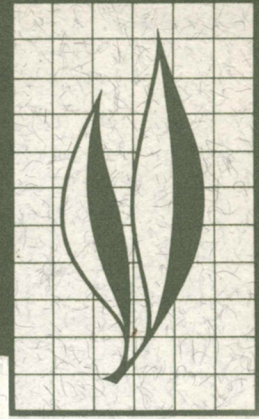


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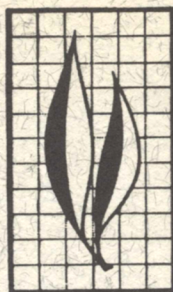
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Observations on the Biology of *Cinara ponderosae* (Williams) (Homoptera:Aphididae) in the Westside Forests of the Sierra Nevada

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Observations on the biology and population dynamics of *Cinara ponderosae* Williams) in the westside Sierra Nevada forests of California are presented.

The species is believed to be anholocyclic, because sexuales, eggs, and fundatrices were absent. In the spring following winter survival on ponderosa pine (*Pinus ponderosa* Lawson) in the foothills, populations migrated up the west slope of the Sierra Nevada. The local population in Blodgett Forest, Eldorado County, began in May with the number of aphids and colonies expanding throughout June and collapsing by the end of July. Detailed study of instar distribution, based on a sampling every four days, showed a gradual increase in older instars until population collapse. First generation 4th instars and apterae moved throughout the tree and began new colonies.

Predators, primary and secondary parasites, and ant associates were noted and discussed.

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Observations on the Biology of *Cinara ponderosae* (Williams) in the Westside Forests of the Sierra Nevada^{1,2}

INTRODUCTION

PALMER (1926) STUDIED the life histories of several species of cinarans (*Cinara*) in Colorado, and Johnson (1965) looked at the effect of heavy infestations of *C. pseudotaxifoliae* Palmer on Douglas-fir seedlings. Otherwise, few studies have been made of the 125 or more species of cinarans named or collected west of the Rocky Mountains in the United States and Canada.

In 1972, we found *Cinara ponderosae* (Williams) to be the most abundant cinaran of the mid-elevation westside Sierra Nevada forests. The aphid was noted only on small specimens (3 m tall or less) of *Pinus ponderosa* Lawson and *P. jeffreyi* Grev and Balf., although trees of all sizes were examined throughout the study. A study of *C. ponderosae* was undertaken from 1973 to 1975 in conjunction with taxonomic and biological studies of other *Cinara* spp. found in this region. Aphids in this genus are potentially important as pests in nurseries and tree plantations.

METHODS

Study area

Blodgett Experimental Forest, located 16 km northeast of Georgetown, El Dorado County, California, in the central Sierra Nevada (Fig. 1) was used for most of the summer observations. The forest is a mixed conifer, predominantly second-growth stand of six principal tree species: ponderosa pine, *Pinus ponderosa*; white fir, *Abies concolor* (Gordon and Glendenning) Lindley; incense cedar, *Calocedrus decurrens* (Torrey) Florin; sugar pine, *Pinus lambertiana* Douglas; Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco; and California black oak, *Quercus kelloggii* Newberry.

Two sites were chosen for sampling in 1974 and for distributional analysis in 1975. One was at the south end of the experimental forest on the southeast slope of Sand Mountain; the other was 3 km east of the forest in the vicinity of Stumpy Meadows Lake. Both sites were characterized by abundant ponderosa pine regeneration.

Sampling, 1974

Ponderosa pines were examined at each site until a branch with a colony was found, placed in a plastic bag, and taken to the laboratory for study. Ten colonies were collected at each site; collections were made every 4 days. Only one colony per tree was taken. In

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Fig. 1. Topographical map of California. Area A indicates foothill region where *C. ponderosae* was collected during the winter. Line B is the approximate location of the elevational transect run in 1975; open circle on line B is Blodgett Experimental Forest.

the laboratory, all aphids, predators, ants, parasites, and mummies were removed. Ants, adult predators, and 1st and 2nd instar aphids were placed in alcohol. Third and 4th instar and adult aphids were put in small petri dishes to await mummification. After 4 to 7 days aphids that had not mummified were pooled with the 1st and 2nd instars. Mummies were placed in gelatin capsules to rear parasitoids. Larval predators were put into gelatin capsules (000) or small petri dishes and fed aphids until mature. The number of each instar, alate or apterous 3rd and 4th instar nymphs, alate or apterous adults, associated insects, and mummies were recorded for each sample.

In addition to and concurrent with the samples taken for the laboratory, 25 colonies, each on small (< 1.5 m) separate trees, were marked and examined *in situ* every fourth day. Thus, each tree could be examined thoroughly, and counts, including associated insects, could be recorded without excessively disturbing the aphids.

Life-table construction

Time-specific life tables were constructed using Hughes's (1962, 1972) technique to predict the parameters of an equivalent sample taken one instar period later. One instar period was taken as the approximate time needed for complete development and moult for any of the first three instars, providing the temperature was above the minimum threshold for development. Life tables assumed a stable instar distribution in the population at the time of sampling. A stable instar distribution occurs if the rate of reproduction remains relatively constant for a time period. The following formula (Hughes 1972) was used to calculate the numbers in the first three instars (I, II, III) expected in a geometric progression based on the number of the first three instars observed in the samples taken.

$$e = \frac{I + II}{II + III} = \text{potential rate of increase}$$

Expected number of aphids in

$$\text{III: } T_1 = \frac{(I + II + III)e^\lambda - 1}{(e^\lambda)^3 - 1}$$

$$\text{II: } T_2 = e^\lambda T_1$$

$$\text{I: } T_3 = (e^\lambda)^2 T_1$$

The number of aphids represented by the geometric progression was then compared with the observed using a χ^2 df analysis. Values greater than 3.84 ($p = 0.05$) were assumed to be evidence that a stable instar distribution did not exist. Data from both sample sites were combined, and each life table was based on a sample of 20 colonies.

Losses due to parasitism was estimated by the number of mummies formed in the laboratory following collection. Losses due to predators were based on the number of aphids of various instars necessary to rear the various predator larvae, collected with the sample, to maturity. Losses due to *Deraeocoris ingens* were estimated. It was assumed that all alaroid 4th instars moulted and emigrated before the next sampling data.

