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AUTECOLOGY OF GONGYLIDIUM RUFIPES (SUNDEVALL, 1829) (ARANEAE, LINYPHIIDAE)

II. Habitatpreference, phenology and life-cycle (*)

BY

L. BAERT (**)

(Avec trois figures dans le texte)

I. INTRODUCTION

During the years 1974, -75 and -76, different woodhabitats, situated in the Hutsepotbos at Zwijnaarde and in Nazareth (both near Gent), were sampled by mean of different sampling methods (e.g. pitfalls, quadrats, handsorting and sweepnet).

The amount of data resulting from these sampling allowed us to determine the life-cycle of *Gongylidium rufipes*. This is the subject this paper treats about. This samplingprogram was combined with rearing experiments. The purpose of these experiments was to investigate (1) the influence of constant temperature-regimes upon the postembryonal developmental rate and (2) the influence of the photoperiod upon the ovarial development of the Erigonid spider *G. rufipes*. The results of these investigations are already published (BAERT, 1978 b, and BAERT, 1980).

II. MATERIAL AND METHODS

The macrohabitats studied were situated at Zwijnaarde (macrohabitats A, B, C, D, F, G) and at Nazareth (macrohabitats H, I). The general characteristics of the macrohabitats are :

(*) Lecture held at the VIIIth International Congress of Arachnology at Vienna (7. — 12. July 1980).
(**) Present address : K. B. I. N. Vautierstraat 29, 1040 Brussel.

A, B, F : beechwood with Rhododendron-undergrowth and thick litterlayer of the mor-type;
  A : strewed with chalk;
  F : litterlayer removed;
D : broad woodaley covered with a herbaceous vegetation;
C : coppiced woodland. The vegetation is composed of elder, alder, chestnut. The litterlayer is of the mull-moder type;
G : pinewood composed of larch with a sparse undergrowth of mapletrees. Thick litterlayer of pineneedles;
H : pinewood of *Pinus sylvestris* with no undergrowth. Thin litterlayer covered with moss;
I : pinewood of *Pseudotsuga mucronata* with dense undergrowth of fens and bramble. Thin litterlayer.

Four pitfalls were arranged in each habitat in two pairs. They were emptied every fortnight.

The quadrat samplingprogram, performed in the coppiced woodland-habitat only, consisted of square quadrats with side measurement of 25 cm (the surface of one quadrat equals thus 1/16th of a square meter).

Catches by hand were only sporadically performed.

During the years 1974, -75, and -76, the temperature was continually registrated between 0 and 20 cm above litterlayer. In Fig. 1, the following measurements are figured : weekly mean maximum and minimum temperature and weekly mean temperature based on registrations made every two hours.

III. RESULTS

Habitatpreference of *Gongylidium rufipes*

The structural characteristics of the different studied macrohabitats are given in table I. This table is completed with data of different studies carried out in our country by students of the « Laboratorium voor Oecologie der Dieren, Zoögeografie en Natuurbehoud van de RUG — Dir. Prof. Dr. J. HUBLÉ — and of a short selection of the most important literature on that matter. Also given is the presence or the absence of the species in those habitats.

From this table it seems clear that *G. rufipes* occurs as well in pine — as in deciduous woods. If the macrohabitat is a deciduous wood, the following structural requirements have to be fulfilled :

(1) the prime vegetation must be composed of trees and/or shrubs;
(2) a dense « bush-shrub » layer (Elton's fieldlayer) must be present;
(3) the presence of a litterlayer is indispensable.

