SOME OBSERVATIONS ON THE BIOLOGY OF CAMISIA CARROLLI (ACARI : ORIBATIDA) 1

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ORIBATID MITE
HABITAT
FOOD

SUMMARY: Camisia carrolli was found to be one of the most abundant mites on Douglas fir (Pseudotsuga menziesii (Mirb.) Franco) in the western Cascade Mountains of Oregon. It occurs at maximum density in the upper portion of the canopy. Five to eight years-old twigs with needles still attached constitute its optimum microhabitat. This mite is mycophagous and probably feeds on pioneer fungi colonizing young twigs. Fungi and other detritus cover it completely and may help it endure drought.

ORIBATE HABITAT COMPORTEMENT ALIMENTAIRE RÉSUMÉ: Camisia carrolli est l'un des acariens les plus abondants sur le pin Douglas (Pseudotsuga menziesii (Mirb.) Franco) dans la chaîne des Cascades (Orégon, U.S.A.). Sa densité est maximale dans la strate supérieure de l'arbre. Les jeunes rameaux encore couverts d'aiguilles et âgés de 5 à 8 ans constituent son microhabitat optimal. Cet acarien est mycophage et se nourrit vraisemblablement des champignons pionniers envahissant les jeunes rameaux. Il est hydrobionte et cesse toute activité en cas de sécheresse. Des champignons et autres détritus le recouvrent entièrement et l'aident sans doute à supporter la sécheresse.

The canopy of large trees has always held promise of interesting arthropod inhabitants; however, the difficulty of access has limited research possibilities. Recently, access techniques have been developed (DENISON et al. 1972) and thus investigations of this habitat are now posible.

A two year survey of the canopy of old growth Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) was carried out in conjunction with a research program on nutrient cycling in canopies of large coniferous trees. A variety of sampling techniques were used and a large number of arthropod species were collected. The Acari were

one of the most abundant and widespread groups; Camisia carrolli André, 1980 was found to be the most abundant of the mites associated with the twig surface. The food preferences, macro- and microdistribution of this mite were examined in some detail.

METHODS

A survey of the Douglas fir canopy arthropods was carried out in old growth trees on watershed 2 of the H. J. Andrews Experimental Forest,

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75 km east of Eugene, OR, U.S.A. in the Cascade Mountains. The trees sampled are located in a stand corresponding to the Tshe/Rhma/Bene community type of FRANKLIN and DYRNESS (1973). Access to the canopy of several trees was available, but the samples used to provide the data for this paper were all taken from one tree (named Neptune, with a dbh of 2 m, height of 80 m and age of approximately 450 years). The techniques used to get up into the canopy are modified from rock climbing and are described in detail by DENISON et al. (1972). Movement up and down the tree is effected on permanently attached ropes, minimizing the impact of repeated climbs.

The structure, biomass and surface area of Neptune have been determined using methods described by PIKE et al. (1977) and sample selections were based on these background data. The data presented here are in part the result of sampling the foliage (twigs and associated needles) during the general canopy arthropod survey. Periodically samples were taken for the sole purpose of determining the microdistribution of *C. carrolli*.

The sampling unit was either a living branchlet, small cuttings of twig and associated needles or a dead branchlet without needles. Samples varied from 10-15 g dry weight and generally contained twigs up to 10 years old. Samples were randomly chosen from branches in three canopy strata: lower (24-54 m), middle (54-65 m) and upper (65-80 m). The strata were delimited such that totals of projected branch area were approximately equal in each (PIKE et al. 1977). Processing samples in the lab consisted of washing each sample thoroughly under a strong jet of water and filtering the wash through a set of nested sieves consisting of 16, 40, 100 and 200 mesh stainless steel cloth (pore size 1.13 mm, 380 μ m, 140 μ m and 74 μ m respectively). The contents of each sieve were examined and all C. carrolli were counted. This technique was found to be more effective than Berlese extraction for removing Camisia from the twig surface (see ANDRÉ and LEBRUN (1979) for Berlese extraction efficiency).