Distributional sampling, 1975

Resource utilization and movement of *C. ponderosae* within the host tree were measured. Fifty ponderosa pines, small enough to examine thoroughly, were marked in each of the two study areas for weekly sampling during 1974 beginning May 11. Trees with aphids on them were mapped, and colonies, aphid forms, ants, predators, and parasites were located (Fig. 7 and 8). Trees were drawn as if sectioned at each internode from bottom to top, each circle (whorl) representing the trunk and each line from it, one branch. Colony locations were designated by solid circles, and aphid morphs, ants, and associated insects were coded for each colony location. Observations continued until *C. ponderosae* was found on only one of the 100 marked trees.

RESULTS

Anholocycly in *C. ponderosae*

During the spring and early summer of 1973, many colonies of *C. ponderosae* were composed of a single alate viviparae and immatures. These were assumed to be at least second generation, because fundatrices are all apterous. In the early spring of 1974, a thorough search was made for eggs, but none could be found. All colonies, when finally observed, were started by alate viviparae. Specific colonies were then followed throughout the summer, fall, and into the winter; no sexuales were found.

Climate at the altitude (1,000 to 2,000 m) of this region of the Sierra Nevada is too severe during the winter months for aphid survival. Heavy snow, freezing temperatures, and winter storms are climatic factors. In light of this, plus the absence of sexuales, eggs, and fundatrices, a source of the spring alatae had to be found. Searches along the foothills (200 to 300 m elevation) during the winter of 1974-75 produced many collections of *C. ponderosae* (Fig. 1). Also, a United States Forest Service nursery at Placerville (located in the foothills of the Sierra Nevada) had a *C. ponderosae* buildup on its small ponderosa pines almost every winter.

In the spring of 1975 a west-to-east elevational transect was run at weekly intervals (Fig. 1). Colonization of ponderosa pine by *C. ponderosae* was observed to move from low to high elevations; this closely matched bud burst in small pines. At this time of the year, prevailing winds from the west may have helped this migratory pattern.

These observations led us to consider *C. ponderosae* to be anholocyclic in this area of the Sierra Nevada.

Instar age distribution of *C. ponderosae*

The 39 instar distributions from sampling in 1974 (Fig. 2) were analyzed for fit to a geometric progression. Twenty-seven, or 67 percent, had X^2 df values low enough for a geometric progression to be assumed (Tables 1, 2). The validity of assuming stable instar age distributions in the sets of data that approximate a geometric pattern has been questioned by Carter, Aikman, and Dixon (1978). They calculated a chi-square heterogeneity test using Hughes's data from 1960 and 1961 and found that, although individual sets of instar distributions reflect a geometric progression, the sum of the X^2 values strongly suggests that the sets of samples are not from a homogeneous population with respect to instar distribution. Table 3 is a similar test that utilized the data given in Tables 1 and 2. Results were similar to those found by Carter, Aikman, and Dixon (1978): that the heterogeneity test suggests that all of the samples were not from a homogeneous population with relation to instar age distribution.

Figure 2 shows that the alatoid 3rds and 4ths fluctuated considerably between sampling dates. Population of 3rd and older instars increased up to mid-June and peaked two weeks after colony size peaked (Fig. 3) but corresponded closely to the peak number of colonies in 1975 (Fig. 4).

Cinara ponderosae Instar Distribution, in % of Total Aphids from Ten Colonies

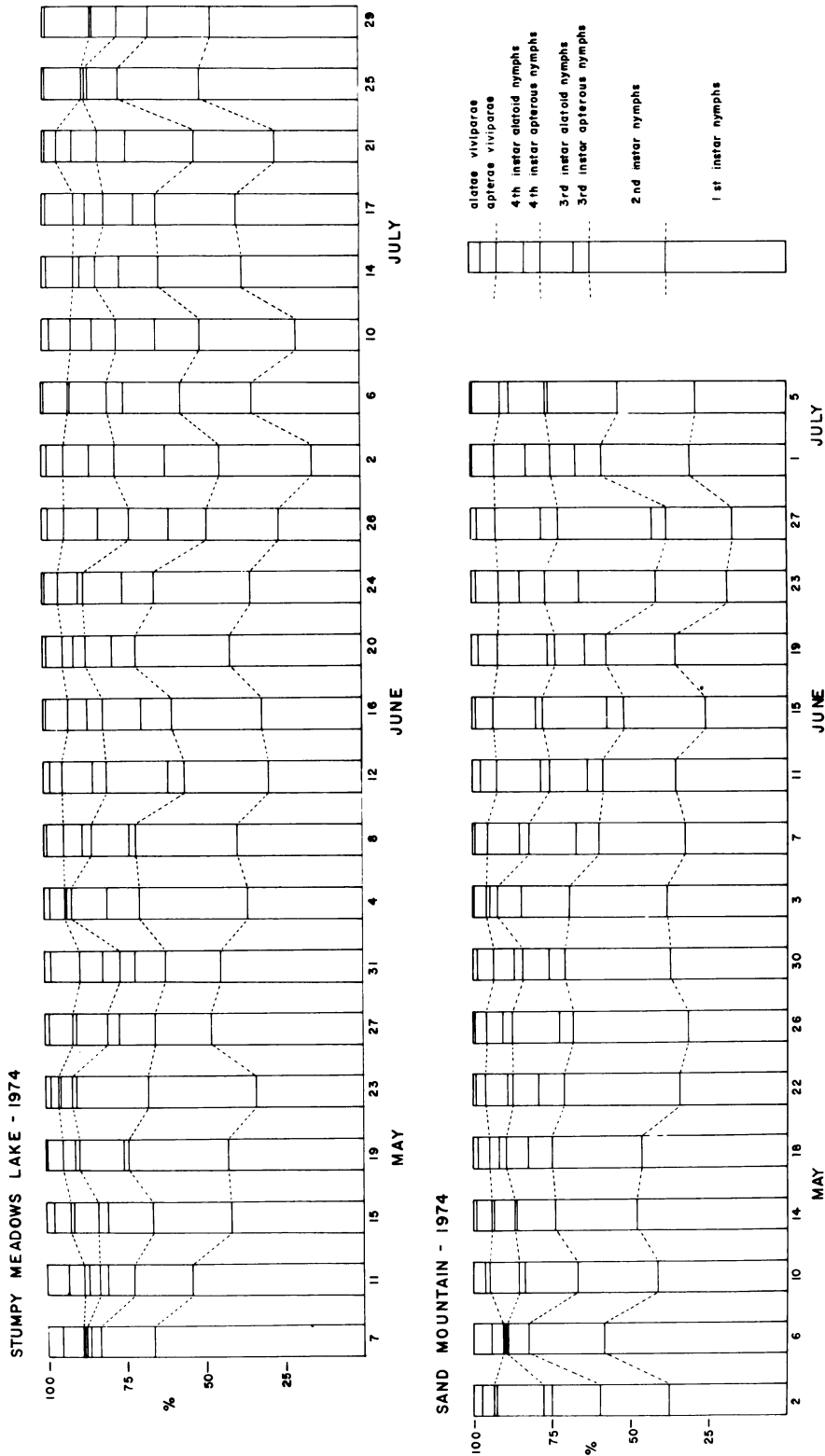


Fig. 2. *Cinara ponderosae* instar distribution from 1974 samples taken for laboratory study at Sand Mountain and Stumpy Meadows Lake sites.