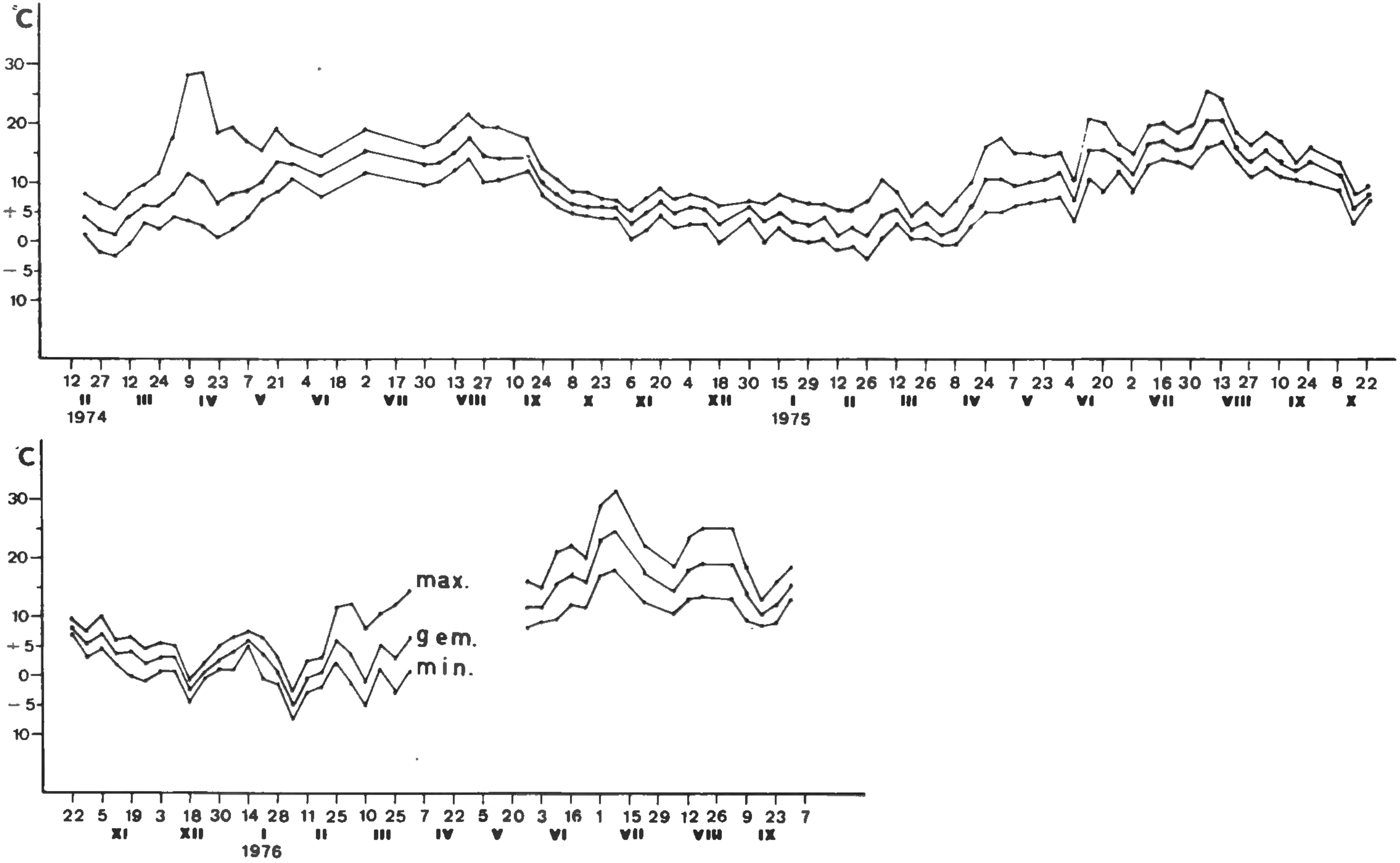

Fig. 1. — Temperatures registrated between 0 and 20 cm above litterlayer (mean value - see text).

TABLE

Synopsis of the Literature data and own observations

Presence of *G. rufipes* (in relatif high numbers in pitfalls)	Macrohabitat	Trees
A. Deciduous woods		
–	Hutsepot A, B, F (beechwood)	++ (beech)
+	Hutsepot C (coppiced woodland)	+ (some oaks, chestnu
–	Hutsepot D (woodalley)	—
+	TURNBULL (1960) (oak-beechwood)	++ (oak and beech)
+	SCHAEFER (1976) *(Melico-Fagetum festucosum)*	++ (beech)
–	SCHAEFER (1976) (Erlenbruchwald - *Alnetum glutinosae*)	–
–	SCHAEFER (1976) (Birkenbruchwald)	+ (*Betula pendula*)
–	LAMPO (1975) (oak-beechwood)	++ (oak and beech)
–	LAMPO (1975) (meadow planted with young hazels)	–
+	HOET (1972) (oak-beechwood)	+ (beeches with some oaks and larches)
B. Pinewoods		
–	Nazareth H	++ (pine)
+	Nazareth I	+ (Douglas spruce-fir)
+	Hutsepot G	++ (larch)
+	SCHAEFER (1976) (Kieferforst)	++
C. Other macrohabitats		
–	VAN PRAET (1975) (marshy meadow)	–
	SCHAEFER (1976)	
–	— Litoraea landscape	–
–	— Hochmor	–
–	— Küstendünen	–
–	— Calluna-heath	–
	HUBLE (1975) (dune habitats)	
–	— Astridpanne	–
+	— Doornpanne	–
+	— Westhoek	–