From Sept. 1976 to Sept. 1977 one living and one dead branchlet were taken from one branch

within each canopy stratum. From Nov. 1977 to Dec. 1978 sampling was more intensive and limited to living branchlets (see Fig. 2 for date and number of samples (n) per date).

In order to study the microdistribution of C. carrolli, sampling was carried out as outlined above but the sorting unit was the twig segment between two adjacent terminal-bud-scale scars. A total of 1838 twig segments were examined. Each segment was placed in an age class following the method briefly discussed in PIKE et al. (1977). Estimates of Camisia abundance and density were made for twigs and needles of ages 1 through 10 years, from several heights in the canopy during 4 successive months (April to July 1978). Samples were directly observed using a 30 × dissecting microscope and the number of Camisia on each segment was recorded. Since branchlet samples dried out rapidly and C. carrolli remains quiescent in dry conditions, it is assumed that the distribution observed in the lab reflects closely that existing in situ. Larvae, nymphs (all 3 stases) and adults were recorded separetely.

Some aspects of the biology of this mite, such as habitat, camouflage and feeding behavior, were investigated. Results obtained from observations in situ were combined with information derived from laboratory studies. In the present case, mites were reared in three different ways: on small pieces of twigs, in small plastic boxes containing a plaster-charcoal substrate, and in concavity slides.

Pieces of twigs were kept moist by soaking and placing them in desiccators partly filled with water. Some samples were immersed in part in the water of the desiccators and remained quite wet. These rearings were used to check the microdistribution of *Camisia* and its range of habitat under wet conditions (in contrast to the fresh samples which were dry).

Immatures and eggs were also reared on a plaster-charcoal substrate until pupation or hatch. Freshly molted or hatched individuals were clean and selected for morphological studies (ANDRÉ, 1980). Some other specimens were caught on twigs and kept in these conditions a few hours

until they produced their faecal pellets. Pellets were at once mounted for subsequent observation under a compound microscope. The plaster-charcoal was kept wet, not merely moist, to insure that the *Camisia* remainded mobile.

To obtain contamination free larvae for feeding studies, fresh eggs were place into water in concavity slides until hatch. The resultant larvae were transferred to new concavity slides, each slide contained a sample of one of the following fungi: Epicoccum purpurascens Ehrenb. ex Schlecht., Cladosporium sp., and Fusarium sp. These three fungi were all isolated from Douglas fir needle- or twig-surfaces and were obtained from the culture collection of the

Department of Biology at the University of Oregon. In addition, a few of the newly hatched larvae were placed in concavity slides containing scrapings from twigs. All test slides were kept in the light at room temperature in desiccators partially filled with water. Daily observations were made to check whether mites were feeding. Faecal pellets produced by these test larvae were collected and observed as described above.

For S.E.M. examination of *C. carrolli* to illustrate *in situ* camouflage, small pieces of bark each containing one specimen were removed from dry twigs. These were placed on "stubs" using silver paint, critical point dried and sputter coated prior to examination.

RESULT AND DISCUSSION

The data gathered during the first year of sampling suggested that C. carrolli was not evenly distributed and that there were more of them in the upper than in the lower portions of the canopy. Data from the first year were not subjected to statistical analysis because of the small sample size but during the second year the sample size was large enough for analysis. Data from the second year were analyzed using the Kruskal-Wallis procedures for k independent samples (GIBBONS, 1976). These procedures calculate an overall statistic that indicates the probability of nonhomogeneous populations, in this case lower vs. middle vs. upper, and also allows direct comparisons between strata. A summary of this analysis is shown on Table 1. In the first column (H values), 7 of the 13 are high enough to reject the hypothesis that the canopy strata were homogeneous for C. carrolli. The 2nd, 3rd and 4th columns are the direct comparisons between strata and give absolute value differences between the means of the ranked samples in these strata. The significant level for this second test is raised so that possible differences may be detected. There are significant differences indicated between the lower and upper canopy in 10 of the 13 sampling dates. The lower and

middle differ in only 4 and the middle and upper differ in only 3 cases. The lower \neq middle \neq upper did not occur on any sampling date. In addition, in Figure 1 it can be seen that the values of C. carrolli per kg of branchlet from the mid canopy samples fluctuate across both the lower

Table 1: A summary of the Kruskal-Wallis statistical analysis based on the ranked means of the number of *C. carrolli*/kg of branchlet for lower, middle and upper canopy levels.

