

Abundance and prey of *Coelotes terrestris* (Wider) (Araneae, Agelenidae) in hedges

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Summary

The influence of structure and microclimate of hedges on the abundance and prey of *C. terrestris* was investigated to show the suitability of hedges as habitats for normally woodland-inhabiting spiders.

In a broad hedge the ground was covered by litter and the microclimate was more like that of woodland. The abundance of *C. terrestris* was relatively high (1.2 webs/m²). The prey spectrum consisted of 34 species, some of them typically inhabiting woodlands.

In a narrow hedge the ground was not covered by litter and the microclimate was more like that of open country. The abundance of *C. terrestris* was relatively low (0.8 webs/m²). The prey consisted of 23 species, some of them typically inhabiting open country.

C. terrestris seemed to prefer, for web-building, places with a higher activity abundance of the potential prey beetles.

It is concluded that hedges can be suitable permanent habitats for normally woodland-inhabiting spiders if they are broad enough to develop a woodland-like microclimate and a layer of litter. Prey supply does not limit the population density of *C. terrestris* in hedges.

Introduction

Until the first half of this century hedges were typical structures of the central European landscape. They formed widely extended networks with their primary functions being demarcation of estates and forming living fences (Röser, 1988). In recent decades many boundary lines, and the hedges on them, disappeared with the increasing intensification of agriculture and associated combination of fields. The remains of the once extended hedge networks are island-like and widely scattered. Today, hedges serve as habitats for many species of plants and animals (Pollard *et al.*, 1974; Tischler, 1948, 1950, 1958; Thiele, 1964), they are more and more places of refuge, and their function of connecting the remaining woodlands is more important (Glück & Kreisel, 1988; Mader, 1980, 1983; Röser, 1988; Rotter & Kneitz, 1977). Nevertheless, very little is known about the ecological requirements of hedge-inhabiting arthropods, especially spiders.

Spiders inhabit almost all terrestrial ecosystems, if some other form of terrestrial life exists (Turnbull, 1973). Physical and biological factors like temperature, humidity, light, wind, vegetation structure, prey supply, competition and predators determine the suitability of a particular habitat for individual species (Foelix, 1979; Rypstra, 1983). It seems that the structures supporting web-construction largely limit the distribution of web-building spiders. The other factors have a subordinate influence on habitat selection according to the physiological needs and tolerances of the species (Schaefer, 1978; Turnbull, 1973). In hedges

the microclimate and vegetation structure can be more or less woodland-like, depending on the hedge's structure and measurements (Glück & Kreisel, 1988; Mader & Müller, 1984). Hence, woodland spiders with their special adaptations are presumably more or less able to inhabit such biotopes.

The aim of this work was to investigate the suitability of hedges for typically woodland-inhabiting spiders, with *Coelotes terrestris* (Wider) serving as the example. The influences of structure and microclimate of hedges on the abundance and prey of the spider were the most interesting subjects of research.

The biology of *Coelotes terrestris*

Coelotes terrestris is a widespread, hygrophilous ground-living spider in Europe, mainly inhabiting the litter of woodlands on mountains and hills (Tretzel, 1952). Its web consists of a sheet of about 5 cm diameter and a funnel-like gallery which leads 10 to 20 cm into the ground. The spider feeds on epigeic active arthropods, which are captured on the sheet and eaten in the gallery; the remains of the prey (elytra, heads, etc.) are stored in a separate part of the gallery (Tretzel, 1961).

The life-cycle of the females is biennial and of the males annual. After mating in the autumn most of the males die. The females hibernate and then build one or two egg-cocoons in May or June of the following year. The spiderlings hatch about four weeks later, stay in their mother's web for some weeks and feed on her prey during this time (Tretzel, 1961). The brood-care period lasts longer if prey is abundant (Krafft *et al.*, 1986). After the death of the mother in the autumn, often her corpse is eaten by the young (Bristowe, 1958) which hibernate in the fifth or sixth instar and complete their development in the following summer. Females attain a biomass (fresh-weight) of 97 ± 12 mg (mean \pm 95% confidence interval, $n = 17$), males 86 ± 33 mg ($n = 5$; own measurements).

Study area

The investigated hedges are situated near Aachen (West Germany) in the Iter-Creek dale (6°1'E., 50°43'N., altitude 250-260 m). The subsoil, consisting of slate and sandstone with a superimposed layer of loess, has developed a Ca-poor brown soil. The climate is temperate with a precipitation of c. 900 mm per year, relatively cool summers and relatively warm winters

		Hedge 1	Hedge 2
Blackberry	<i>Rubus</i> sp.	×	×
Blackthorn	<i>Prunus spinosa</i>	××	×
Common Elder	<i>Sambucus nigra</i>	×	×
Dog Rose	<i>Rosa</i> sp.	×	×
Gooseberry	<i>Ribes uva-crispa</i>	×	×
Hazel	<i>Corylus avellana</i>	××	—
Hawthorn	<i>Crataegus monogyna</i>	×	×××
Traveller's Joy	<i>Clematis vitalba</i>	×	—
Hop	<i>Humulus lupulus</i>	×	—
Oak	<i>Quercus robur</i>	×	—
Guelder Rose	<i>Viburnum opulus</i>	×	—

Table 1: Woody plants of the studied hedges. × = infrequent, ×× = frequent, ××× = abundant.