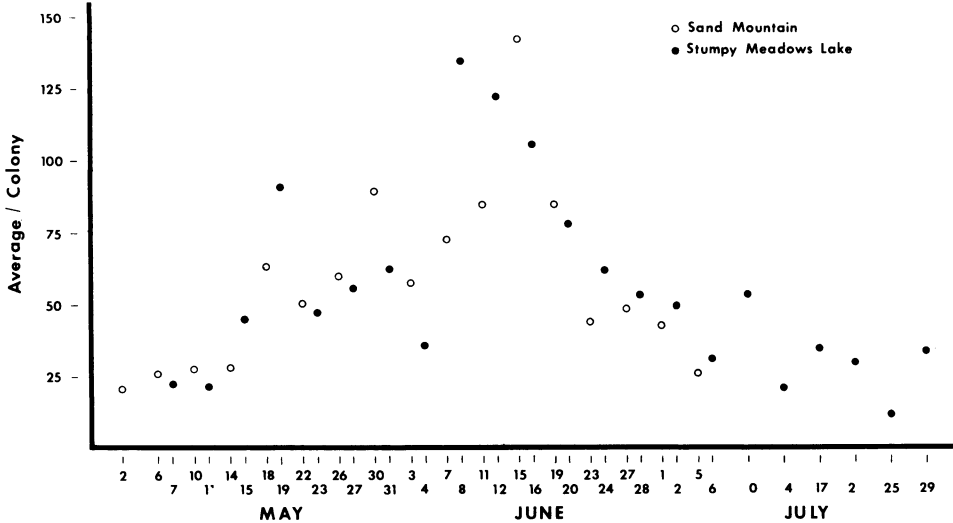


Fig. 3. Average number of *C. ponderosae* per colony for the Sand Mountain and Stumpy Meadows Lake sampling sites, 1974.

TABLE 1.
OBSERVED AND PREDICTED STABLE INSTAR DISTRIBUTIONS OF
CINARA PONDEROSAE POPULATIONS ON *PINUS PONDEROSAE* AT
STUMPY MEADOWS LAKE, 1974

Sampling date	Number of individuals/instar stage/sample*						e ^λ	X ² **
	Observed			Predicted (first 3 instars)				
	1st	2nd	3rd	1st	2nd	3rd		
May 7	152	39	10	151	39	10	3.90	0.01
May 11	119	41	24	109	44	18	2.46	3.12
May 15	189	112	79	185	117	74	1.57	0.82
May 19	392	285	142	400	252	159	1.58	6.03
May 23	160	162	114	164	140	120	1.16	3.85
May 27	267	99	84	257	128	64	2.00	13.62
May 31	302	117	97	291	149	76	1.95	13.09
June 4	130	122	77	138	109	86	1.27	2.96
June 8	530	431	190	551	356	230	1.54	23.56
June 12	375	322	302	384	344	307	1.12	1.70
June 16	331	301	230	336	283	237	1.19	1.43
June 20	324	235	123	331	212	136	1.56	3.89
June 24	216	189	138	227	180	145	1.24	1.01
June 28	136	120	128	125	119	113	1.05	2.88
July 2	76	142	161	87	121	168	0.72	5.33
July 6	109	72	73	104	83	67	1.25	2.24
July 10	108	165	134	132	145	159	0.91	11.05
July 14	78	55	42	77	57	41	1.36	0.06
July 17	133	86	56	132	86	56	1.54	0.01
July 21	77	74	89	83	88	96	0.92	3.17
July 25	57	29	12	57	27	11	2.09	0.23
July 29	157	66	33	156	69	31	2.25	0.27

*Each sample consisted of 10 colonies.
**For values of X²_{df} < 3.84 the observed instar distribution approximates a geometric progression.