I

about the habitatpreference of *G. rufipes*

Shrublayer	Bushlayer	Herblayer	Litterlayer
–	–	–	++ (mor)
++ (alder, elder, *Prunus* sp., maple)	–	–	+ (mull-moder)
–	–	+	+ (leaves of beeches of adjacent beechwood B)
+ (hawthorn)	+	+	+
–	–	+	++ (dense)
++ (alder)	–	+	++ (dense)
–	+ (ling)	+ (*Eriophorum vaginatum* L.)	thin – peat-mor
+ (thin - rowan)	–	–	+
+ (young hazels)	+	+	– (or thin)
+ (hornbeam and rowan)	–	thin	++ (mor)
–	–	–	+ (pineneedles)
–	– (locally blackberry)	++ (ferns)	+ (pineneedles + ferns)
+ (maple)	–	–	+ (pineneedles + leaves of maple)
–	++	++ (ferns)	+ (deciduous and pine-litter)
–	–	++	–
–	–	++	–
–	–	++	–
–	–	++	–
–	–	++	–
+	+	+	+
+	+	+	+
+	+	+	+

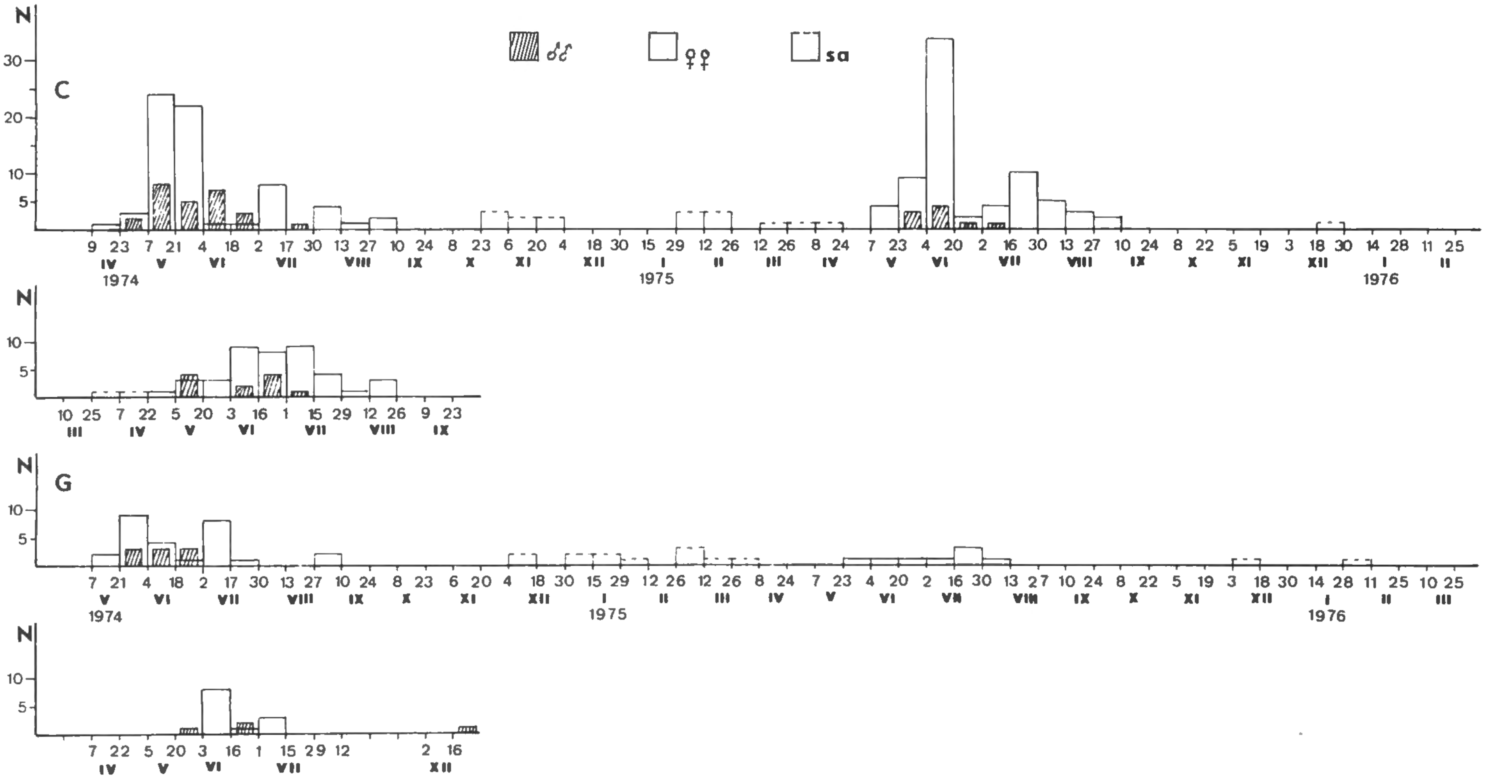

Fig. 2. — Phenology of *Gongylidium rufipes* (activitydensities) in the habitats « C » (Coppiced woodland) and « G » (Larchwood) (sa = subadult stage = third instar).

As we shall see below, the presence of these three structural elements is closely related with the season-bound vertical migrations of the spiders, in function of their life-cycle. The sampled coppiced woodlandhabitat C is the only deciduous woodhabitat fulfilling these requirements. In this habitat we found G. *rufipes* in relatif high abundancies (see Fig. 2 and Table II).

The three structural requirements, enumerated above, must also be fulfilled in pinewoods, as is the case in habitat G (see Table I). If the « bush - shrub » layer is absent, as in habitat I, a herblayer composed of ferns has the same effect.

Meadows, even marshy, are not suitable habitats for G. *rufipes*. This is clearly demonstrated by the works of HOET (1972), VAN PRAET (1975) and LAMPO (1975) for our country. No specimens of this species were caught in such habitats.