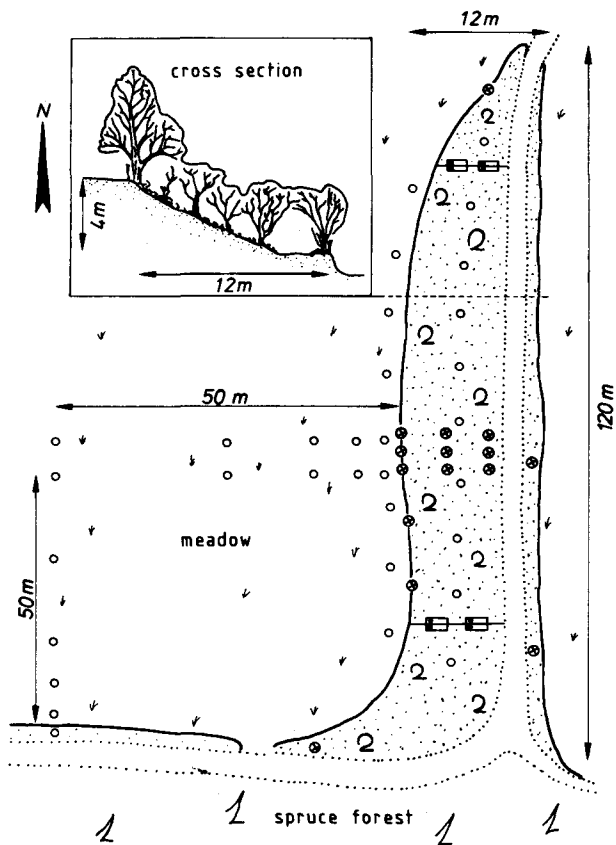


Fig. 1: Map of hedge 1 with pitfall-trap arrangement and cross-section. Open circles = single-traps; crossed circles = cross-traps; rectangles with closed circles = groove-traps.

(Pflug *et al.*, 1978). Hay-meadows, cut in May or June and then grazed by cows later in summer and autumn, and pastures, grazed by cows from spring to autumn, are the main agricultural uses of the region.

Hedge 1 lies between meadows on the western slope of the dale and covers an area of about 1,000m² (length 120m, width 8-12m; see Fig. 1). It is traversed by a c. 2m wide track and adjoins a spruce forest at the southern end. The hedge contains eleven species of woody plants, dominated by blackthorn and hazel (Table 1), which form a closed canopy of c. 5m height over the whole hedge. The ground is covered by a layer of litter (c. 5cm).

Hedge 2 encloses a pasture of c. 90 × 50m and covers an area of about 100m² (length 170m, width 0.5-1.2m; Fig. 2). About half of the hedge was cut to a height of c. 1.2m in the year before this investigation, the rest is 3-5m high. It contains only six species of woody plants (mainly hawthorn; Table 1), and its edges are thickly covered by nettles (*Urtica dioica* and *U. urens*; cross-sections in Fig. 2). The ground is not covered by litter.

Materials and methods

The investigation period lasted from July to November 1986 (140 days in total).

The microclimate at about 20cm above ground-level was recorded using 7-day recording thermohygrographs (Co. Lambrecht, Göttingen) and then digitalised with a micro-computer system (Tektronix). For further

analysis, the absolute and average weekly (Monday to Sunday) minima and maxima of temperature and relative humidity were evaluated.

The abundance of *C. terrestris* was determined by counting weekly the webs of the spider on fixed patches. These patches covered an area of 85m² (hedge 1) and 7m² (hedge 2), corresponding to about 8% and 6% of the total area of the hedges. This seemed to be enough to obtain reliable results (cf. Reise & Weidemann, 1975). Each web found was individually marked with a numbered flag (height c. 5cm) to examine how long the webs were occupied and how many new webs were built in the course of the study. Occupied webs can be distinguished easily by their bright and clean threads (cf. Tretzel, 1961).

The potential prey of *C. terrestris* are in principle all arthropods of appropriate size which contact the webs (Turnbull, 1973), especially carabids and other epigeic active beetles. The activity abundances of the ground-living beetles were therefore measured with pitfall traps.

Three trap types, single-traps, cross-traps and groove-traps were used. A single-trap consists of a metal cylinder (diameter 9.5cm, height 16.5cm), sunk into the soil to ground-level, containing a rubber-ringed marmalade-jar and with a plastic roof (12 × 12cm) to protect the trap from precipitation. A cross-trap consists of two crossed plastic strips (length 71cm, height 10cm), sunk c. 2cm perpendicularly into the

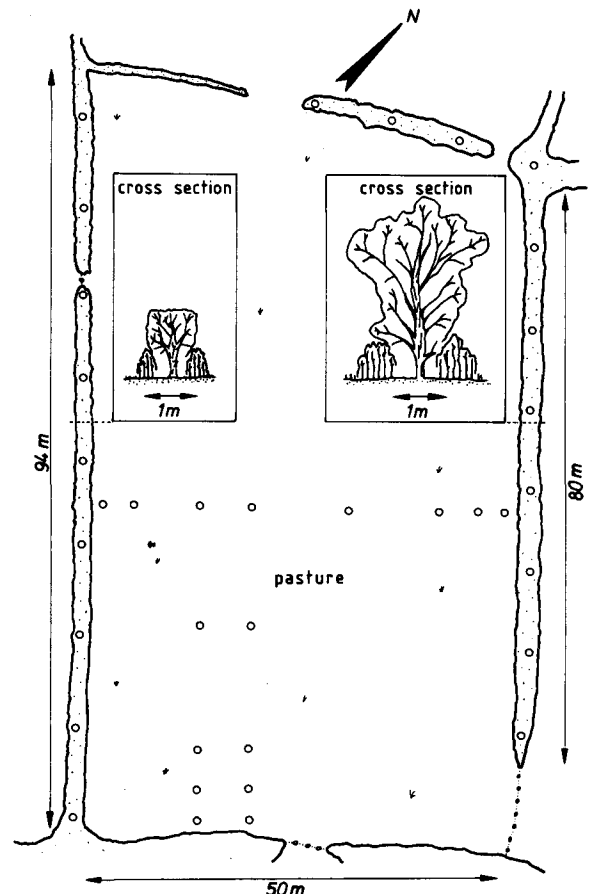


Fig. 2: Map of hedge 2 with pitfall-trap arrangement and cross-sections. Open circles = single-traps.

ground. In each of the four corners of the cross one single-trap (as described above) was installed. A groove-trap consists of a parallel double-chambered plastic groove (length 100cm, width 2×10 cm, height 8cm) sunk into the soil to ground-level. One single-trap (as described above) was placed at the end of each chamber.

