5/ 6/ 7/ 8/ 9/ 10/ 11/ 12/ 13/ 14/ 15/ 16/ 17/
Date : 28 V - 12 VI/ 25 VI/ 14 VII/ 30 VII/ 12 VIII/ 5 IX/ 17 IX/ 2 X/ 21 X/ 4 XI/ 18 XI/ 4 XII/ 16 XII/ 30 XII 1986/ 26 I 1987/ 12 II/ 24 II/
Periodnumber : 19/ 20/ 21/ 22/ 23/ 24/ 25/ 26/ 27/
Date: 10 III - 27 III/ 7 IV/ 21 IV/ 5 V/ 20 V/ 2 VI/ 16 VI/ 13 VII/ 28 VII/

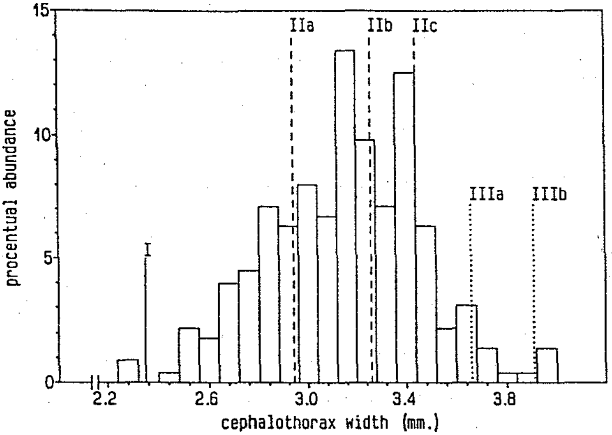
The analysis of the frequency distributions of the male cephalothorax width (table 2, figure 3) indicates that five (exceptionally six) size groups are present. We interprete these groups as follows : a first age group (I) of small specimens contains one size group, a second age group of medium-sized specimens contains three size groups which differ only very little (IIa, IIb, IIc) and a third age group of large specimens containing one (III) or two (IIIa, IIIb) size groups. The subdivision of the age groups is present in the males as well as in the females.
We interprete the age group II as being formed by individuals from the first brood of the previous year, who have reached maturity in their second year. The subdivision of this age group is a consequense of the variability in moults before reaching maturity. Individuals from later broods which reach maturity in their second year form age group I, while age group III is made up of individuals which have hibernated twice as juveniles and have reached maturity only in their third year. Also in this case, the subdevision of the age group is a result of the variability in the number of instars, required to reach maturity. Specimens of age group I seem to be absent in the population, sampled at Ferrières. Furthermore, the proportion of the animals, belonging to age group III (a and b) is high in Ferrières as compared to the Zoniën forest. This may be caused by unsuited climatological conditions which prevent the "short" life cycle to occur in the Ardennes.

Table 2. : Results of the analysis of the frequency distributions of the adult male cephalothorax width in Coelotes terrestris

Locality :	Cohorte :	I	IIa	IIb	IIc	III		Value of G (1)
						a	b	
Station A (1985-1986)	(2)	2.5	19.5	29.6	43.5	4.8		15.45 (19)
(n = 160)	(3)	2.44±0.28	3.07±0.14	3.34±0.16	3.63±0.16	4.03±0.04		
Station A (1986-1987)		2	11.8	51.7	31.0	3.5		4.56 (16)
(n = 148)		2.88±0.21	3.11±0.06	3.46±0.15	3.77±0.1	3.98±0.06		
Station A (1987-1988)		2.5	8.8	19.5	51.2	18		22.64 (16)
(n = 152)		2.62±0.11	2.99±0.13	3.16±0.06	3.45±0.11	3.75±0.06		
Station F (1985-1986)		4	31.7	35.4	20.3	8.7		0.41 (17)
(n = 184)		2.38±0.10	2.74±0.29	2.97±0.12	3.26±0.09	3.57±0.07		
Station F (1986-1987)		7	16.7	54.7	17.5	3.8		15.51 (18)
(n = 192)		2.53±0.07	2.68±0.09	3.02±0.15	3.45±0.06	3.79±0.07		
Station F (1987-1988)		4	25	42.6	19.6	8.8		1.09 (16)
(n = 188)		2.30±0.12	2.64±0.08	2.90±0.08	3.13±0.07	3.39±0.12		
Station K (1986-1987)		2	49	24.5	18.4	4.3	1.8	26.78 (20)
(n = 224)		2.35±0.25	2.94±0.21	3.26±0.08	3.44±0.08	3.67±0.07	3.91±0.02	
Station K (1987-1988)		5	36.1	28.9	24.9	5.1		23.06 (19)
(n = 224)		2.34±0.05	2.74±0.12	2.99±0.10	3.24±0.10	3.54±0.22		
Station L (1986-1987)		3	18.4	33.0	36.5	9.1		12.77 (17)
(n = 241)		2.62±0.03	2.82±0.08	3.10±0.08	3.38±0.11	3.60±0.18		
Station L (1987-1988)		8.5	48.5	30.1	9	3.9		15.55 (15)
(n = 209)		2.48±0.04	2.82±0.10	3.08±0.10	3.12±0.26	3.45±0.07		
Ferrières Station II		-	35	40.3	13.6	10	1.1	6.30 (16)
(n = 151)			2.46±0.11	2.67±0.09	3.02±0.08	3.21±0.15	3.54±x	

