

FIELD OBSERVATIONS ON THE POPULATION STRUCTURE OF THREE CTENID SPIDERS (*CUPIENNIUS*, ARANEAE, CTENIDAE)

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ABSTRACT. The population structure of three large species of the genus *Cupiennius* was evaluated. Although solitary, 45% of *C. coccineus*, 40% of *C. salei* and 30% of *C. getazi* spiders were found on plants together with one or more conspecifics. The adult sex ratio (males : females) was 1:1.2 for *C. salei* (1989, $n = 52$), 1:1.3 for *C. coccineus* (1990, $n = 75$) and 1:1.6 for *C. getazi* (1990, $n = 29$). The ratio of adults : immatures was 1:0.5 for *C. salei*, 1:1.8 for *C. coccineus* and 1:1.3 for *C. getazi*. The two sympatric species, *C. coccineus* and *C. getazi*, sometimes occur on the same plants and are therefore considered syntopic. In all three species spider density is correlated with the number of the retreats offered by their dwelling plants. We found up to 0.2 adults/plant for *C. salei* and 0.3 adults per plant for *C. coccineus* and *C. getazi*. *Cupiennius* spiders, particularly the males, change their dwelling plants quite often. On average, *C. salei* males could only be found for 0.5 day on the same plant without interruption (five days observation time), *C. coccineus* males for one day (21 days observation time) whereas females with eggsacs of these two species stay significantly longer (3.5 days and 8 days, respectively; 21 days observation time). Considering the rather high population density and the frequent changes of the dwelling plants (the males in particular), interactions between spiders seem very likely. In the lab, male competition in addition to courtship between the sexes is elicited by male vibratory courtship signals. Overt fights between males were observed in the field.

Wandering spiders of the genus *Cupiennius* Simon 1891 (Araneae, Ctenidae) are solitary and nocturnal. They live on monocots, such as bromeliads and banana plants. The leaves of these plants provide protective retreats for the spiders at their base where they form narrow spaces (chalices) with openings only at their upper side (see Fig. 2). During the day the animals hide in these spaces (Barth et al. 1988b). At night the spiders come out of their retreats to ambush, to prey and to court on their dwelling plants. Upon contact with female silk, the male is aroused and emits vibratory courtship signals. These are propagated across the plant and elicit vibratory responses in a female if she is motivated and within the reach of the male vibrations (Barth 1985; Rovner & Barth 1981). The male courtship signals elicit competition behavior in other males. Rivals approach each other and fight, the winner then copulates with the female (Schmitt et al. 1992). Adult *Cupiennius* males show higher locomotor activities than females without an egg-sac. It is suggested that this is due to sexually motivated searching behavior (Schmitt et al. 1990). Between the sympatric species *C. cocci-*

neus and *C. getazi* several ethological mating-barriers are known to exist and only 13% of the females of these two species respond to the courtship signals of males of the other species (Barth & Schmitt 1991).

The study of questions related to sexual selection (Schmitt et al. 1990, 1992) and species recognition (Barth & Schmitt 1991), which are currently the focus of our interest, requires not only quantitative analysis of behavior in the laboratory as mentioned above but also information on the density and structure of spider populations and information on intra- and interspecific interactions in the field. Do the spiders live densely enough to make male-male interactions likely? When males meet, do they actually fight for females, as shown in the lab? In search for females, do males change their dwelling plants more often than females? Do the sympatric species actually share their dwelling plants, i. e., are they syntopic?

Here we report on field observations made in Central America on the three large species of the genus, *C. salei*, *C. coccineus* and *C. getazi* (Lachmuth et al. 1984). The ranges of *C. salei* and of

Table 1.—Population densities of three *Cupiennius* species (maxima observed in the wild). (1) *Musa sapientium* ($n = 167$); (2) *Aechmea mexicana* ($n = 86$); (3) *Aechmea maria reginae* ($n = 12$), *Vrisea regalis* ($n = 14$); (4) *Aechmea mexicana* (1989: $n = 17$; 1990: $n = 37$), *Guzmania zani* ($n = 8$); (5) *Xanthosoma sagittifolium* (1989: $n = 46$; 1990: $n = 144$); (6) *Gynerium sagittatum*; —data not available.