Cross-traps and groove-traps have a higher trapping efficiency than single-traps because of their greater edge-length (Luff, 1975). In order to enable a direct comparison of the results from all traps, the catches were normalised on the single-traps. Ten single-traps, six cross-traps and four groove-traps installed in the central part of hedge 1 (Fig. 1) were compared, presuming the environmental conditions of these traps to be homogeneous. For each beetle species and each trap type, the catches over the whole investigation period were summed, treating the four jars of each cross-trap and the two jars of each groove-trap as one catch. The totals were first divided by the numbers of traps and then normalised using the single-trap value. The result gave 1:C:G (single-traps to cross-traps to groove-traps) with C and G being the factors used to standardise the catches of the cross-traps and groove-traps with respect to the single-traps.

In hedge 1 and the adjacent meadow a total of 32 single-traps, 15 cross-traps and four groove-traps were installed, and 36 single-traps were placed in hedge 2 and the adjacent pasture. These traps were arranged in such a manner that it was possible to discriminate between the activity abundances of the ground-living arthropods in the middle of the hedge, at the edge and at different distances in the meadow (hedge 1; Fig. 1)

and pasture (hedge 2; Fig. 2). All traps were emptied weekly; no preservative fluid was used.

Because the biomass of the potential prey could be another important criterion for its attractiveness for *C. terrestris*, some individuals of the most frequent beetle species were weighed (Sartorius 4501 Micro balance, $d = 0.001$ mg).

In order to determine the prey caught by *C. terrestris*, 59 webs from hedge 1 and 14 webs from hedge 2 were completely removed from the ground. In the laboratory the remains of the prey were dissected and identified. The hard parts of beetles (elytra, heads, etc.) were identified by comparison with a beetle collection.

The statistical evaluation was performed with the U-test (two-sample comparisons), the H-test and the Dunn-test (multiple-sample comparisons; see Sachs, 1978 and Gibbons, 1976).

Results

Microclimate

The temperature and relative humidity were less variable in hedge 1 than in hedge 2 (Fig. 3). Because of the lower surface/volume ratio of hedge 1 the take-up and loss of heat and the exchange of air were less than in hedge 2. Thus, the extremes of temperature and relative humidity were considerably greater in hedge 2 than in hedge 1 (Fig. 3). In hedge 2 the temperature maxima were up to 6°C higher and night frosts in late summer and early autumn appeared earlier and more often. The relative humidity reached 100% every night, whereas it was nearly always lower in hedge 1. During the day the air in hedge 2 was often more than 10%

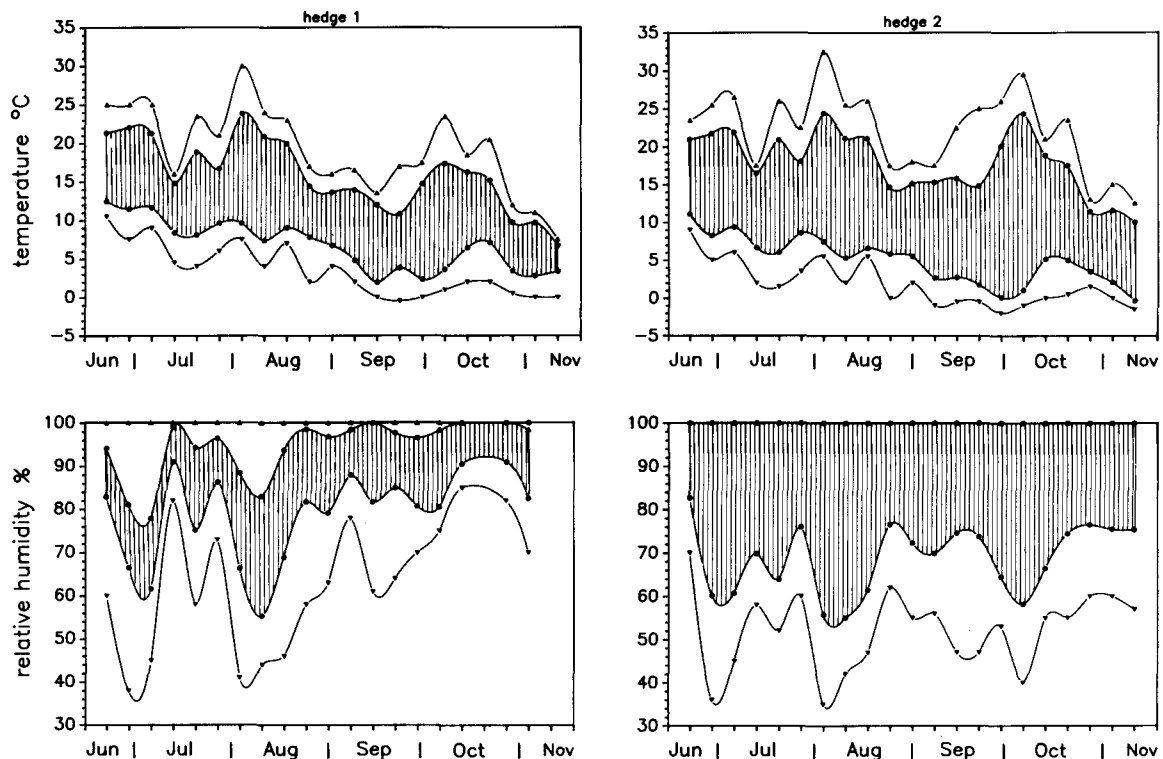


Fig. 3: Temperature and relative humidity in hedge 1 (left) and hedge 2 (right). Hatched area = range between average weekly minimum and maximum; triangles (top and bottom lines) = weekly absolute maximum and minimum.