Date	H value	$ \bar{R}_1 - \bar{R}_2 $	$ \bar{R}_1 - \bar{R}_3 $	$ \bar{R}_1-\bar{R}_3 $
16-xi-1977	4.68	4.8	8.5**	3.7
16-хп-1977	18.04*	9.3*	15.9**	6.7
12-1-1978	10.19*	3.9	12.2**	8.2**
26-r-1978	4.54	4.7	6.3**	1.7
2-ш-1978	10.98*	1.5	8.0**	9.5**
7-IV-1978	3.24	4.9	2.1	2.8
28-iv-1978	3.70	6.0**	4.8	1.2
26-v-1978	0.79	2.3	0.5	2.8
5-vn-1978	5.72	3.8	7.3**	3.5
2-vш-1978	9.23*	5.5	9.0**	3.5
30-viii-1978	10.70*	4.8	8.5**	3.7
11-x-1978	10.35*	1.5	7.0**	8.5**
18-хи-1978	10.53*	6.2**	8.2**	2.0

^{*} significant at the .05 level

^{**} significant at the .20 level

 $[\]bar{R}_1$ = mean of the ranks of the lower canopy samples \bar{R}_2 = mean of the ranks of the middle canopy samples

 $[\]bar{R}_3$ = mean of the ranks of the upper canopy samples

Statistical procedure from Gibbons, 1976.

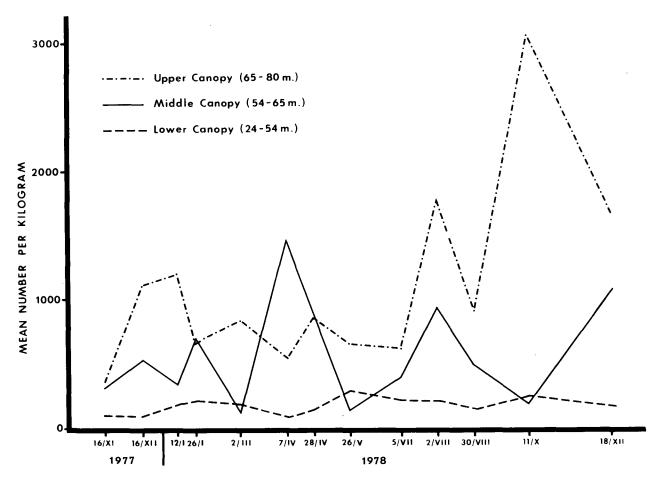


Fig. 1: Mean values of number of *Camisia carrolli* per kg of branchlet for each canopy stratum, shown for slightly more than one annual cycle.

and upper values but that the lower and upper values remain rather distinct from each other. This suggests that the distribution pattern of *C. carrolli* could be considered a continuum between low population density in the lower canopy to higher population density in the upper canopy.

In Figure 2, the number of C. carrolli per kg of branchlet is shown as a function of the distance from the top of the tree. The line represents best fit to a power curve for the data points shown. It can be noted that the slope in all cases is negative and the exponent is fairly close to -2 in many of the cases. A generalization might be that density of C. carrolli varies as the square of the distance from the top of the tree. The r values show that this decrease in density from

upper to lower canopy is significant for 11 of the 13 sample sets.

The heterogeneous distribution of *C. carrolli* can be seen by examining the variability of the samples taken from one branch system (see Fig. 2). On 7-IV-1978 (second vertical row of points) sample counts were: 0, 91 and 1435 *C. carrolli* per kg of branchlet. It can also be seen that there were other cases where several samples from one branch system had approximately equal densities of *C. carrolli*.