TRETZEL (1952) gives the following habitatpreferences : « Lebst Vorzugsweise auf Ufergebüsch (Alnus, Salix, Corylus) an Flüssen und Waldbächen sowie an Gebüsch und im Laubstreu in Erlenbrüchen. Vom Ufergebüsch geht sie mitunter in die Ufervergetation oder auf Uferwiesen », and WIEHLE (1960) : « Die Art lebt auf Ufergebüsch (gelegentlich auch an Boden sehr feuchter Waldstellen) oder auf Wiesen in unmittelbarer nähe der Gewässer ».

In the description given by TRETZEL, the three structural aspects enumerated above are considered, but as WIEHLE, he stresses upon the hydrobiont character of G. *rufipes*. Out of the former data it seems clear that not the hydrobiont character of the species plays a prevalent role in its habitatpreference, but well the presence of the three structural elements given above.

Phenology

The highest relative abundances were found in habitat C (Table III). A characteristic feature of this species is the higher relative abundance of females in the pitfalls.

In Fig. 2 the availability-distribution is showed for the habitats C and G. In the year 1974 a female activity started half April, atteined a peak during the month May and ended begin September. In 1975 the activity began somewhat a month later, atteined an activity-peak during the first samplingperiod of June and ended in September. The availability-distribution of 1976 is comparable with the one of 1975, except for its lower activitydensities.

We cannot truly speak of a male activity-peak but only of a little activity raise. In 1974 their activity began somewhat end April - begin May and ended end June. In 1975 their activity began also a month later and ended a samplingperiod later. In 1976 their activity began a sample-period earlier.