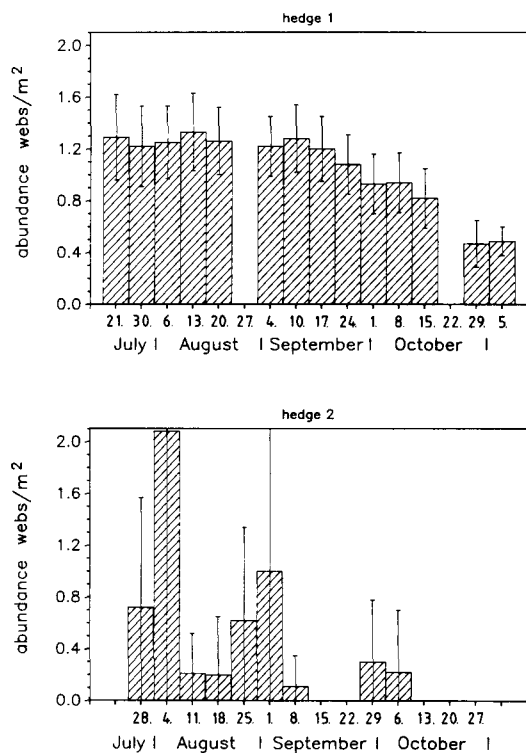


Fig. 4: Abundance of *C. terrestris* in hedge 1 (top) and hedge 2 (bottom) (mean \pm 95% c.i.). On 27 August, 15 September, 20 and 22 October no measurement could be carried out.

drier. The organisms here consequently have to tolerate greater differences in climatic conditions compared with those in hedge 1.

The litter-free soil of hedge 2 dried down to a depth of several cm in summer, as was noted while counting and removing the webs. In hedge 1, however, the litter-covered soil was always damp.

In sum the microclimatic conditions in hedge 1 can be described as woodland-like, whereas in hedge 2 they were more similar to those of open country.

Abundance of *C. terrestris*

During summer, the abundance of *C. terrestris* in hedge 1 reached a relatively constant value of about 1.2 webs/m² (Fig. 4, top). During autumn, the abundance decreased continuously to 0.4-0.5 webs/m², corresponding to less than half of the summer values. In hedge 2, the abundance of *C. terrestris* during summer reached an average of 0.8 webs/m², significantly lower than in hedge 1 (U-test, $p < 0.0001$). In addition the values were very variable from week to week (Fig. 4, bottom) and during autumn the abundance decreased to such an extent that no webs could be found after mid-October.

Because of the greater width of hedge 1 it was possible there to investigate how the webs of *C. terrestris* were distributed. In summer, the abundance of *C. terrestris* was significantly higher at the edge than in the middle of the hedge, and near the track significantly lower than in the other regions (H-test, $p < 0.001$; Dunn-test, $p < 0.05$; see Fig. 5, top). Later in

summer and autumn the abundance decreased more strongly at the edge than in the middle (Fig. 5, middle and bottom). On average, webs were not occupied for longer than 54 days (Fig. 6). At the edge of hedge 1 and near the track (but not in the immediate vicinity) *C. terrestris* stayed longer than in the middle and in the immediate vicinity of the track. Conversely, most of the newly built webs were found in the middle and not at the edge. This suggests that the spiders probably prefer the middle of the hedge for hibernation.

The prey of *C. terrestris*

From the 73 webs collected in both hedges the remains of 306 arthropods belonging to 38 species were dissected. Of these 64% were beetles (with carabids alone 31%) and 17% dipterans. *Forficula auricularia* accounted for 8% of the spider's prey, and the remaining 11% were other arthropods (Fig. 7).

C. terrestris captured arthropods of very different taxonomic groups and did not reject species capable of producing venomous or distasteful secretions (e.g. Julidae, Heteroptera, Carabidae; see Table 2). The spectrum of prey in hedge 1 with 34 species was considerably richer than in hedge 2 (23 species). Five mainly woodland-inhabiting carabids (*D. quadri-*

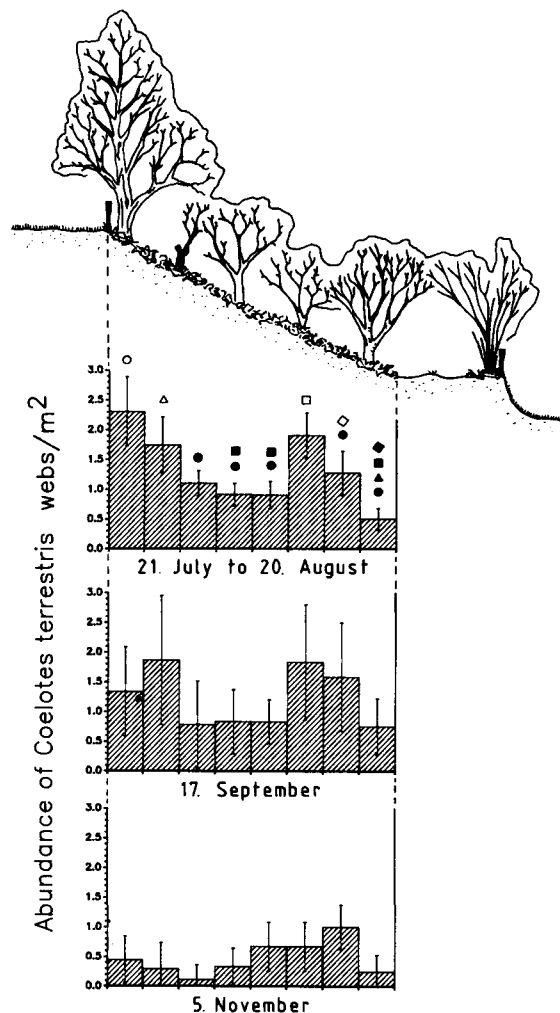


Fig. 5: Distribution of *C. terrestris* in hedge 1 in the course of the study (mean \pm 95% c.i.). Open symbols = abundance was significantly higher than in regions with corresponding closed symbols.