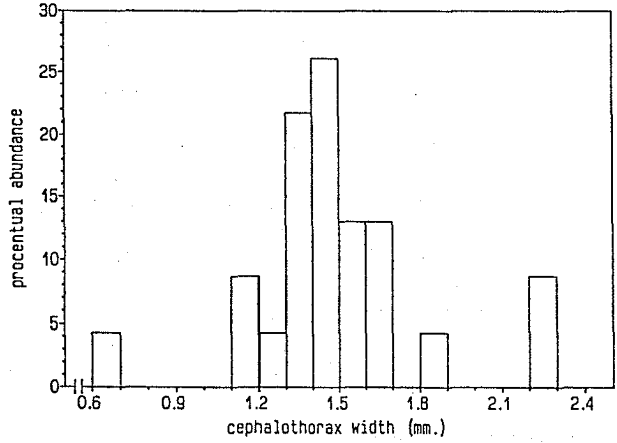
(1) : degrees of freedom
(2) : procentual abundance of specimens in this group
(3) : mean value (± standerd deviation) of the cephalothorax width of specimens in this group

Figure 3.
Emperical frequency distribution of the measurements of the cephalothorax width of males (in mm.) of *C. terrestris*, caught in station K (1986-1987) with indication of the mean cephalothorax width of the different age groups



A possible test for this hypothesis is that it implicates that during the hibernation period, three groups of juveniles should be present, *i.e.* a large group of medium-sized specimens from the first broods of the season just passed, a small group of small specimens from the subsequent broods of this season and a small group of large specimens from the previous season. The presence of these three groups could indeed be shown (figure 4).

Figure 4.
Frequency distribution of the measurements of the cephalothorax widt of *C. terrestris* juveniles (in mm.), caught while sieving litter in Station J on 29 November 1989 (n=30)



Tretzel (1961) believes that the captures of males during spring are made up of individuals who passed through a so-called "Frügentwicklung", this is a development in which certain individuals were found (under laboratory conditions) to reach maturity after fewer and shorter instars than normal. They were supposed to reach maturity already in spring following their first hibernation. According to Tretzel (1961), these specimens can be recognised by their small size. He also believes that males who reached maturity in September all die before the winter, which he bases on the obervation that males are not found in hand-captures during winter.
We do not agree with this hypothesis and falsify it based on the following observations.
1) We believe that the presence of overwintering males is adequatly shown by their presence in pitfall-traps before, during and immediatly after the winter. Furthermore, one male specimens was found hibernating on 29 November 1989 under a log of dead wood. However, it is true that only females are found commonly during winter.
2) The size of males, caught during spring does not differ distinctly of that of males, caught during the main activity period.
3) No subadults or newly moulted adult males could be found during the period in which they should be present according the hypothesis of Tretzel (1961) (see table 1).
4) The "Frügentwicklung" as observed by Tretzel (1961) seems to occur only under the experimental conditions applied by him (variable temperature, room temperature during winter, natural photoperiod), and not under the experimental conditions as applied by us (constant temperature and photoperiod). Presumably, the observations of Tretzel (1961) on the "Frügentwicklung" are due to an abnormal development caused by a deficient photoperiod induced hibernation system in some individuals.