TABLE

Number of caught *G. rufipes* in the deciduous woodhabitat (habitat C)

Month	I	II	III	IV	V
1974		21-II (30') : 1 (♀)	19-III (1 h) : 8 (♀) + 2 (♂) 28-III (1 h) : 3 (♀) + 3 (♂)		30-V (1 h) : 5 (♀) + (♂)
1975	8-I (m²) : 6 (♀) + (♂) 16-I (5 Q) : 2 (♂) 23-I (3 Q) : (♀) 29-I (5 Q) : (♂)	12-II (6 Q) : 2 (♀) + 3 IInd 26-II (6 Q) : 2 (♀)	5-III (4 Q) : 2 (♀) + (♂) 12-III (7 Q) : (♀) 26-III (7 Q) : (♀)	3-IV (6 Q) : — 17-IV (5 Q) : 2 ♀* 22-IV (8 Q) : 3 ♀ + ♂ + (♀)	14-V (1 h) : 8 ♀ + 3 ♂ 15-V (m²) : 7 ♀ + 2 ♂ 27-V (m²) : 5 ♀ + ♂
1976		25-II (6 Q) : —	1-III (6 Q) : — 4-III (6 Q) : 1 (♂) 9-III (6 Q) : 1 (♀) 11-III (6 Q) : — 15-III (6 Q) : 2 (♀) 18-III (6 Q) : — 22-III (6 Q) : 1 (♂) 29-III (6 Q) : 1 (♀)	I-IV (6 Q) : 1 (♂) 5-IV (6 Q) : 1 (♂) 6-IV (6 Q) : — 7-IV (6 Q) : — 12-IV (6 Q) : 2 (♀) 13-IV (6 Q) : — 15-IV (6 Q) : 1 (♀) 20-IV (6 Q) : 1 (♀) 21-IV (6 Q) : 1 (♀) 26 & 27-IV (6 Q) : — 29-IV (6 Q) : —	On 3 and 5-V (6 Q) : — 10-V (6 Q) : ♀ 11, 13 & 17-V (6 Q) : — 18-V (6 Q) : ♀ 24, 26, 28 & 31-V (6 Q) : — end May : at the feet of elder : 2 ♀ with cocoon.

* = just moulted; IInd = second instar; third instar juveniles indicated between braquets = (♂)

II

by way of handcatchings (h), Sweepnet (Sw) and Quadratsamplings (Q)

VI	VII	VIII	IX	X	XI	XII
12-VI (1 h) : —	(17 Q) : —	6-VIII (1 h) : ♀ 13-VIII (1 h) : 2 ♀ + (♂) (16 Q) : 1 IInd 13-VIII (Sw) : 11 IInd	(12 Q) : 2 IInd	(3 Q) : —	6-XI (B) : 17 (♀) + (♂) 20-XI (B) : 3 (♀) + (♂) (12 Q) : —	4-XII (3 Q) : 2 (♀) 18-XII (3 Q) : 1 IInd (12 Q) : —
1 & 9-VI (6 Q) : — 15 & 16-VI (6 Q) : —		5-VIII (Sw) : IInd + ♀ between 9 & 23-VIII (45 Q) : — 23-VIII : cocoon 25-VIII (Sw) : 1 IInd	(28 Q) : — 15-IX (Sw) : IInd (B) : (♂) + (♀)	(20 Q) : —	3-XI (10 Q) : —	
		22-VIII-1977 (Sw) : 13 IInd				

& (♀); B = bags; (1 h) = handcatchings during one hour; (30′) = idem during 30 minutes.

TABLE III

Numbers of caught *G. rufipes* in each studied macrohabitat

	A	B	C	D	F	G	H	I
1974	—	—	26 ♂♂/67 ♀♀ (93)	—	—	9 ♂♂/27 ♀♀ (36)	not sampled	not sampled
1975	1 ♂	—	9 ♂♂/73 ♀♀ (82)	—	—	/ 8 ♀♀ (8)	—	2 ♂♂/ (2)
1976	—	—	11 ♂♂/41 ♀♀ (52)	—	1 ♂	3 ♂♂/12 ♀♀ (15)	2 ♂♂/2 ♀♀ (4)	10 ♂♂/15 ♀♀ (25)

Comparing the availability-distributions (Fig. 2) with the meteorological data (Fig. 1), we find that the activity always starts when the mean temperature nearly atteins a value of ca. 10 °C. There is an activity drop when the mean temperature drops beneath the temperature level of ca. 15 °C. In 1974 the maximal temperatures reached higher values in the period preceding the activity start (April), so that this could be the cause of the earlier activity observed then.