maculatus, *N. biguttatus*, *P. strenuus*, *S. nivalis* and *T. nitens*) were found only in webs from hedge 1. In comparison, *B. tetracolum* was recorded only in the prey in hedge 2. Here a greater influence of the grass-land-inhabiting species was evident, being shown for example by the higher proportion of *Tipula* spp. (adults and larvae) and *Platynus dorsalis* in the prey.

Of the carabid species occurring as prey in both hedges, the spiders in hedge 2 mostly captured more individuals per web, giving a total of about 50% more carabid individuals per web as compared with hedge 1 (Table 2). Nevertheless, *C. terrestris* in hedge 1 caught nearly the same total amount of Coleoptera individuals per web by catching a high proportion of the scarabaeid *Serica brunnea*. This indicates that the spiders use the species-richer prey supply in hedge 1, and can compensate for the reduced number of prey species in hedge 2 by capturing more individuals of each species.

Corresponding to its greater abundance in hedge 1, *C. terrestris* captured about 40% more prey items per square metre than in hedge 2. This could indicate a greater influence of the spider in the food-web of the community there.

According to their biomass the most frequent potential prey beetles can be divided into three groups (Table 3): (1) 'heavy beetles' like *Pterostichus madidus* (F.) and *P. melanarius* (Ill.), which at 113 and 158 mg are about 30-60% heavier than *C. terrestris*; (2) 'medium-weight beetles' like *Aphodius rufipes* (L.), *P. oblongopunctatus* (F.) and *Platynus assimilis* (Payk.), which reach about 50-70% of the spider's fresh-weight;

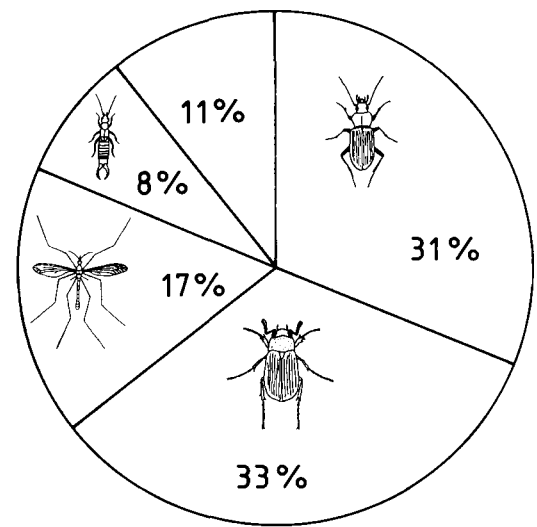


Fig. 7: Prey composition of *C. terrestris*. Carabids 31%, other Coleoptera 33%, Diptera 17%, *Forficula auricularia* 8% and other Arthropoda 11%; 100% = 306 individuals.

(3) 'light beetles' like *Sphaeridium scarabaeoides* (L.) and *Bembidion lampros* (Hbst), which are less than 30% of the weight of the spider.

Most of these beetles reached very different activity abundances in the two hedges. For example, *P. melanarius* and *Nebria brevicollis* were considerably more frequent in hedge 2 (Table 3); obviously, species like these which typically inhabit open country or edges of woodlands can invade a narrow hedge more effectively than a large one. On the other hand, typically woodland-inhabiting species like *P. madidus* and *S. brunnea* were considerably more frequent in hedge 1.

In both hedges *C. terrestris* captured nearly the same amount of prey individuals and biomass per web, but the composition of the prey was different (Table 4). No web contained the remains of a 'heavy beetle'; of the 'medium-weight beetles', *C. terrestris* preferred *S. brunnea* to the equal-weighted *N. brevicollis* in hedge 1. On the other hand, *N. brevicollis* was the predominate prey of the spiders in hedge 2. Individuals of the 'light beetles' were captured in both hedges and amounted to c. 22% of the beetle biomass caught. Remarkably high was the catch of *P. vernalis* in hedge 2, because this species was not captured there with the pitfall traps.

C. terrestris used the species-richer prey supply in hedge 1 and consequently had a more extensive prey spectrum there than in hedge 2. Nevertheless the feeding success of the spider was similar in both hedges, as expressed by nearly the same amount of captured biomass.

The beetle biomass captured by *C. terrestris* was higher near the edges of hedge 1 than in the middle. This was in agreement with the activity abundances of the potential prey beetles (positive edge-effect; see Fig. 8), indicating that the spiders (at least in summer, see Fig. 5) prefer locations for web-building with a relative high activity abundance of the potential prey.