Spiders	Plants	Year	Adults (n)	All (n)	Density of adults per			Density of all spiders per		
					m ²	plant	retreat	m ²	plant	retreat
<i>C. salei</i>	banana plants (1)	1989	37	47	0.04	0.2	0.2	0.1	0.3	0.3
	bromeliads (2)	1989	15	35	1.7	0.2	—	3.9	0.4	—
<i>C. coccineus</i>	bromeliads A (3)	1989	8	25	0.3	0.3	—	0.8	1.1	—
		1990	5	26	0.2	0.2	0.01	0.9	1.0	0.04
	bromeliads B (4)	1989	8	12	0.5	0.3	—	0.8	0.5	—
		1990	5	10	0.3	0.1	0.01	1.5	0.2	0.03
<i>C. getazi</i>	Araceae (5)	1989	14	42	0.5	0.3	—	1.4	0.9	—
		1990	14	189	0.1	0.1	0.01	1.1	1.3	0.2
	Poaceae (6)	1989	0	0	0.0	—	—	0.0	—	—
		1990	9	54	0.5	—	—	2.8	—	—

the other two species do not overlap whereas *C. coccineus* and *C. getazi* live sympatrically (Barth et al. 1988b).

METHODS

Spiders were observed mainly during the night between 1900 h and 2400 h. This is the period of maximum locomotor activity (Barth & Seyfarth 1979; Schmitt et al. 1990) when the spiders leave their retreats to prey and court on the leaf surfaces. Plants with easy-to-inspect retreats, such as those of *Xanthosoma* and *Musa*, were searched for spiders during the day, too. In accordance with our experience in the field all leaf bases forming openings 20 mm or more in width were considered potential retreats. Spiders were marked with small color spots (correction fluid) on their prosoma and/or opisthosoma and/or legs.

Cupiennius salei.—Observations were carried out in Mexico (Fortin de las Flores in the state of Veracruz) between 10–14 February 1989. We investigated an untended patch (9 m²) of 86 bromeliads (for names of plant species see Table 1) and an untended site of banana plants (1000 m²), the latter forming 24 groups each consisting of 3–15 individual plants. The banana plants were up to six m high. We searched for spiders up to a height of approximately two meters. We counted the number of individuals found in the 24 groups of banana plants (9 counts in 4 days) and correlated the mean number of spiders of each group with the number of plants and retreats.

Cupiennius coccineus.—Spiders of this species were observed in the south-west of Costa Rica at the Wilson Botanical Garden of the Organisation for Tropical Studies (OTS), near San Vito, Coto Brus, between 5–15 March 1989 and between 3 January–25 February 1990. Two patches with bromeliads planted on the ground (A = 30 m², B = 15 m², see Table 1) and four small groups of banana plants were investigated. Most of the bromeliads had been untended from two months prior to our investigations onward. In patch B, 20 bromeliads, which had been planted only three days before investigations in 1990 started, were not treated separately from the untended bromeliads in our observations. In a homogeneous group of 12 bromeliads (*Vrisea regalis*, part of patch A) the plants were assigned to two categories based on the number of retreats (category 1: ≤ 21 , category 2: > 21 retreats; 6 plants per category). The mean numbers of animals encountered on each plant and day (\bar{x}) of both categories were compared. *C. coccineus* was also observed at the OTS station in La Selva and near Cahuita, Costa Rica and near Colon and Portobello in Panama (for details see below).

Cupiennius getazi.—We observed *C. getazi* in the north-east of Costa Rica at the La Selva Biological Station of the OTS between the 26–27 February 1989 and between the March 1–April 6, 1990. Data were obtained from four patches (1989: 30 m², 1990: 98, 46, and 28 m²) in a dense stand of *Xanthosoma* and from a 20 m² patch in a temporary swamp covered with grass in the

primary forest (see Table 1). The swamp had dried up four weeks and one week before our investigations in 1989 and 1990, respectively. We searched for spiders along roughly 2000 m (1989) and 3000 m (1990) of wayside of the trails of La Selva up to a height of approximately two meters. Several small groups of banana plants near the forest were also investigated.

All *Xanthosoma* patches were examined for spiders three times within a week, except one patch which was examined only once in 1990. The number of spiders per plant and the number of retreats per plant did not differ significantly among the patches. For each year we summed up all counts of all patches in order to get sufficient data for statistical analysis, resulting in a total of 135 plants and 94 spider counts in 1989, and 507 plants and 326 spider counts in 1990. The plants were grouped to form seven categories having from 2–8 retreats per plant.