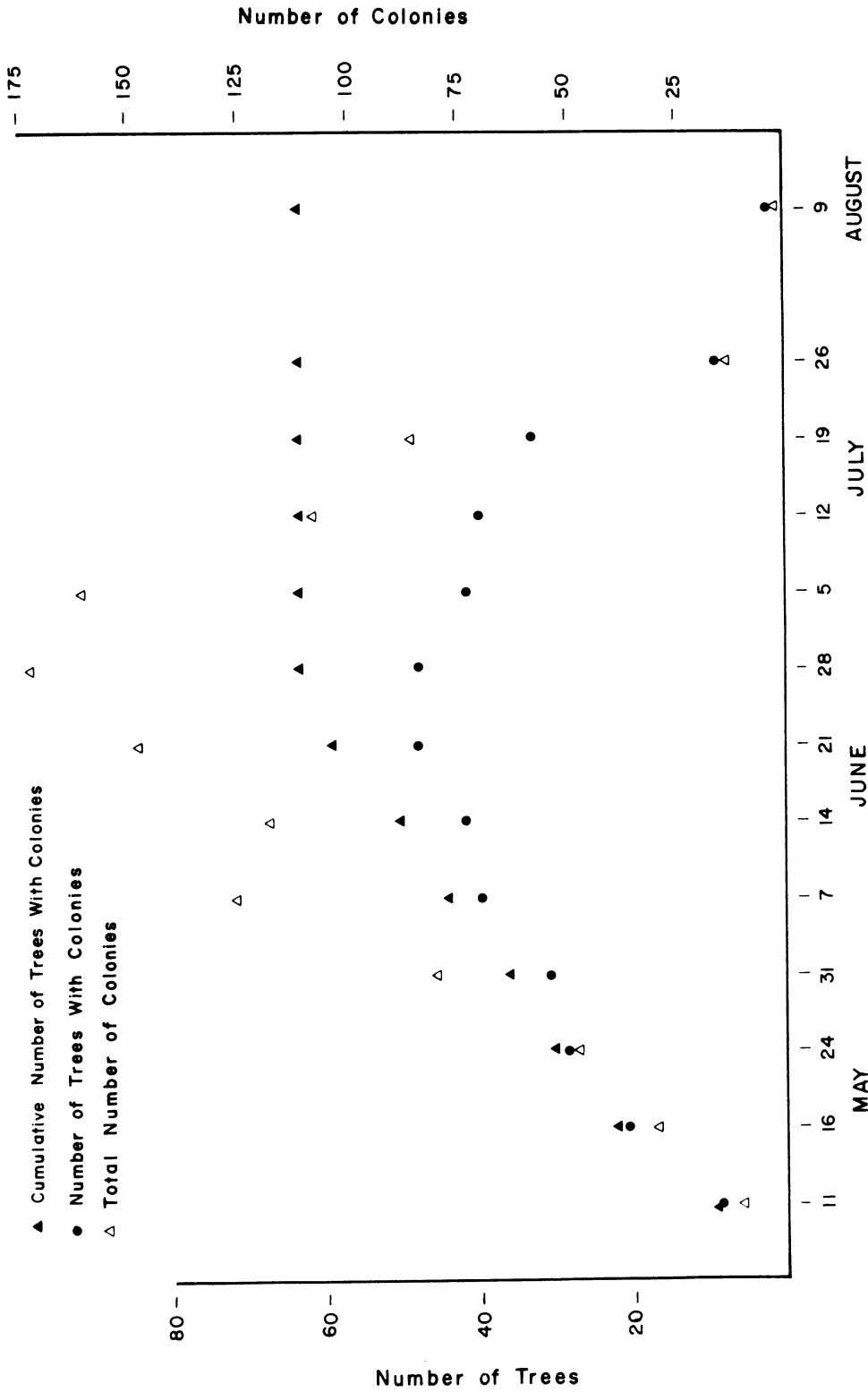


Fig. 4. Data from distributional sampling, 1975, showing number of trees with colonies at each sampling date, cumulative number of trees number of trees used by *C. ponderosae* to that date and total number of colonies on occupied trees on that sampling date. Data from Sand Mountain and Stumpy Meadows Lake are combined.

TABLE 2.
OBSERVED AND PREDICTED STABLE INSTAR DISTRIBUTIONS OF
CINARA PONDEROSAE POPULATIONS ON *PINUS PONDEROSAE* AT
SAND MT., 1974

Sampling date	Number of individuals/instar stage/sample*						e	X ² **
	Observed			Predicted (first 3 instars)				
	1st	2nd	3rd	1st	2nd	3rd		
May 2	79	47	38	77	52	35	1.48	0.79
May 6	151	62	18	152	57	21	2.66	0.87
May 10	114	70	51	112	74	48	1.52	0.44
May 14	131	71	35	132	70	36	1.91	0.05
May 18	293	180	93	296	171	99	1.73	0.87
May 22	173	183	82	189	141	105	1.34	18.90
May 26	187	215	115	208	171	140	1.22	17.91
May 30	335	301	120	359	238	157	1.51	27.00
June 3	220	178	130	220	171	132	1.29	0.32
June 7	237	202	163	236	195	163	1.20	0.26
June 11	307	201	145	307	209	142	1.47	0.37
June 15	370	367	367	371	370	368	1.00	0.03
June 19	304	192	139	303	202	135	1.50	0.62
June 23	85	101	159	78	110	153	0.72	1.60
June 27	86	102	169	75	108	156	0.69	3.03
July 1	133	123	71	140	106	80	1.32	4.09
July 5	74	64	60	71	64	57	1.11	0.28

*Each sample consisted of 10 colonies.

**For values of $X^2_{idf} < 3.84$ the observed instar distribution approximates a geometric progression.

TABLE 3
HETEROGENEITY CHI-SQUARE CALCULATIONS USING THE SAND MOUNTAIN AND
STUMPY MEADOWS DATA GATHERED IN 1974 AND SHOWN ON TABLES 1 AND 2

Item	Sand Mountain (pooled X ²)			Stumpy Meadows (pooled X ²)		
	1sts	2nds	3rds	1sts	2nds	3rds
Observed	1955	2659	3279	2388	3264	4418
Expected	2000	2580	3321	2357	3232	4432
Total X ² values = 77.43 > X ² _{17 df} = 40.80 at .001 level						
100.33 > X ² _{22 df} = 48.27 at .001 level						
100.33 - .514 = 99.82 > X ² _{21 df}						
Heterogeneity X ² * = 77.43 - 4.19 = 73.24 > X ² _{16 df} = 46.80 at .001 level						
= 39.25 at .001 level						
.514 X ² _{1 df} = 3.84 at .05 level						
X ² = 4.19 X ² _{1 df} = 3.84 at .001 level						
Heterogeneity X ² * = Total X ² values - Pooled X ²						

*Reject assumption that all samples are from a homogeneous population when Heterogeneity X² greater than the maximum table values.

Life tables

Life tables were developed from the 39 instar distributions shown in Figure 2. Life tables for three dates in the sampling program are shown in Figure 5. Instar distributions on these dates met the criteria outlined above for assuming a stable age distribution. Columns A and D are the total number of aphids sampled on the dates shown. Column B is all of the aphids in Column A plus a predicted number of first instars. In B, losses of the various instars are indicated. These losses are assumed to have taken place before the next sampling date. Column C is Column B minus the losses. In the transition from A to B, it was assumed that all of the 1sts from A became 2nds in B, and all the 2nds became 3rds, etc.

The first life table (Figure 5A) was based on the May 14 and 15 data and predicted May 18 and 19. At this time of the year the population was growing very rapidly both in colony size and in number of colonies. Prediction in Column C was much smaller than that observed on May 18 and 19.

The second life table (Fig. 5B) was based on the June 11 and 12 data and predicted June 15 and 16. These dates coincided with maximum population size both in the number of colonies and numbers per colony. Prediction shown in Column C is somewhat larger than the observation.

The third life table (Fig. 5C) was based on June 23 and 24 data and predicted June 27 and 28. This time period corresponded to the rapid decline in number of aphids per colony (Fig. 3), and the calculated value of $e\lambda$ was less than one.

In-situ observations and counts, 1974

In situ observations and counts of aphids in premarked colonies provided clues as to the movement of aphids, especially later instars, to different areas on the tree. Close scrutiny with the hand lens required to make accurate counts in the field usually disturbed the aphids and caused them to run or drop off the trees. Counts of two colonies that remained in a fixed location are shown in Table 4. Older instars continually left the colony, a constant in all the colonies observed. In some cases, aphids were assumed to have joined one of the other colonies located in the tree. Colony AI-74-20 (Table 4) contained over 100 individuals, including a large number of 1st instars. In four days, despite thorough examination, not an aphid could be found on the entire tree. We had no explanation for this.