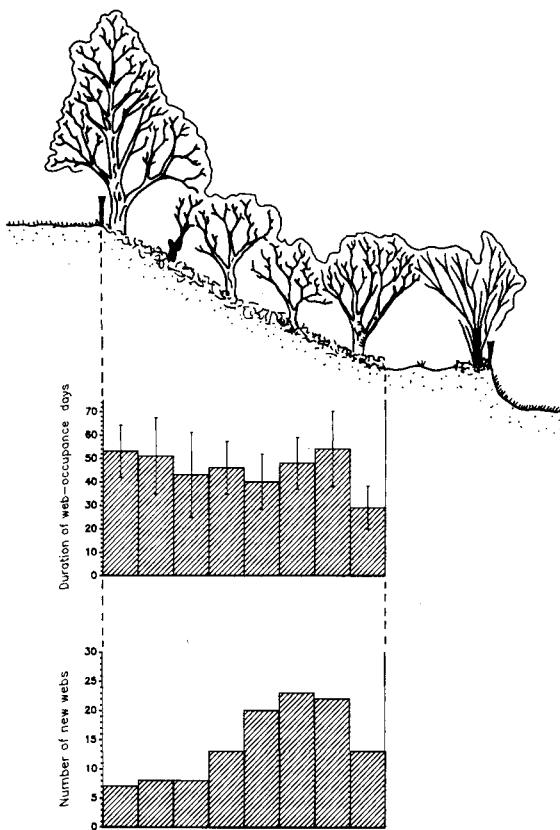


Fig. 6: Duration of web occupancy (mean \pm 95% c.i.) of *C. terrestris* in hedge 1 and number of newly built webs in the course of the study.

Discussion

The abundance of *C. terrestris* in the hedges investigated here (maximum 5 webs/m² in hedge 1) was relatively low, compared with results from beech forests, e.g. in the 'Solling' 15 individuals per square metre were found (Ellenberg *et al.*, 1986). The more montane climate and the deeper layer of litter there could be the reasons for the higher abundance of spiders. In a pine forest Tretzel (1961) found only 0.41 webs/m². Obviously deciduous woodlands are more suitable habitats for *C. terrestris* than coniferous forests. Investigators of hedges have mostly used pitfall-trapping to measure activity abundances (e.g. Blick, 1988; Tischler, 1948, 1950, 1958) or focused their interest on the higher strata (e.g. Zwölfer *et al.*, 1984); consequently their data cannot be used for a direct comparison here.

One main reason for the higher abundance of

C. terrestris in hedge 1 as compared with hedge 2 in summer is certainly the more woodland-like microclimate there. In addition to this microclimatic difference caused by the different measurements of the hedges (compare Mader & Müller, 1984) the exchange of air and soil moisture in hedge 2 was not hindered by litter. This direct loss of soil moisture led to the desiccation of the ground. Because *C. terrestris* depends on humidity-saturated air (Tretzel, 1961) it can be concluded that the soil in hedge 2 probably was too dry for permanent inhabitation (at least in the relatively warm and dry summer of 1986). However, the layer of litter in hedge 1 did not allow such a desiccation of the soil. The temperatures in both hedges did not imperil the spider's existence, since danger to life for *C. terrestris* by extreme temperatures occurs only above 43°C (Tretzel, 1961) and below -5.3°C (Kirchner, 1973).

The litter not only influenced the soil moisture, but

	Hedge 1		Hedge 2	
	Ind./web	Ind./m ²	Ind./web	Ind./m ²
Arthropoda total	4.03	5.12	4.86	3.74
Opiliona spp.	0.02	0.03	0.07	0.05
<i>Mitostoma chrysomelas</i> (Hermann)	0.02	0.03	—	—
<i>Paranemastoma 4-punctatum</i> (Perty)	—	—	0.07	0.05
Araneida: <i>Oxyptila praticola</i> (C. L. Koch)	—	—	0.07	0.05
Isopoda spp.	—	—	0.07	0.05
Myriapoda: Julidae sp.	0.03	0.04	0.14	0.11
Heteroptera spp.	0.08	0.10	0.07	0.05
Homoptera spp.	0.02	0.03	—	—
Hymenoptera spp.	0.03	0.04	0.07	0.05
<i>Myrmica</i> sp.	0.05	0.06	—	—
Diptera spp.	0.46	0.80	0.57	0.72
<i>Tipula</i> sp. adults	0.17	0.22	0.21	0.16
<i>Tipula</i> sp. larvae	—	—	0.14	0.11
Dermoptera: <i>Forficula auricularia</i> L.	0.32	0.41	0.43	0.33
Coleoptera total	2.69	3.40	2.86	2.20
Carabidae total	1.22	1.51	1.86	1.43
<i>Agonum muelleri</i> (Herbst)	0.07	0.09	0.07	0.06
<i>Amara</i> spp.	0.03	0.04	0.07	0.06
<i>Bembidion tetracolum</i> Say	—	—	0.07	0.06
<i>Dromius quadrimaculatus</i> (L.)	0.03	0.04	—	—
<i>Leistus ferrugineus</i> (L.)	0.02	0.03	0.07	0.06
<i>Loricera pilicornis</i> (F.)	0.17	0.22	0.21	0.17
<i>Nebria brevicollis</i> (F.)	0.25	0.32	0.71	0.55
<i>Notiophilus biguttatus</i> (F.)	0.07	0.09	—	—
<i>Platynus dorsalis</i> (Pontopp.)	0.14	0.17	0.21	0.17
<i>Pterostichus strenuus</i> (Pz)	0.02	0.03	—	—
<i>Pterostichus vernalis</i> (Pz)	0.32	0.41	0.43	0.33
<i>Synuchus nivalis</i> (Pz)	0.03	0.04	—	—
<i>Trichotichnus nitens</i> (Heer)	0.07	0.09	—	—
Hydrophilidae				
<i>Megasternum boletophagum</i> (Marsh.)	0.03	0.04	—	—
<i>Sphaeridium scarabaeoides</i> (L.)	0.03	0.04	—	—
Staphylinidae spp.	0.47	0.60	0.43	0.33
Elateridae spp.	0.05	0.06	0.07	0.05
<i>Agriotes pallidulus</i> (Ill.)	0.03	0.04	—	—
Tenebrionidae				
<i>Scaphidema metallicum</i> (F.)	0.02	0.03	—	—
Lagriidae: <i>Lagria hirta</i> (L.)	0.02	0.03	—	—
Pythidae: <i>Rhinosimus</i> sp.	0.02	0.03	—	—
Scarabaeidae: <i>Serica brunnea</i> (L.)	0.42	0.53	—	—
Curculionidae spp.	0.08	0.10	0.07	0.05
<i>Barypeithes araneiformes</i> (Schrk.)	0.08	0.10	0.14	0.11
Coleoptera indet. spp.	0.20	0.25	0.21	0.16
Insecta indet. spp.	0.15	0.07	—	—