Summarized, the life cycle of *C. terrestris* is as follows. Cocoons are produced mainly during May, the juveniles from these cocoons start living an independant life from July or August onwards. Juveniles from a second cocoon, produced in August or the beginning of September, leave their mother before winter or stay together in their mothers' web to hibernate. Growth is resumed from May onwards. Some specimens hibernate a second time as juvenile. From August onwards but mainly in the beginning of September the animals reach maturity and start copulating immediatly. Males can still be caught till as late as August of the following year, they presumably remain active as a possible inseminator of subsequent broods. Fertilised females overwinter and start producing a first cocoon in May.

B) *Cœlotes inermis*

The temporal distribution of the captures of *C. inermis* is presented in the figures 5, 6 and table 3. Males of this species are captured mainly during two periods per year, *i.e.* one during autumn (September to December) and one during spring (January to June). The results in figure 7 indicate that the relative importance of these two periods varies from year to year. This pattern is interpreted as that of a winter-adult species whose activity is strongly dependant of temperature. In this case - copulatory activity from September till June - we expect that females collected during winter will not all be able to produce fertilized cocoons. Of the two such specimens available, none did produce a fertile cocoon.
Females of *C. inermis* were caught in low numbers only. During the months September and October, newly moulted females showing only a beginning of egg-development were caught. In the period from April to May, the females caught had maturing or mature eggs (table 3). A small number of subadults were caught in September. The phenological pattern as described here has also been found by several authors (Tretzel 1954, 1955, Dumpert & Platen 1985), our interpretation of

this pattern is however different of that of Tretzel (1954, 1955).

Figure 5.
Phenology of both sexes of *C. inermis* in Station F (1986 - 1987)

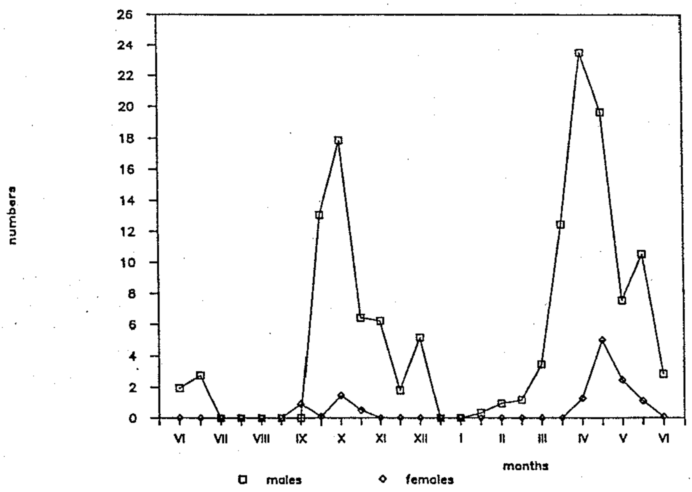
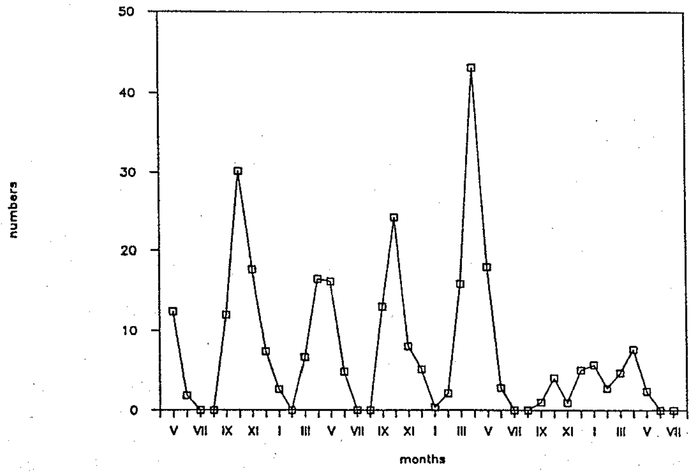