Third instars (Table II) were captured from November till April. Pitfalls showed that this instar exhibited a little activity during the winter months, certainly during the warmest period of a warm winterday.

Following Table II, *G. rufipes* reaches the adult stage in the second half of April. Following SCHAEFER's classification of the types of annual cycles of spiders, *G. rufipes's* annual cycle can be described as one belonging to the type II annual cycle e.g. a stenochronous species reproducing in spring and summer and hibernating as juveniles or subadults.

Absolute densities

The quadrat sampling data of Table II, expressed per surface unit (/m^2) is given in Table IV.

The absolute densities registrated in 1976 were lower than in 1975. In analogy with this finding we also observed a lower activity-density, but there is no true correlation between those two facts.

The absolute female densities lays much higher than those of the males. During the months of highest activity, e.g. June and July (1975 and 1976), the lowest absolute densities were recorded. This can surely be correlated with the search of a suitable place for cocoonconstruction by the females (on places not accessible for sampling feet of bushes, shrubs and young trees).

TABLE IV

Absolute densities

	Jan.	Feb.	Mar.	Apr.	Mai	Jun.	Jul.	Aug.
1974	—	—	5.5 (♀♀) 2.5 (♂♂) (2m^2 h)	—	5 ♀♀ 1 ♂ (1 m^2 h)	nih. (1 m^2 h)	—	1.5 ♀♀ 0.5 (♂♂)
1975	5 (♀♀) 1.1 (♂♂) (29 Q)	5.3 (♀♀) (12 Q)	3.6 (♀♀) 0.9 (♂♂) (18 Q)	0.8 (♀♀) 4.2 ♀♀ 0.8 ♂♂ (19 Q)	6.7 ♀♀ 1.7 ♂♂ (3 m^2 h)	—	nih. (17 Q)	—
1976	—	nih. (6 Q)	1.3 (♀♀) 0.7 (♂♂) (48 Q)	1.1 (♀♀) 0.4 (♂♂) (72 Q)	0.7 ♀♀ (66 Q)	0.5 ♀♀ (30 Q)	—	nih. (45 Q)

Q = number of quadrats taken; third instars between brackets; h = handcatchings.

Captures by hand clearly demonstrated that the females lays their eggs and construct their cocoons at the feet of shrubs and bushes (in this habitat mainly elder) or perhaps even within the canopy of these shrubs, bushes and young trees (see Table II).

Seasonal-bound vertical migration

Sweepnet captures, exhibited throught the shrubs during the month Augustus, showed us that the IInd Instar stage is spend in the canopy of shrubs (habitat C).

After leaving the cocoon, the spiderlings exhibit an active vertical upward migration. This migration could be a sort of (evolutive) adaptation against the harsch competitive pressure, with which they are (were) confronted when leaving the save cocoon. This competitive pressure could be exhibited by the little Erigonid spiders as *Monocephalus fuscipes*, *Dicymbium nigrum* and *Diplocephalus picinus* which reach relatif high populationdensities in this period.

A possible competitive pressure for place emanating from typical web-sharing species as Tetragnathids and Araneids within the shrubs is to be neglected since the fundamental difference in spacial construction of their webs. Tetragnathids and Araneids construct webs overthrowing space between twigs. Juvenile *G. rufipes* construct, on the contrary, their webs on the underside of leaves. They have in other words a different spacial niche than the Tetragnathids and Araneids. The vertical migration towards the soil happens on a passive way during the leaffall. The spiderlings (IInd or IIIrd instars) fall together with the leaves.During the period of leaffall, great bags were put underneath the shrubs to intercept the falling leaves. When sorting them, many IIIrd instar spiders were found. The IIIrd instar spiderlings hibernate in the litterlayer and become adult during the second half of April.

About G. *rufipes*, TURNBULL (1960) speaks of a resident species of the shrub-layer, being capable of emigration to the adjacent ground- or herblayer.

SCHAEFER (1976) speaks of a species living within the vegetation and, during the winter, within the litterlayer, with a possible exchange between those two layers.

Annual cycle — life-cycle (Fig. 3)

— During the months May and June, the males run actively on the soil in search of a suitable mating partner.