Table 2: Prey of *Coelotes terrestris* from analysis of 73 webs (hedge 1: 59 webs, hedge 2: 14 webs). 306 prey items in total (hedge 1: 238, hedge 2: 68); number of prey caught per m² calculated from abundance 1.27 webs/m² (hedge 1) and 0.77 webs/m² (hedge 2).

also its structure, making many gaps and hollow spaces, offered the spiders many places for web-construction (Stippich, 1986). Therefore, the well-developed layer of litter in hedge 1 was also a direct cause for the higher abundance of *C. terrestris*.

Prey supply in the hedges investigated here cannot have been a limiting factor for the population density of *C. terrestris*, because no web contained remains of *P. melanarius* or *P. madidus*. Both species were among the most frequent beetles in the hedges, but it is known from laboratory experiments that *C. terrestris* only catches and feeds on them after long periods of starvation (Tretzel, 1961, and own experiments). Particularly in hedge 2 prey was abundant, as shown by the considerably higher activity abundances of the potential prey beetles, especially *N. brevicollis*, as compared with hedge 1.

The results show that carabids and other Coleoptera formed the basis of the food of *C. terrestris* (64% of prey individuals). The results of other authors confirm this: Tretzel (1961): 47% Coleoptera; Nentwig (1981): 70-80% Coleoptera; Nyffeler & Benz (1981): > 80% Coleoptera.

The detailed composition of the prey is determined by the species present locally. *S. brunnea* occurred almost exclusively in hedge 1 and was the most frequent prey species of *C. terrestris* there, whereas this was *N. brevicollis* in hedge 2. Obviously, the spider here could compensate for the low numbers of *S. brunnea* by increased predation on *N. brevicollis*. A comparison with a more distant investigation area shows the local influence more clearly. It was found in the 'Solling' that the most frequent prey species of *C. terrestris* are *Phyllobius argentatus* (L.) (Curculionidae), *Othius punctulatus* (Gze.) (Staphylinidae), *Athous subfuscus* F. (Elateridae) and *Pterostichus oblongopunctatus* (F.) (Carabidae) (Ellenberg *et al.*, 1986).

Apart from activity abundance, ease of handling of

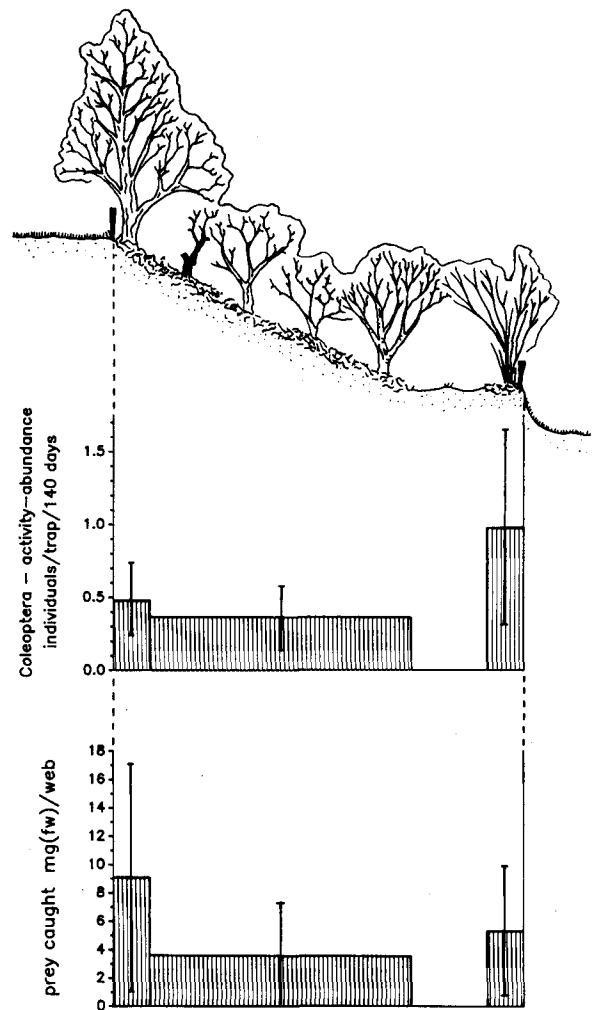


Fig. 8: Distribution of activity abundance of potential prey (top) and prey caught by *C. terrestris* (bottom) in hedge 1 (mean \pm 95% c.i.).