C. getazi spiders were also observed near Colon in the Panama Canal Zone on grass at the edge of a forest (150 m²), near Portobello, Panama, in a patch densely overgrown with *Xanthosoma* and *Heliconia* (800 m²) and near Cahuita, Costa Rica, in a patch very similar to that of Portobello (900 m²). These patches, in which we expected *C. getazi* to live syntopically with *C. coccineus*, could be searched for spiders only once.

RESULTS

***Cupiennius salei*.**—The dense bromeliad patch in Fortin de las Flores had the highest population density found for any of the *Cupiennius* species (adults: 1.7/m²; total: 3.9/m²; Table 1). On banana plants, population density is highly correlated with the number of the available retreats (Pearson's $r = 0.87$, $n = 24$, $P < 0.001$). The number of spiders and the number of available plants are more weakly correlated ($r = 0.47$, $n = 24$, $P < 0.05$).

The sex ratio of adults was 1:1.2 (males : females; $n = 52$). Of all the spiders observed, 32% were juveniles. Each time we found a spider we recorded the simultaneous presence of conspecifics on the same plant. All counts were summed (Fig. 1). Most of the juveniles were found alone on their dwelling plants, but about 28% and 18% of the adults were found to share their dwelling plant with conspecific females and males, respectively (Fig. 1). We also observed two males courting and fighting close to a retreat occupied by a female (Fig. 2).

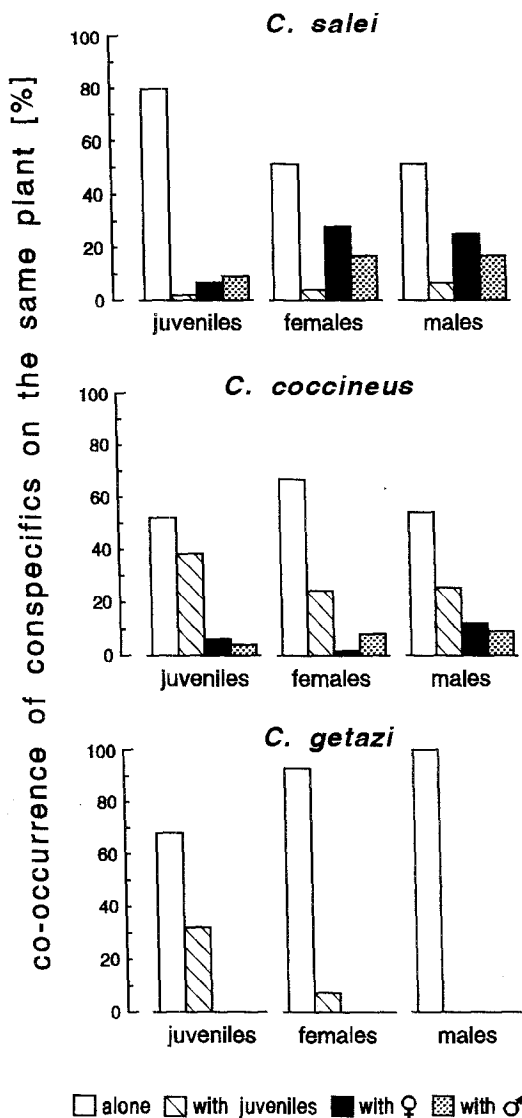


Figure 1.—Co-occurrence of conspecific individuals on the same plant (banana plants, bromeliads, yantia plants (*Xanthosoma*)) evaluated for three species of the genus *Cupiennius*. N = number of observed spiders, n = number of observations. *C. salei*: $N = 47$, $n = 47$; *C. coccineus*: $N = 107$, $n = 673$; *C. getazi*: $N = 146$, $n = 334$.

Females of *C. salei* carrying an eggsac usually close their retreat firmly with a sheet-web and do not leave it until the spiderlings hatch (Melchers 1963). In two cases, however, we observed males courting and then copulating with a female carrying an eggsac.