Some laboratory tests showed us that :

(1) the same male is able to mate subsequently with different females without interruption (all females were fertilised);

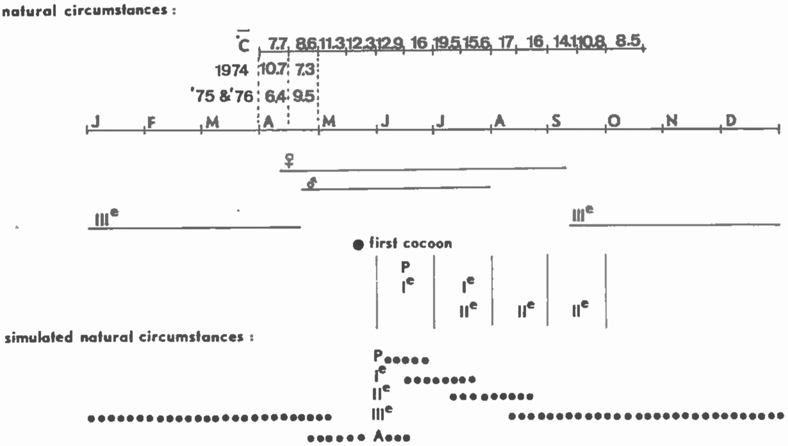

Fig. 3. — Life-cycle of *Gongylidium rufipes* under natural and simulated (temperature) natural circumstances.

(2) there is no cannibalistic aggressivity of the females towards the males. After copulation male and female can live close together till their death. Such lifehabits are advantageous to the survival of the species. We already saw that the male densities in a habitat are very low compared with those of the females. The lack of any cannibalistic aggressivity of the females towards the males, allows the males to fertilise more than one female, so that the difference between male and female densities is in some way uplevelled;

- — The female activity observed from May till Augustus is the result of an active search for a suitable place for cocoonconstruction.
- — Cocoons are build from half May till June-July. This occurs mainly in the vicinity (at the feet) of bushes and or shrubs. Laboratory tests showed that a female can build three to four cocoons (in captivity). The number of laid eggs varied between 13 and 68 (mean value : 37,1 ± 13,1; No. 36 cocoons).
- — The first juvenile stages exhibit an active upward migration towards the canopy of bushes, shrubs and young trees. In times of leaffall (late summer, autumn) the elder juvenile stage (presumably the third instar) drops to groundlevel by mean of a passive nearward migration (with the falling leaves).
- — The third instar spiders spend the winterperiod in a sort of quiescence state within the litter layer. Handsorting of the litter in this period resulted in many catches of lethargic third instar spiders.
  Pitfall catches demonstrated that at some times an activity of these spiderlings occurs during the winter. This is certainly correlated with an active search of food during warm moments of hot winterdays.
- — Between half and end April, the third instars moult for their last time. The adult stage is attained. Quadrat samples taken on April the 17th of 1975 furnished two adult females just moulted.
- — The males are directly running off in search of a female.

Life-cycle under simulated natural circumstances

Parallel with the experiments with constant temperatureregimes (BAERT, 1980), 26 spiders were reared under simulated natural circumstances. The temperatures at which the spiders were successively reared were based upon mean temperaturerecords of the year 1971 (normal climatic year) (see Table V).

A full account of the rearing method is given in BAERT, 1978 a and b, and BAERT, 1980. We started on the assumption that the first eggs are laid half May (cocoon used was laid on the 21st of May 1975) and that the first juveniles leave their cocoon at the beginning of june (during this experiment the juveniles left their cocoon on the 2nd of June 1975).

The following results were found :

(1) When second instar spiders were brought from a regime of 15 (± 1) °C to a regime of 12,5 (± 0,5) °C they immediately began to moult, and within a short time they reached the third instar (the total experimental population reached the third instar stage after twenty days).