	mg fresh-weight			Activity abundance			
	mean	95% ci	n	Ind./trap/140 days			
				Hedge 1	Meadow	Hedge 2	Pasture
<i>Pterostichus madidus</i>	133	6.4	14	1.29	0.00	0.15	0.00
<i>Pterostichus melanarius</i>	158	24.9	7	0.58	10.29	5.45	19.50
<i>Aphodius rufipes</i>	69	—	1	0.55	0.19	0.20	0.00
<i>Serica brunnea</i>	63	—	1	0.58	0.00	0.05	0.00
<i>Nebria brevicollis</i>	61	1.9	167	1.57	9.05	6.05	6.82
<i>Calathus fuscipes</i>	61	—	1	0.10	0.24	0.05	0.00
<i>Pterostichus oblongopunctatus</i>	54	9.3	7	0.03	0.00	—	—
<i>Platynus assimilis</i>	52	7.8	3	0.38	0.00	—	—
<i>Sphaeridium scarabaeoides</i>	28	—	1	0.31	0.24	—	—
<i>Amara spp.</i>	24	5.3	18	0.20	0.67	—	—
<i>Agonum muelleri</i>	21	2.4	15	0.10	0.57	0.35	0.63
<i>Loricera pilicornis</i>	15	1.2	4	0.17	0.14	0.10	0.19
<i>Pterostichus vernalis</i>	14	1.0	30	0.17	0.29	—	—
<i>Pterostichus strenuus</i>	11	4.9	4	—	0.09	—	—
<i>Trichotichnus nitens</i>	11	—	*	0.86	0.05	—	—
<i>Notiophilus biguttatus</i>	6	0.5	11	0.07	—	—	—
<i>Leistus ferrugineus</i>	4	—	1	0.10	—	—	—
<i>Bembidion lampros</i>	3	0.1	27	—	0.10	0.05	0.19
Total	—	—	—	5.77	21.92	12.30	27.33

Table 3: Biomass (mean \pm 95% confidence interval) and activity abundance of potential prey (Coleoptera) of *Coleotes terrestris*. * = biomass estimated from body length.

the prey determines its attractiveness for *C. terrestris*. This is influenced by e.g. biomass, body length, hardness and mobility of each prey species. *S. brunnea* is less armoured and less mobile than *N. brevicollis* and was therefore captured in hedge 1 in a considerably higher proportion than the carabid, despite its three-fold lower activity abundance. Similarly, the relatively high proportion of *Forficula auricularia* in the prey of the spider might be the consequence of its short elytra, which leave most of the abdomen unprotected. *P. madidus* and *P. melanarius* obviously are so heavy that *C. terrestris* does not catch them if other prey are abundant.

In conclusion, the spider seems to prefer prey species with high activity abundances and a biomass of about two-thirds of its own (*F. auricularia* has a fresh weight of $73 \text{ mg} \pm 15 \text{ mg}$ ($n = 6$)). This conclusion is confirmed by Nentwig & Wissel (1986) who found arthropods with a body length of 50-80% of the spider's to be the most frequent prey.

C. terrestris is described by some authors as a specialised beetle feeder (Nyffeler & Benz, 1981). Of course the meaning of such a specialisation, if it exists at all, must be understood as the spider's reaction to the prey supply and not as an active preference for beetles. The capture of a well armoured carabid is not easy, although for a robust spider like *C. terrestris* it does not pose an insurmountable problem. Preference can easily be shown by offering the spider soft-skinned arthropods, e.g. beetle larvae, which it prefers over hard-shelled ones (Tretzel, 1961, and own experiments; compare also Turnbull, 1973).

C. terrestris seems to react to local differences of prey supply. Its higher abundance at the edge of hedge 1 in summer can be interpreted as a numerical reaction to the higher prey activity abundance. This interpretation is confirmed by results of laboratory experiments, where *Amaurobius similis* (Blackwall) and

Achaearanea tepidariorum (C. L. Koch) built their webs in locations with higher prey supply (Gillespie, 1981; Turnbull, 1964, and other authors; synopsis in Riechert & Harp, 1987), and by the positively correlated activity abundances of epigeic spiders and their potential prey (Nentwig, 1982). In contrast to this Greenstone (1978) after field studies on *Pardosa ramulosa* (McCook) indicated that numerical reactions of spider populations under natural conditions are not provable, because prey are abundant. Of course, the foraging strategies of *P. ramulosa* and *C. terrestris* are quite different and consequently cannot be compared directly.

The results of this work demonstrate that hedges can be suitable habitats for normally woodland-inhabiting spiders. It is apparent from this study that a hedge should have a width of several metres to enhance the possibility of development of a layer of litter and a woodland-like microclimate (compare also Glück & Kreisel, 1988). Nevertheless, a very narrow hedge can be colonised by *C. terrestris* in climatically suitable years, but longer periods of warm and dry weather cause desiccation of the soil and increasingly unsuitable conditions for hygrophilous organisms. If a hedge contacts other woodlands, it can be newly settled or recolonised from there, or it can serve as a connecting element between two woodlands. Such contacts are especially important for narrow hedges.

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	Hedge 1		Hedge 2	
	Ind./web	mg/web	Ind./web	mg/web
<i>Pterostichus melanarius</i>	—	—	—	—
<i>Pterostichus madidus</i>	—	—	—	—
<i>Aphodius rufipes</i>	—	—	—	—
<i>Serica brunnea</i>	0.42	26.80	—	—
<i>Nebria brevicollis</i>	0.25	15.61	0.71	43.84
<i>Calathus fuscipes</i>	—	—	—	—
<i>Pterostichus oblongopunctatus</i>	—	—	—	—
<i>Platynus assimilis</i>	—	—	—	—
<i>Sphaeridium scarabaeoides</i>	0.03	0.96	—	—
<i>Amara</i> spp.	0.03	0.82	0.07	1.52
<i>Agonum muelleri</i>	0.07	1.44	0.07	1.52
<i>Loricera pilicornis</i>	0.17	2.55	0.21	3.22
<i>Pterostichus vernalis</i>	0.32	4.52	0.43	6.02
<i>Pterostichus strenuus</i>	0.02	0.19	—	—
<i>Trichotichnus nitens</i>	0.07	0.75	—	—
<i>Notiophilus biguttatus</i>	0.07	0.40	—	—
<i>Leistus ferrugineus</i>	0.02	0.06	0.07	0.25
<i>Bembidion lampros</i>	—	—	—	—
Total	1.47	54.10	1.56	56.37

Table 4: Prey (Coleoptera) caught by *Coelotes terrestris*. Individuals per web and mg (fresh weight) per web.

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