During the initial canopy it was noted that *C. carrolli* appeared to be more abundant on living than on dead branchlets. Twenty six paired samples (dead vs. living, from a common branch system) for each canopy stratum were analyzed

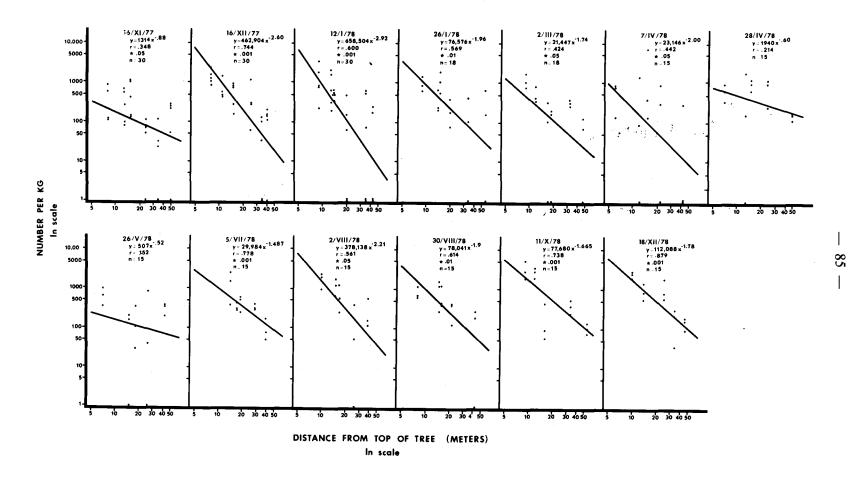


Fig. 2: The number of Camisia carrolli per kg of branchlet plotted against the distance from the top the tree ($\ln \times \ln$). Each line represents best fit to a power curve with the equation given for each date and r value plus significance levels .05 or greater. Each vertical line of points represents the samples taken from one branch system.

using the paired t test. The calculated t values were all significant at the .005 level, supporting the observation of a higher density of *C. carrolli* on living than on dead branchlets. From the

upper to the lower stratum, the estimated mean density of *C. carrolli* on living and dead branchlets are respectively: 401 vs. 115, 185 vs. 45 and 68 vs. 10 mites per kg of branchlet.

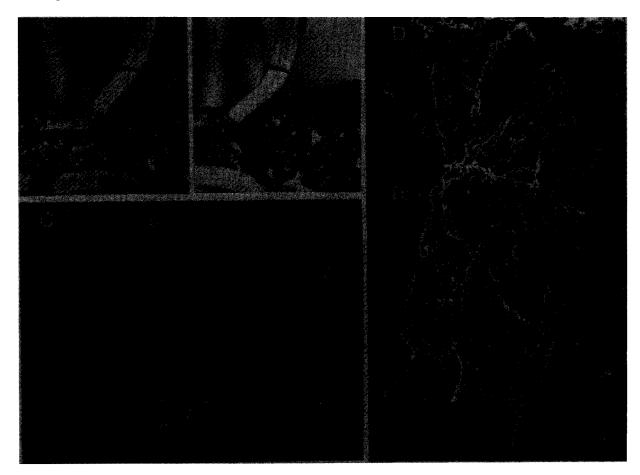


Fig. 3: A: C. carrolli quiescent nymph at the axil of a needle (indicated by an arrow); B: The same specimen after the twig was soaked (the arrow indicates the water meniscus); C: C. carrolli adult in situ (a: base of a needle; b: base of a bud); D: C. carrolli nymph in situ (fp: faecal pellet) (C and D are scanning electron micrographs; magnification: 84 × and 166 × respectively).

This observation led us to study the microhabitat and microdistribution of *C. carrolli*. In dry samples, such as they were collected *in situ*, the Oribatid mites were always found on the twigs themselves. Therefore, additional experiments were carried out in the laboratory to determine their behavior in moist conditions. Some mites were thus observed on twigs soaked, put in desiccators and partly immersed in water. All were seen wandering on the twig, some left the sample

but none of them was observed on a needle. This suggest that the microhabitat of *C. carrolli* is restricted to the twig itself.