Parasitoids were often observed ovipositing in colonies, but few or no mummies were found in the colony or anywhere on the tree. Observations of parasitized individuals the following year showed that they left the tree completely; in one location, these parasitized individuals were found mummified on the trunk obscured under a thick layer of litter at the base of the tree. In another case, an entire ring of mummies was discovered around the trunk at ground level. We also noted that parasitized immigrant alatae remained in the colony until mummified.

Distribution of *C. ponderosae* on host trees

Figure 4 shows the number of trees with aphids for each date and the cumulative number of trees which had been used by *C. ponderosae*. Of the 100 trees, a maximum

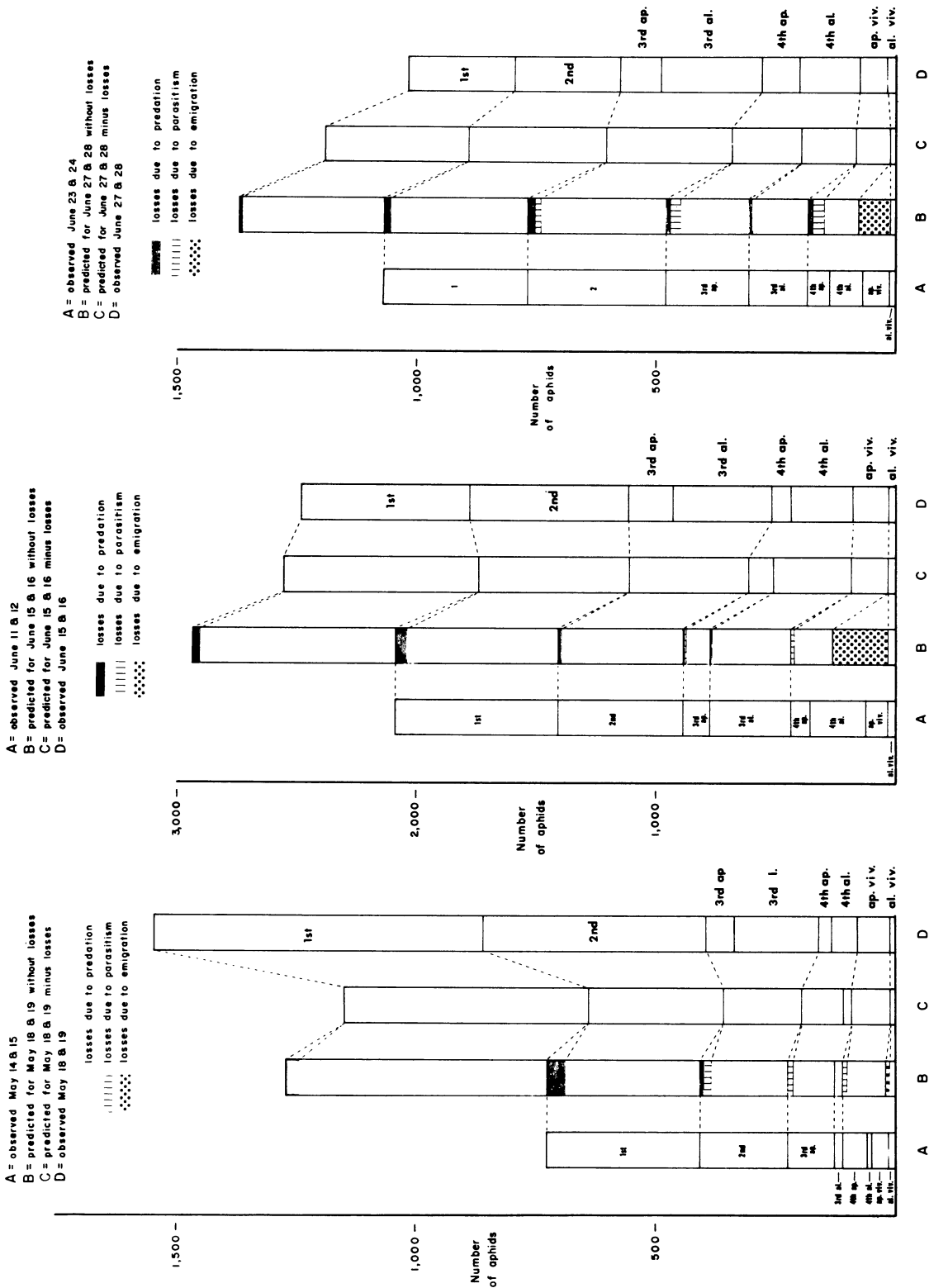


Fig. 5. Life tables constructed after Hughes (1972) from data gathered in destructive sampling, 1974.

TABLE 4.
COUNTS OF *CINARA PONDEROSAE* AND ATTENDANT INSECTS* OBSERVED
IN TWO *IN SITU* COLONIES. SAND MOUNTAIN, 1974

Collection date	Total no. aphids	<i>C. ponderosae</i> /instar stage†								Parasitoids	Predators
		1st	2nd	3rd		4th		ap. viv.	al. viv.		
				ap.	al.	ap.	al.				
Colony A1-74-25											
May 1	12	3	6	0	0	0	0	0	3		
May 5	34	15	10	6	0	0	0	0	3		
May 9	44	17	15	6	0	4	0	0	2		
May 13	40	1	10	16	3	6	1	3	0	syrphid, 1 imm, 2e	
May 17	55	9	11	12	9	7	1	5	1	<i>Pauesia</i> , 1f	
May 21	64	20	12	7	2	14	7	0	0	<i>Scymnus</i> , 1 imm.	
May 25	43	21	8	6	2	3	0	2	1		
May 29	5	1	2	2	0	0	0	0	0		
June 2	0	0	0	0	0	0	0	0	0		
Colony A1-74-20											
April 30	14	6	6	0	0	0	0	0	2		
May 5	30	6	11	11	0	0	0	0	2		
May 9	40	9	9	10	0	9	0	0	3		
May 13	36	5	13	7	0	9	0	1	1	syrphid, 3e	
May 17	35	16	9	3	0	2	0	4	1		
May 21	65	37	10	12	0	3	2	0	1		
May 25	0	0	0	0	0	0	0	0	0		