For how long do spiders dwell on the same plant without interruption (hereafter called res-

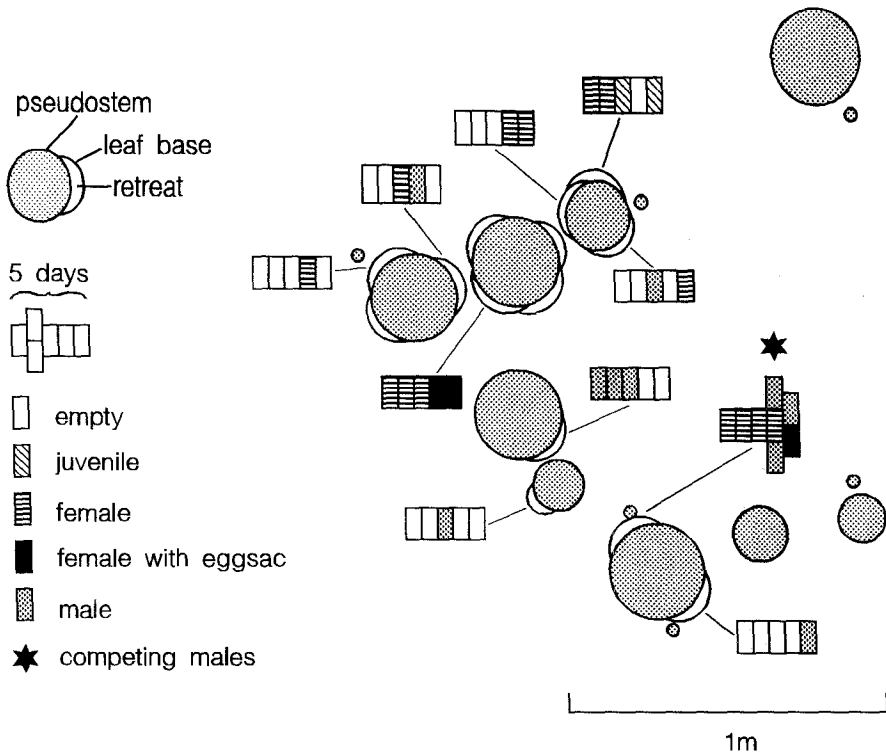


Figure 2.—*C. salei* spiders found on a group of banana plants. The locations of females, males and juveniles are shown over a period of five days. Two of the females built an eggsac during the observation period. Two males were fighting close to a female sitting in her retreat (see asterisk). All observations were made at night.

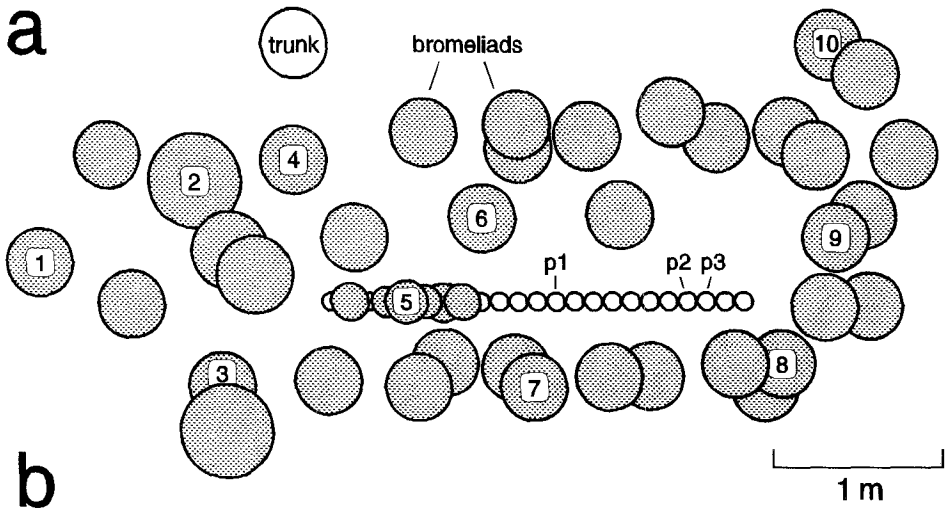
idence time)? On banana plants (observation time five days), females with eggsacs stay significantly longer than both females without an eggsac and males; females with eggsacs: median = 3.5 days, range 1.5–5 days, $n = 7$; females without eggsac: 0.5 day, 0.5–5 days, $n = 16$; males: 0.5 day, 0.5–3.5 days, $n = 14$; ($df = 2$, $P < 0.005$; Kruskal-Wallis analysis of variance, Siegel & Castellan 1988). Residence times of females without eggsac and of males do not differ from each other (observation time 5 days).