In addition, it was noticed that, on samples brought back to the laboratory, *Camisia* specimens were rather regularly found in the axil of a needle or sometimes aggregated under the withered scale of an old terminal bud. When such a sample is soaked, microepiphytes on twigs swell and retain a thin layer of water; further, a menis-

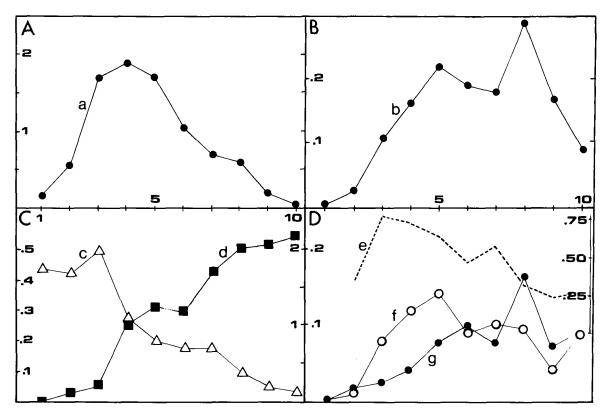


Fig 4: Age-specific distribution (from 1 to 10 yrs) of some variables. a: C. carrolli abundance (number of individuals. sample-1); b: C. carrolli density (number of individuals. segment-1); c: needle density (millions of needles. m-2 of twig); d: microepiphyte density on twigs (cm3. m-2 of twig); e: ratio I/T (Immature/Total number of mites); f: immature density (number of individuals. segment-1); g: adult density (id.).

cus of water forms in the axil of each needle and constitutes a reserve of water as well as real reservoir for the mite it shelters (Fig. 3A, B). In contrast, needles shed water because of the cuticle, and consequently water trickles down either to the tip or to the petiole of needles. The hydrophilic character of twigs and their epiphytes in contrast to the hydrophobic property of needles could explain the restricted microhabitat of *C. carrolli*. However, needles may exert a beneficial effect by prolonging or increasing the water retention on twigs.

This hypothesis is strengthened by observations on the microdistribution of *C. carrolli*. Data are summarized in figure 4. Fig. 4A shows the distribution of mite abundance by twig-age class. The abundance of *C. carrolli*, expressed as the total number of mites on segments of a given age, has increased by age 3 to a level which is sus-

tained until year 5. However in a sampling unit, there are more segments in the younger age classes than in the older. Therefore, total mite abundance as expressed above must be corrected and the ecological density, expressed as the total number of mites found on the segments of age X/number of segment of age X, should be preferred. The mite ecological density is illustrated in figure 4B and its distribution appears to be bimodal. The mite density has increased by age 5 to a value of about 22 individuals/100 segments; after a slight decrease, the density reaches a second peak at age 8 (about 29 individuals/100 segments) after which it decreases.

The increase of *Camisia* density could be explained by the increase of resources available, i. e. the microepiphyte volume on old twigs (Figure 4C, curve d; data from PIKE et al. 1977). However, the decrease of *Camisia* density seems to be

hardly explicable by the same factor. On the contrary, the hypothesis advanced above, namely the beneficial effect of needles on water retention, should well explain this decrease on the older twigs: needles are dropping (see Fig. 4C, curve c; data from PIKE et al. 1977) and water retention should decrease, restricting the microdistribution of *C. carrolli*.

In addition, the bimodal pattern of mite density demands an explanation. It is given by figure 4D where densities of the adults and immatures (nymphs and larvae) are considered separately. The first peak of mite density coincides with the maximum density of the immatures (at age 5 yrs.) while the second peak coincides with that of the adults (at age 8 yrs.). Figure 4D shows also the age-specific distribution of the ratio I/T (number of immatures/total number of Camisia). It suggests that the adults have a wider range of distribution than the immatures and should be less dependent of the water retention. Adults should be the pioneers colonizing new habitats where they would deposit eggs.

TABLE 2: Camisia feeding in culture with fungus.