(2) The third instars spend the simulated winterperiod in an inactive state (quiescence). During this period the following feeding frequencies were observed :

- — food uptake is high at 12,5 (± 0,5) °C;

TABLE V

Constant temperatureregimes used for the simulation of natural circumstances

Period		Temperatureregime
02-VI	till 01-VIII	15 (± 1) °C
01-VIII	till 01-IX	12.5 (± 0.5) °C
01-IX	till 01-XI	9.5 (± 1.5) °C
01-XI	till 17-XI	4 (± 1) ° C
17-XI	till 15-XII	1 (± 1) °C
15-XII	till 02-I	4 (± 1) ° C
02-I	till 05-II	alternated : 1 (± 1) °C ←→ 4 (± 1) °C every 7 days
05-II	till 08-III	4 (± 1) ° C
08-III	till 08-IV	9.5 (± 1.5) °C
08-IV	till 08-V	12.5 (± 0.5) °C
08-V	till 23-V	15 (± 1) °C
23-V	till 07-VI	20 (± 1) °C
07-VI	till †	15 (± 1) °C

— food uptake remains high during the first ten days of the 9,5 (± 0,5) °C regime; after that period it lowers;

— when the temperature lowers beneath the 5 °C range (successive regimes : 4 (± 1) °C ←→ 1 (± 1) °C, see Table V) there is only a sporadic food uptake;

During this alternated phase (from 2 January till 5 February) an increased food uptake was observed at 4 (± 1) °C. This points towards an adaptation. After a prolonged action of low temperatures, *G. rufipes* is able to increase her feedingfrequency at minute temperature changes in positive way (this means from 1 (± 1) °C to 4 (± 1) °C).

— When the temperature raises back, the food uptake raises also.

(3) Fifteen days after the day the third instars were transferred from the 9,5 (± 0,5) °C regime to the 12,5 (± 0,5) °C regime the first individuals moulted. In ten days time the total experimental population reached the adult stage. In this experiment the adult stage was reached half April, which is in good agreement with our field records (see Table II).

(4) Mean duration per instar see Table VI. The short S. D. shows there was a good timing of the moulting.

Out of these results we can conclude that :

(1) Theoretically pre-instar juveniles can be found in June; first instars in June-July; second instars in July-Augustus-September and third instars from September till April of the next year.
(2) When the mean end - summer begin - fall temperature decreases to a value of ca. 12,5 °C, the second instars pass into the third instar stage.
(3) The third instars reach the adult stage when the mean spring temperature raises to a maximum value of ca. 12,5 °C.

TABLE VI

Developmental time of the different instars during the experience with simulated natural circumstances (for definition of P see BAERT, 1980)

P : 19.7 ± 6.6 days
I : 24.3 ± 4.4 days
II : 29.9 ± 4.8 days
III : 254.7 ± 5.5 days

P + I : 44 ± 5 days
\+ II : 74.2 ± 5 days
\+ III : 328.8 ± 3.4 days

RESUME

Le cycle vital de l'Erigonine *G. rufipes* a pu être déterminé grâce à l'emploi de différentes méthodes de capture effectuées dans divers habitats boisés.

Nous avons complété les données ainsi obtenues à l'aide d'une simulation des circonstances climatiques (ici seul le facteur température était variable) existant dans l'habitat ou l'araignée a été capturée le plus abondamment. La durée du cycle postembryonnaire — c'est-à-dire de la sortie du cocon jusqu'à la mue finale — ainsi obtenue, coïncide largement avec celle trouvée sur le terrain.

Les températures constantes appliquées, ainsi que la durée de leur application, sont basées sur les données émanant d'un enregistrement continu des températures régnant sur le terrain.

Les résultats obtenus à l'aide de nos différentes méthodes de capture nous ont démontré que les juvéniles et les sub-adultes effectuent une migration verticale au cours de leur cycle selon les saisons.

La phénologie ainsi que le cycle vital de l'espèce sont décrits.

ABSTRACT

By means of different sampling methods (e.g. pitfalls, handcatchings,...) performed in different woodhabitats, combined with rearing experiments, we were able to dertermine the life-cycle of *Gongylidium rufipes*.

First of all we tried to find out which habitat this species prefers. For this purpose we compared our results with those found in the literature.

The results of our sampling showed there was a seasonal bounded vertical migration.

With rearing experiments we tried to simulate the environmental temperature conditions. Therefore the spiders were submitted to a series of alternating constant temperatures. Each temperature was applicated during a well determined period. The duration of these periods were based on data from constant temperature registrations made during a whole year in the habitat in which the spider was caught the most abundantly.

The phenology and life-cycle of the spider is described.

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Laboratorium voor Oecologie der Dieren
Zoögeografie en Natuurbehoud (R. U. G.)
Dir. Prof. Dr. J. HUBLÉ
K. L. Ledeganckstraat 35 — 9000 Gent.