***Cupiennius coccineus*.**—The population density of adults in bromeliad patch B in Las Cruces was higher in 1989 than in 1990 (0.3 and 0.1 adults/plant, respectively, Table 1). In the primary forest of La Selva we roughly estimated one adult *C. coccineus* every 50 m along the trail in 1989. In 1990 the only *Cupiennius* spider we found was one *C. coccineus* female along the entire stretch searched. On bromeliads we found significantly more animals on plants of category 2 with more retreats ($\bar{x} = 1.24 \pm 1.02$, $P < 0.01$) than on those of category 1 with fewer retreats

($\bar{x} = 0.23 \pm 0.46$, t -test, $df = 102$; 149 encounters in 17 days).

The sex ratio of adults was 1:1.3 (males : females; $n = 75$). Of all the spiders observed, 63% were juveniles. *C. coccineus* was more often co-occurring with conspecifics than *C. salei*. Still about 60% were sitting alone on their plant (Fig. 1). The maximum accumulation of spiders we observed was on a big bromeliad (*Aechmea mexicana*, diameter 2 m) where three males courted and fought in the presence of one female and one juvenile.

Females with eggsacs had their retreats closed by a sheet-web. Unlike *C. salei*, eggsac-carrying females of *C. coccineus* leave their retreats temporarily. We found the retreat (and dwelling plant) of such a female (female B, Fig. 3) empty on 2 February at 1815 h, but the same day at 2120 h the female had returned. Nevertheless, females carrying an eggsac are similar to *C. salei* in remaining significantly longer on the same plant (median = 8 days, range 2–12 days, $n = 5$) than both females without eggsac (median = 2 days,



location	day of february															
	1	2	5	6	8	10	12	13	14	16	17	18	19	21	23	24
1						5						H				
2		4						H	H	H			H	H		
3	A	A	A	A	A	A	A	A	A		A	A	A	G	G	
4							G	G								
5	1	1	1	1	1	1	1	1								
6						G										
7	B	B														
8	2															
9		E	E													
10	3				F	F		F			F	F	F	F	F	F
trunk	C	C										G				
p 1			D													
p 2	D															
p 3		D														

Figure 3.—*C. coccineus* spiders dwelling on bromeliads (see bromeliads B, 1990, Table 1). (a) The site with 8 *Guzmania zani* growing on approximately 1.5 m high bamboo posts (p) and 37 *Aechmea mexicana* growing on the ground. Labels of bromeliads (1–10) and posts (p1–p3) refer to location codes in (b). (b) The locations of adult females (A–G) and males (1–5) were observed over a period of 24 days (juveniles not shown). Females A and B were carrying eggsacs and were sitting in retreats closed by loose sheet-webs. All observations were made at night.

range 1–13 days, $n = 14$) and males (median = 1 day, range 1–12 days, $n = 19$, Kruskal-Wallis test, $df = 2$, $P < 0.05$). Residence times of females without eggsac and males do not differ from each other (Kruskal-Wallis test, ns ; observation time 21 days).

Cupiennius getazi.—Spider density was calculated for the *Xanthosoma* area and the swamp area (Table 1). Dramatic differences between the two observation years were found in the swamp area. Whereas in 1990 spider density was high, in 1989 we did not observe a single specimen.

In the primary forest we found *C. getazi* on a few bromeliads growing on the ground. In the *Xanthosoma* patches the number of spiders per plant was positively correlated with the number of retreats on the plants (1989: Spearman's $r_s = 0.94$, $P < 0.05$; 1990: $r_s = 1.0$, $P < 0.01$), but not with the number of plants (1989: $r_s = -0.66$, ns ; 1990: $r_s = -0.39$, ns).

The sex ratio of *C. getazi* was 1:1.6 (males : females; $n = 29$). Of all the spiders observed, 93% were juveniles. Fig. 1 shows that only juveniles co-occur on the same individual plant to

any appreciable extent (max. three juveniles). We observed two pairs copulating and one courting male in front of a female sitting in her retreat. *C. getazi* (like *C. salei* and *C. coccineus*) is able to form retreats by drawing together leaves and joining them with threads but eggsac-carrying females were rarely observed to close their retreats with a sheet web.

Syntopy.—In all four areas within the geographic range of *C. getazi* and *C. coccineus* (La Selva, Colon, Portobello and Cahuita), we found both species on the same plant species and sometimes on the very same plants. There is no evidence that the different species use different parts of the plants. In La Selva we found *C. getazi* living syntopically with *C. coccineus* on banana plants. In the primary forest of La Selva *C. coccineus* and *C. getazi* were found only at a distance of at least 8 meters and never on the same plants.