Fungal species	Number of positive observations/total	Total number of pellets	Number of larvae reared
Fungal scrapings:			
Atichia glomerulosa	6/13	41	2
Fungi from culture :			
Cladosporium sp.	5/21	130	3
Fusarium sp.	3/37	14	5
Epicoccum purpurascens	4/38	6	6

Data relating to the feeding behavior of *C. carrolli* are summarized in table 2. Sixteen larvae were reared in concavity slides during about 3 weeks. Periodical observations were carried out to observe whether larvae were eating (positive response) and to count the numbers of excreted faecal pellets. In addition, 16 faecal pellets

excreted by nymphs and adults reared on twigs were collected and analyzed. Some contained pigmented cell walls destroyed beyond recognition, but in most cases contents were identifiable as spores and trichomes of fungi belonging to the family Metacapnodiaceae, thalli of Atichia glomerulosa (Ach. ex Mann) Stein. and unknown mycelium. Everything suggests that C. carrolli is mycophagous and is grazing the fungi which colonize the young twigs.

Scanning electron micrographs (Fig. 3C, D) show that Camisia (adults and especially nymphs) are covered by adherent dirt, fungi and even faecal pellets over a gummy cerotegument. Even eggs are covered in the same way. As a result, when a larva hatched in a cavity slide, it collected fungi from the egg envelope (unfortunately it was not observed whether the transfer was active or only passive). Moreover, a few hyphae collected by a larva reared in water were sufficient to colonize the specimen as fungi are growing and expanding all over the animal. Such a phenomenon is usually considered as a camouflage device. However, the layer of fungi and dirt could perform another function. In Bdelloidea, a family of rotifers particularly well adapted to desiccation through anhydrobiosis, revivification is possible only if dessication occurs slowly and if animals are protected from the air by a layer of detritus. The fungal cover of C. carrolli could play a similar role, especially in immatures².

CONCLUSIONS

This preliminary study of the biology of *C. carrolli* reveals several features in common with that of *C. segnis*, described by GRANDJEAN (1950). Like *C. segnis*, *C. carrolli* is arboreal (as suggested by its macrodistribution) and hydrobiontic. In addition, *C. carrolli* is mycophagous. The latter 2 characteristics should explain its macro- and

^{1.} As a consequence, C. carrolli would not account for the decrease in microbial cell volume observed by CARROLL (1979) on 4-year-old neddles; nor the reverse.

^{2.} MADGE (1964) carried out several experiments on trito- and deutonymphs of *Belba geniculosa* Oudemans (= *Damaeus onustus* C. L. Koch), another oribatid species whose immatures are covered with cast skins, dirt and detritus. Those experiments suggest that such a cover might play a role in the regulation of the water loss.

microdistribution. The microhabitat of *C. carroli* is restricted to the young twigs (roughly from 3 to 10 years aged); on the younger twigs fungi are lacking while, on the older one needles are dropping and water retention would be reduced.

C. carrolli seems well adapted to endure drought and/or desiccation and becomes quiescent when a period of dryness occurs. Such behavior is also known among Bdelloidea (rotifers) and "terrestrial" tardigrades living in mosses (cryptobiosis, anabiosis...). Like Bdelloidea, C. carrolli, particularly the immatures, are covered by fungi and detritus. This may be a device to endure dryness.

Mites such as C. carrolli and C. segnis pose some problems of terminology. They are usually considered to be terrestrial, or even xerophilous. However, BERTRAND (1977) working on "terrestrial" tardigrades living in mosses suggested that it is nonsense to apply the terms "terrestrial" or " xerophilous " to hydrobiontic animals such as tardigrades. The same remark applies to C. segnis, C. carrolli and some other oribatid mites as Ommatocepheus ocellatus (Michael). Such animals, which are hydrobiontic (i. e. living in water) but which are also able to endure a period of dryness and/or desiccation, should rather be called either "enantioxerantic" as proposed by BERTRAND (1977) or "anectoxerous" as proposed by TRAVÉ (1963).

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^{1.} From Greek εναντιος meaning opposite and ξηραντικός which dessicates. The term "énantioxérie" was coined in 1939 by a lichenologist (Duguy, 1939 quoted by Travé, 1963 : 62).

^{2.} Coined by Travé (1963: 116, footnote 1); from Greek ανεχτικός, able to endure and ξήρος, not wet, dry.