Figure 6.
Phenology of males of *C. inermis* in Station F (May 1985 - September 1988)



able 3. : Summary of the observations on Coelotes inermis in station F (1986-1987)

Number of specimens caught in 7 pitfall traps :

eriod :		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
dults :	MM	1	4						14	23	1	7	1	5			1	1	1	8	16	23	16	4	11	2
	FF							1		2												2	6	1	1	

Maturation stage of eggs in ovaria of dissected females :

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
ature																							3	1	1
aturing																					2	3			
eginning							1		2																

egend : MM : males; FF : females. Periods : see table 1

The analysis of the frequency distributions of male cephalothorax width reveals three to five size groups (figure 7, table 4). We interprete these groups as follows. A first age groups (I) of small animals, which can be subdivided in two (Ia and Ib) consists of animals who reached maturity already in their first year. A second age group (II) of larger specimens consists of animals who have reached the adult instar in their second year. This age group can be subdivided in three groups (IIa, IIb and IIc). As in *C. terrestris*, the subdivisions of the age groups is due to the fact that specimens can reach maturity after a varying number of moults (7, 8 or 9 for both sexes). This interpretation is supported by the results of comparative breeding experiments between *C. terrestris* and *C. inermis* (figure 8). Under the same experimental conditions, the development of *C. inermis* is a little slower than that of *C. terrestris*, but the number of moults required to reach maturity normally is lower in *C. inermis* than in *C. terrestris*. As the growing season in the field is longer for *C. inermis* than for *C. terrestris* (the latter becoming adult from August onwards, the former from September onwards and the period in which cocoons are produced for both species presumable equal, see table 1, 3), we may assume that *C. inermis* can reach maturity in their first year.
The procentual proportion of age group I seems to vary to a very great extent, even when comparing captures of the same year in two forest stands from the same locality (Zoniën forest) : this proportion varies form 58.8% of the total in stand A (catches of 1986-1987) to 3% in stand F (catches of 1985-1986). This age group is absent (Moha) or present (Ferrières) in populations from the Ardennes. A possible explanation for these observations is that only in suited habitats, some specimens can reach a sufficiently large size during their first growing season to reach maturity in their first year. Climatological factors can not account for the observed differences in procentual proportion as they can not explain the differences between populations from different stands in the same forest.
The life cycle of *C. inermis* is summarized as follows. Cocoons are produced from May onwards. As in *C. terrestris*, brood care also occurs in *C. inermis*. The juveniles begin to leave their mothers' web after the second moult. Some specimens can, in suited circumstances, reach maturity in their first year, some to all only reach maturity in September of the following year, after a hibernation period and a second growing season. Copulation takes place from September to May (possibly June), with an interruption during the coldest months. There are no indications in favour of the presence of a second brood, but this presumably does occur.

Figure 7.
Emperical frequency distribution of the measurements of the cephalothorax width of males (in mm.) of *C. inermis*, caught in station A (1985-1986) with indication of the mean cephalothorax width of the different age groups

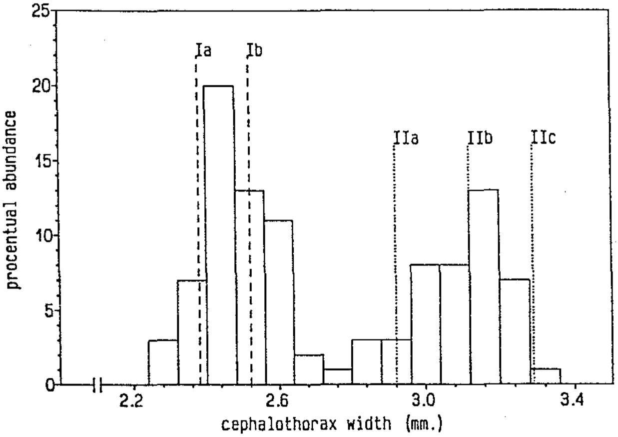
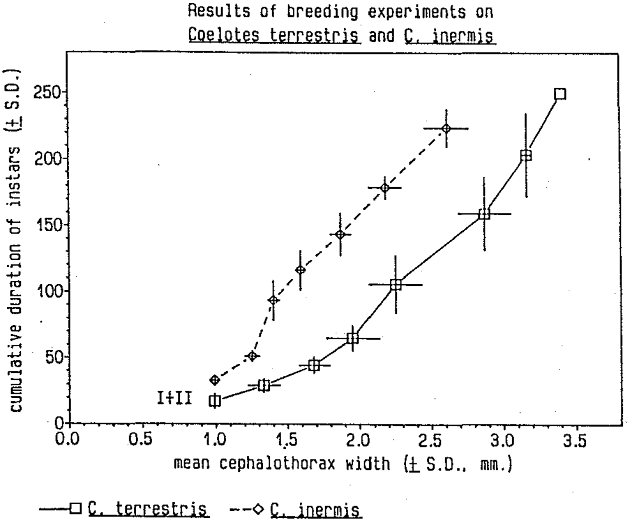