DISCUSSION

Encounters.—When moving about, females leave pheromone-laden draglines on the plant. Since *Cupiennius* spiders quite often change their dwelling plant and locomotor activity is particularly high in males (Schmitt et al. 1990), a male is quite likely to come across female threads when wandering. Upon contact with these threads the male starts courting and a series of behavioral mechanisms ensures species recognition and reproductive isolation (Barth & Schmitt 1991). The vibratory courtship signals emitted by the male and the female spread in the plant (Barth et al. 1988a) for several meters. Considering the spider densities reported here it is very likely that not only females but also other males perceive these signals. From behavioral experiments with *C. getazi* in the lab we know that males perceiving male courtship signals react to these with vibratory competition signals. Rivals approach each other and fight, the winner then copulates with the female (Schmitt et al. 1992). Although the time periods of our observations in the field were limited (e. g., five days for *C. salei*) we did observe fighting *C. salei* and *C. coccineus* males in the presence of a nearby female. High population densities reported in this paper (e. g., 0.2 adults per plant for *C. salei*) are within the range found by Barth & Seyfarth (1979) on banana plants in Guatemala (0.4 adults per plant). Considering the high population densities and that the signals can be detected by the spiders at least four meters away from the source (Schmitt et al. pers. obs.); we suggest that encounters and fights between

males are frequent and that the behavioral scenarios examined in the lab are highly significant.

Retreats.—*Cupiennius* hides in retreats during the day. Protection from predators and from desiccation are proposed to be the main reasons for this behavior (Barth et al. 1988b). As shown here the number of available retreats rather than the number of available plants correlates with spider density. Curiously, we found *C. getazi* living densely in a swamp in 1990 (La Selva) where vegetation provided no leafsheath-like retreats (Table 1). Spiders sat on the leaves clearly visible even during the day. High density of prey animals may have led to high spider densities despite the lack of retreats in this area (Wise 1993). The swamp had dried up only one week prior to our investigations, and there was a large number of dragonflies on which the spiders preyed. In 1989 the swamp had already been dry for four weeks before our inspection. Dragonflies were lacking and we found no *C. getazi* in this area. *C. getazi* spiders were also reported to dwell densely in the swamp area in 1985 (Barth et al. 1988b) at a time when it had not dried up yet (Barth, pers. obs.).

Juveniles.—In contrast to the juveniles of the other two species, the majority of the juveniles of *C. salei* was found alone on their plants (Fig. 1). This finding may be an artifact, however, resulting from our method of investigation. The banana plants, on which our data for *C. salei* were obtained, could be searched for spiders only up to a height of approximately two meters. This is the area of the big leaf bases which form retreats suitable for adult spiders. The smaller juveniles preferably occur in higher regions of the plants or in the leaf litter on the ground (Barth & Seyfarth 1979). Accordingly, only 32% of *C. salei* spiders observed in the bananas were juveniles. Percentages of juvenile spiders found on other plants were 57% for *C. salei* in bromeliads, 63% for *C. coccineus* in bromeliads and 93% for *C. getazi* in *Xanthosoma*.

Life cycle.—In the lab, *Cupiennius* lives for about two years. Maturation takes place at an age of approximately nine months. The spiders court, copulate and build eggsacs during any time of the year. In the field, spiders of different sizes, ranging from newly hatched spiderlings up to adults co-occurred in all areas investigated between January and April. The general impression was the same during a visit to Costa Rica in the summer months (Barth pers. comm.). Details were never quantified, however. Maturation of

Cupiennius seems not to be synchronized in either the laboratory or the field.

Sex ratio.—In all three species we found more females than males. This may have two possible causes, which are not mutually exclusive. First, due to their higher locomotor activity (Schmitt et al. 1990) males might be preyed upon more often (sometimes even by the females during courtship). Second, this finding might be an artifact. At night females usually sit in or near their retreats, which can be inspected quite easily. Males have a higher locomotor activity and change their dwelling plants more often than the females. When wandering about on the plant or on the ground the males might be more easily overlooked than the females in their retreats. Considering this possible error the sex ratio measured by us may be slightly balanced towards the females.

Sympatry and syntopy.—Observations in Panama and Costa Rica prove the syntopy of the two sympatric species, *C. coccineus* and *C. getazi*. In the dense *C. getazi* populations of La Selva (*Xanthosoma*, grass), however, we never found *C. coccineus*. Populations of different species might overlap only at their peripheries.

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