**T. sessile* was the ant species attending colonies at all times.

† ap = apterous, al = alatoid, ap.viv. = apterous viviparae, al.viv. = alate viviparae

of 48 aphids on them at one time, and 62 were used at one time or another throughout May, June, and July. The last time a new tree was occupied (June 28) was just before the dates in 1974 when colony size was at a maximum (Fig. 3). This also corresponded to the maximum number of colonies per tree (Fig. 6) and the maximum cumulative number of colonies on all trees combined (Fig. 4). The tree maps (Figs. 7 and 8) show the movement of aphids and the establishment of new colonies at other points on the tree. Tree 58 (Fig. 7) had its first colony on whorl IV and when first seen had an alate and nymphs. On May 31, the alate was not to be found, and the remaining aphids had moved to the tip of the tree. On June 7, or during the previous week, another alate arrived on the tree and during the following week two more alatae arrived. This tree was colonized by four separate alatae. Tree 2 (Fig. 8) showed a similar pattern. On June 7 two alatae were recorded; none were found on May 31. In both examples the original colony location was occupied for less than 3 weeks, supporting observations made of marked colonies the previous year. The phenomenon was observed many times: several migrants colonizing one tree, while many other small ponderosa pines available in close proximity had no aphids on them.

Although 62 percent of the potential host trees were occupied, the majority of the usable locations on any tree did not have aphid colonies on them. At the maximum infestation levels observed in this study, *C. ponderosae* did not seem to be limited by its food resource.

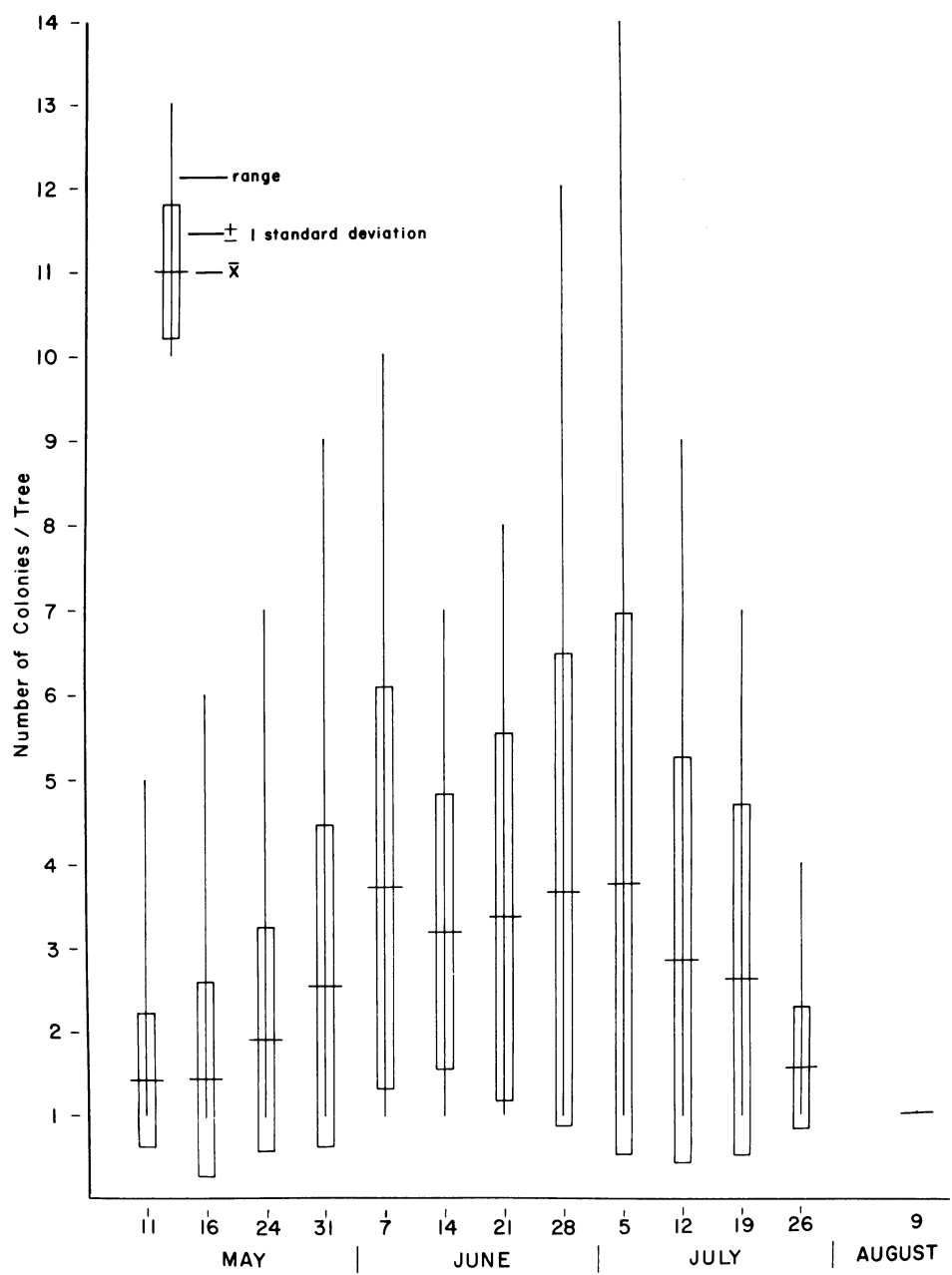


Fig. 6. Number of colonies per tree as observed in the distributional sampling, 1975. Data combined from both Sand Mountain and Stumpy Meadows Lake.