Table 4. : Results of the analysis of the frequency distributions of the adult male cephalothorax width in <u>Coelotes inermis</u>

Locality :	Cohorte :					
	Ia	Ib	IIa	IIb	IIc	Value of G (1)
Station A (1985-1986) (n = 100)	(2) 17 (3) 2.38±0.07	40.1 2.52±0.10	9 2.92±0.09	27.8 3.12±0.09	6.1 3.29±0.02	5.03 (13)
Station A (1986-1987) (n = 98)	25 2.39±0.06	33.8 2.63±0.11	5.8 3.04±0.03	33.7 3.17±0.06	1.8 3.55±0.02	4.22 (15)
Station F (1985-1986) (n = 115)	3 2.49±0.02		43.7 2.92±0.09	40.0 3.08±0.07	13.3 3.20±0.05	3.56 (10)
Station F (1986-1987) (n = 100)	11 2.50±0.19		22.3 2.89±0.11	30.0 3.00±0.16	36.7 3.15±0.08	19.52 (12
Moha Station II (n = 203)			42.0 2.50±0.10	54.5 2.70±0.07	3.5 2.95±0.06	14.75 (9)
Moha Station III (n = 114)			48.0 2.46±0.08	45.6 2.72±0.08	6.2 2.88±0.15	4.54 (10)
Ferrières Station II (n = 106)	11.0 2.26±0.04	5.3 2.46±0.04	26.8 2.64±0.05	48.4 2.83±0.10	8.5 3.05±0.02	15.41 (11

(1) : degrees of freedom
(2) : procentual abundance of specimens in this group
(3) : mean value (± standard deviation) of the cephalothorax width for specimens in this group

Figure 8.
Mean cephalothorax width after moulting (in mm.) versus mean cumulative duration of the instars (in days, beginning point : size of third instar, duration of first and second instar)



Conclusions

The most striking result of our study is, irrespective of the similarity of the overall life cycle patterns of these two species, the importance and implications of the differences which were found.
The life cycle of these two species differs only in few aspects. We summerise these aspects and their implications on the life cycle of the two species as follows.
1) Specimens of *C. inermis* reach maturity about a month later than specimens of *C. terrestris*. As a result, the growing season of the former lasts about a month longer than that of the latter. The difference in main copulation period between the two species, which is restricted to September in *C. terrestris* and (as a result of the higher incidence of unsuited climatological conditions later?) is spread over the rest of autumn, winter and spring in *C. inermis*, may also be a result of this.
2) Differences in the development of the two species are that *C. terrestris* grows faster than *C. inermis*, but the former requires more moults than the latter to reach maturity. Specimens of *C. terrestris* are, at any instar, larger than specimens of *C. inermis* (figure 7).
The longer growing season and the shorter juvenile life of *C. inermis* result in the latter species having the possibility of living an annual life cycle, which is not the case in *C. terrestris*.
The hypothesis, postulated to provide an explanation to the variability in procentual abundance of the age groups found, is different for both species. In *C. terrestris*, climatological factors are believed to be most important, instead of environmental factors of the habitat in *C. inermis*. It is clear that this hypothesis is not complete. Further research, including breeding experiments, have been carried out in order to formulate a more detailed explanation to this problem.

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