Tree No. 58

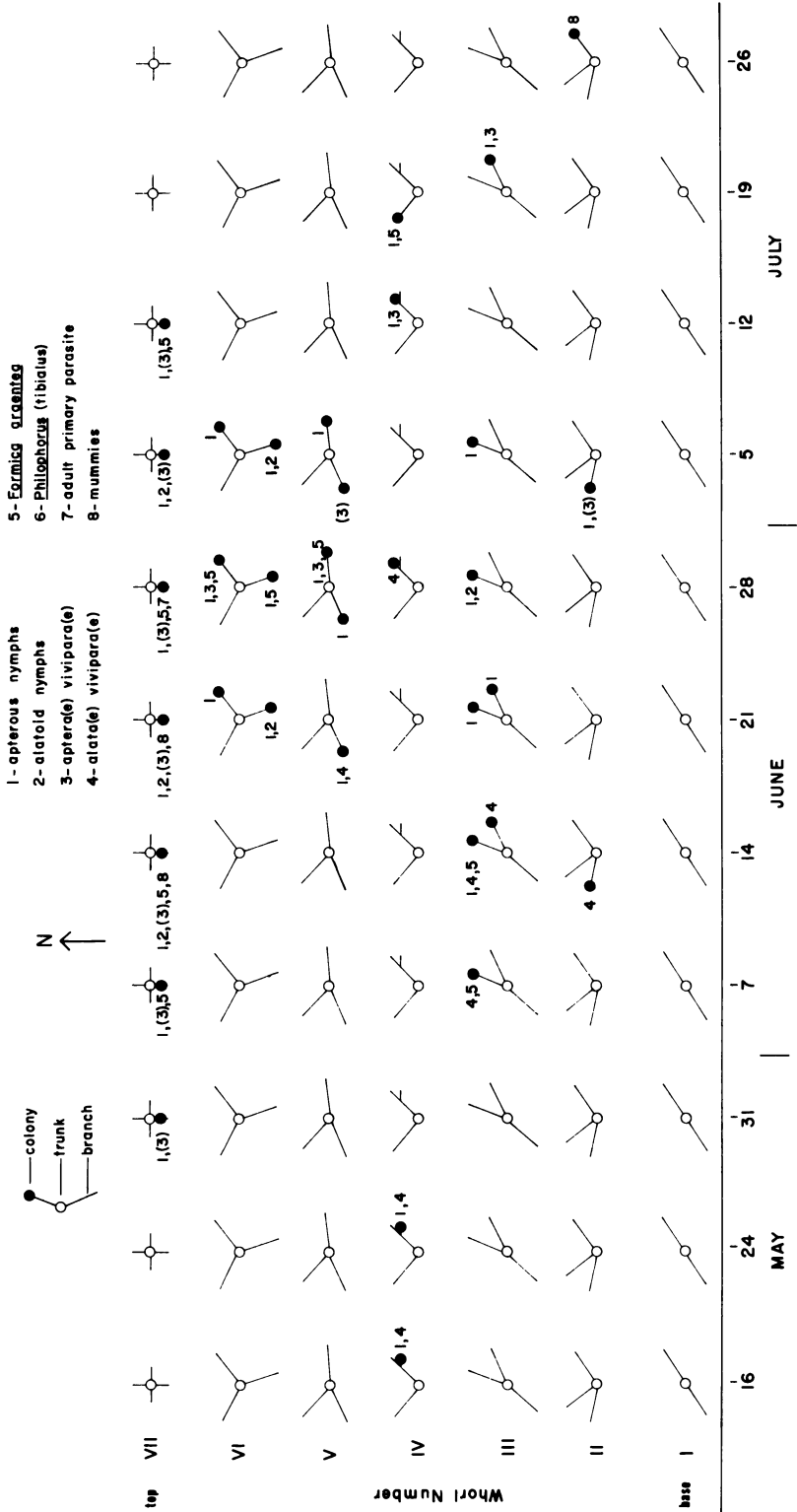


Fig. 7. Example of schematic tree map indicating presence and location of *C. ponderosae* from the point of initial colonization to extinction to extinction on that tree.

Associated insects

Ants. Seven species of ants, *Camponotus modoc* Wheeler, *C. vicinus* Mayr, *Formica argentea* Wheeler, *F. nevadensis* Wheeler, *F. sp.*, *Liometopum occidentale* Emery and *Tapinoma sessile* (Say) were observed attending *C. ponderosae* colonies in the study area. *Cinara ponderosae* did not seem to be as attractive to ants as were other cinaran species. About half of the colonies had no ants present. The relatively small number of aphids in these colonies may have reduced their attractiveness to ants. On the other hand, some of the larger colonies of *C. ponderosae* and other *Cinara* spp. had so many ants in attendance that aphids were scarcely visible.

All the above ant species varied in their behavior in the presence of aphid colonies. *Tapinoma sessile* leaves the colony when disturbed. *Camponotus vicinus*, *C. modoc* and *Formica argentea* are moderately aggressive against adult predators. *Formica nevadensis*, *F. sp.* and *Liometopum occidentalis* are very aggressive, and fewer predator larvae were collected with colonies attended by these species. None of the species were able to prevent parasitoids from gaining access to the colony although the ants' rapid movement was observed to interfere with the parasitoids enough to make them leave the colony. Individuals of *F. nevadensis* were observed palpating adult parasitoids with their antennae while the parasitoids were ovipositing, but no aggressive behavior was exhibited.

Parasitoids

Four primary parasitoids were reared from *C. ponderosae* mummies: *Xenostigmus bifasciatus* (Ashmead), *Pauesia laricis* (Haliday), *P. ponderosae* Muesebeck and *P. sp.* The genus *Pauesia* is mainly limited to *Cinara* spp., and *Xenostigmus* to the Lachninae (Mackauer and Sary, 1967). Two secondary parasitoids, *Euneura lachni* (Ashmead) and

TABLE 5
PRIMARY AND SECONDARY PARASITIDS EMERGED FROM MUMMIES OF
CINARA PONDEROSAE COLLECTED WITH AND REARED FROM LIVE APHIDS
IN THE COLONIES TAKEN TO THE LABORATORY, 1974

Source of mummies	Species				No emergence
	<i>Alloxysta</i>	<i>Euneura</i>	<i>Xenostigmus</i> and <i>Pauesia</i> spp.		
			male	female	
Stumpy Meadows Lake:					
Taken with colonies	2	61	6	18	13
Developed in petri dishes	39	0	153	258	59
Sand Mountain:					
Taken with colonies	3	37	11	24	24
Developed in petri dishes	56	2	90	172	30

Alloxysta lachni (Ashmead) were also reared. Fewer mummies were taken with the colonies than were reared from the aphids in the laboratory (Table 5). This supports observations *in situ* that parasitized aphids do not generally remain in the colony (also documented by Scheurer, 1964). Movement of parasitized individuals out of the colony and even off of the host plant would serve to remove the parasitoid from other potential hosts (of benefit to the aphid population). Removal would also prevent predation on the aphid before mummification; it may also reduce exposure of the parasitoid to secondary parasitoids.

No teneral alatae and very few alatoid nymphs mummified. Some mechanism may prevent parasitoid egg hatch until the alatae have flown and begun to feed. We observed no discrimination between alatoid and apterous nymphs in ovipositing primary parasitoids.

Predators

The following predators were found feeding on *C. ponderosae* in the westside Sierra Nevada: Syrphidae: *Eupeodes volucris* O.S., *Metasyrphus lapponicus* (Zett.) *Metasyrphus* (s.s.) sp., *Scaeva pyrastris* (L.); Chamaemyiidae: *Leucopis americana* Malloch; Coccinellidae: *Scymnus solidus* Casey and *Hippodamia convergens* Guerin; Miridae: *Deraeocoris ingens* Van Duzee, *Philophorus* sp., and *Dacerla* sp.; Neuroptera: *Chrysopa carnea* Stephens and *Hemerobius kokeneeanus* Currie; Araneae: *Phidippus johnsoni* Peckham, *Metaphidippus* sp., and *Linyphia* sp.; Acarina: *Allothrombium* (s.l.) sp.

Bradley and Hinks (1968) considered the omnipresent spiders (not counted in this study) to be major predators of cinarans, although they rarely observed spiders feeding on aphids. We observed webs of the dome-forming spiders, Linyphiidae, with alatae caught on the underside of the dome. Predators other than those observed undoubtedly occur.

Larval *Scymnus solidus* was the most common predator collected; they feed by biting an appendage and sucking the body fluids.

Hippodamia convergens migrate to the Sierra Nevada in the late spring and form aggregations (Hagen, 1962). At this time they have been observed to decimate *C. ponderosae* populations near an aggregation site.

The predatory mirid, *Deraeocoris ingens*, is very common on small ponderosa pines during the late spring. They are fast, adept at avoiding ants, and equally adept at preying on aphids, which they can carry on the end of their rostrum as they feed.

Syrphid larvae were not abundant, and none were collected with colonies later than the end of June. Laboratory-fed larvae of *Scaeva pyrastris* and *Eupeodes volucris* consumed 40 to 50 3rd and 4th instars of *C. ponderosae* from hatch to pupation. Small colonies were observed to be completely decimated by syrphid larvae.

Chamaemyiid larvae, *Leucopis americana*, are so small that they act like ectoparasites riding on the dorsum of the aphids while they feed. Rearing records indicated they will mature after feeding on two of each nymphal instar of *C. ponderosae*.

DISCUSSION

Sampling

The technique for taking samples to study in the laboratory (destructive sampling) was designed by the senior author during the summer of 1973 after personal observations of the local *C. ponderosae* population. The large number of ponderosa pines in both sampling areas made it possible to take colonies from a different set of trees each sampling period, until near the end of July, when it was necessary to search the entire area to find 10 colonies. The decision to take the first colony observed was to eliminate bias in selecting among the several colonies that may have been present on the tree. In the previous season, we also observed that when several colonies were located on a tree, instar distribution was much the same among them. Thus, samples were taken from 10 different trees each sampling date; each tree, in all probability, had been colonized at a different time (Fig. 4).

Life tables

Although Hughes's (1962, 1972) time-specific life tables and the underlying assumptions have been criticized (Carter, et al, 1978), the method can still be useful for examining sequential samples such as were gathered during this study. (See the three graphical life-table representations in Fig. 5).

In the early spring observation (May 14 and 15) (Fig. 5A), the estimated population is far less than that observed 4 days later. Most likely, one instar period during this time of the year is less than the 4-day interval between samplings. Observations in the spring of 1975 show that instar periods could be as short as 2.5 days, which would cause the observed numbers to be much larger than predicted numbers.

In early June (Fig. 5B) the predictions were larger but close to observed numbers. This suggests that one instar period may have been longer at this time, that is, approximately equal to the 4-day sampling interval. Possibly, some mortality factor was underestimated.

In Figure 5C, an $e\lambda$ value of less than one suggests a significant loss of 1st instars or a reduction in the number of producing adults. The latter is more likely, because the majority of the potential adults were altoid and did not remain in the area. It seems likely that some mortality factor was overlooked or underestimated for this period, because the observed numbers were considerably less than in the prediction column. At this time most of the predation must be done by adult predators, because few larvae were found in the colonies.

Annual cycle of *C. ponderosae*

The annual cycle for *C. ponderosae* may be summarized as follows:

November to March.—Colonies can be found on small ponderosa pine at its lowest elevation in the foothills of the Sierra Nevada.

April to June.—Alatae migrate up the west slope of the Sierra Nevada. The advancing edge of this migration is closely correlated with bud burst in ponderosa pine. Upper elevations (1,800 to 2,000 m) are reached by mid June.

July to August.—Continual migration of the third generation occurs throughout the area. Colonies become increasingly scarce during this period. Those colonies which survive are usually large and well attended by ants.

September to December.—Colonies that survive the late summer will remain on host trees at the upper elevations, until the severe weather kills them.

We have observed that this annual pattern is different from those of other cinarans in the same area. The most obvious difference is anholocycly which one might expect in the milder climatic areas of California, such as the Coast Range, but hardly in the Sierra Nevada, where winter weather can be very severe. This species forms sexuales in the Rocky Mountain Region (Palmer, et al. 1926), so anholocycly must be an adaptation to the climatic conditions of California.

Certain advantages could be proposed for evolving complete anholocyclic populations in areas with a mild climate. Sexuale production would be an unnecessary expenditure of energy, if they are unnecessary for survival. The number of males produced reduces the number of reproducing forms, and the oviparae produce fewer eggs than the viviparae produce live nymphs by at least one-third (Scheuer, 1964). Another advantage would be the possibility of utilizing lower temperatures, below the threshold at which natural enemies function, for feeding and reproduction. Predators and parasites of aphids generally have higher developmental thresholds than their host aphids (Bodenheimer and Swirski, 1957; Neuenschwander, Hagen, and Smith, 1975). The aphid is at an advantage during the colder parts of the year, depending on the magnitude of the difference between the two thresholds and providing its own host plant is available. Indications are that *Cinara ponderosae* appears to withstand low temperature, and its population appears to suffer minimal predatory interference throughout late fall, winter, and early spring. Birds, such as the mountain chickadee (*Parus gambeli*), that exhibit bark-gleaning behavior take aphids during the winter months (Dahlsten and Copper, 1979) and could cause significant losses. The consequences of growth during lower temperatures would be the availability of a large number of alate viviparae for the migration and colonization of the west slope of the Sierra Nevada every spring.

The local population of *Cinara ponderosae* is also different from other cinarans. Colonies rarely get very large and are continually moving on the host tree. Almost all of the third generation emigrates, which may minimize the impact of natural enemies, because the aphids do not seem to be very well protected by ants. Losses sustained by the migratory alatae are impossible to quantify, but the difficulty of locating new colonies started by alatae after mid July suggests that mortality must be extremely high.

Samples gathered for the construction of life tables indicate that predator and parasitoid mortality is comparatively low. It becomes a factor in reducing or decimating a local population only after a majority of the third aphid generation has emigrated.

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