DAILY AND SEASONAL INTERACTIONS BETWEEN SALMONBERRY

(RUBUS SPECTABILIS) AND BUMBLEBEES (BOMBUS SITKENSIS)

IN SOUTHWESTERN BRITISH COLUMBIA.

by

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Abstract

My study was designed to answer two main questions:

1.) Do the bees, through their foraging behavior, alter the rates of salmonberry nectar productivity?

2.) Do the plants, through their rates of nectar secretion, alter the foraging behavior of the bees?

Since there are well-documented examples of morphological coadaptations between plants and their pollinators, it was reasonable to suppose that physiological/behavioral coadaptations exist as well. Thus I hypothesized that the above questions would be answered in the affirmative. Though the two questions have been individually studied by several biologists, I felt it important to examine the possible reciprocal responses of plants and pollinators as they occur in a natural community context.

Nectar productivity of salmonberry flowers (Rubus spectabilis, Pursh) was investigated using flowers isolated for various lengths of time from insect visitors. Nectar volumes were extracted using micropipettes and sugar concentrations were determined with a hand refractometer. Volumes and sugar concentrations were then used to calculate calories/hour. Nectar standing crop (calories/flower) was similarly derived using unbagged flowers. During the study I monitored temperature, sunshine levels, relative humidity, date of sampling, time of sampling, and the androecium diameters of all flowers sampled.

It was found that an increase in experimental extraction rate brought about a corresponding decrease in productivity.

This result is opposite to that reported by other authors, yet it was found that this result was not due to flower damage or to artificial fertilization of flowers. This flower response to simulated visitation frequency may be of competitive advantage to flowers not being used by pollinators present in the area.

Productivity and nectar standing crop decreased as the salmonberry flowering season progressed, and decreased throughout the course of each day as relative humidity fell and air temperatures increased. This decline in productivity reflected decreases in volumes of nectar secreted, though sugar concentrations increased with increasing sunshine levels. Younger flowers apparently secreted calories/hour at higher rates than older flowers, this again reflecting trends in volumes of nectar secreted.

In each sample of ten flowers, there were four which secreted at rates significantly higher than the remaining six. Further, the four most productive flowers secreted at more predictable rates in terms of the environmental variables monitored during the study.

Throughout the season there was a dramatic increase of bumblebees (Bombus sitkensis, Nylander) observed at patches of salmonberry flowers. Throughout each day, the bees increased in density as sunshine levels and temperatures increased and relative humidity fell. The bees foraged from the more productive younger flowers more frequently than older flowers, and increasingly foraged from older flowers as nectar abundance in all flowers declined through the day and season. In addition, they may also have been avoiding increasing numbers of flowers

they approached, though this conclusion must remain tentative. Bumblebee behavior was more predictable during the early morning hours of each day as opposed to hours in the afternoon. It is postulated that this was because bumblebees experience more uniform energy conditions in the morning.

Based on the distribution curves of nectar resources and bee density, it is postulated that plants compete for pollinators early in the day and early in the season, while bees compete for nectar later in the day and later in the season. This hypothesis is further supported by observations on the shifts in bee foraging behaviors.

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I. General Introduction

Many flowering plants and the animals which pollinate them are mutually dependent. Flowering plants of many genera utilize animals to transport pollen between flowers, evolving methods to better attract pollinators while at the same time losing the capacity to utilize alternative modes of pollination such as water and wind (Percival, 1965; Faegri and van der Pijl, 1978). From the plant's viewpoint, these animals can thus be considered a resource which may be present in surplus amounts or may be a limiting factor in plant reproduction (Levin and Anderson, 1970; Lack, 1976). Many pollinator species, on the other hand, have evolved various characteristics allowing them to be very efficient at utilizing the food and sometimes shelter that the plants provide as "rewards" for pollination services (Heinrich and Raven, 1972), while at the same time losing their ability to live independent of the plants. The number of flowers available and the food and perhaps shelter they provide can thus be considered as resources from an animal's viewpoint, and can again be scarce or present in surplus amounts (Mosquin, 1971; Pojar, 1974; Heinrich, 1976a).

This "coevolution" to the point where mutual dependence is achieved affects morphological, physiological and behavioral characteristics of both components of the plant-pollinator relationship. Studies of morphological "fit" between plants and their pollinators are quite common. "Bird flowers" are generally characterized by vividly colored petals, long corollas and

elongated sexual parts. Bird pollinators, on the other hand, show a sensitivity for red and have long bills and tongues. Bird flowers are also odorless, while bird pollinators have scarcely any sense of smell (Baker, 1961; Grant, 1966; Carpenter, 1976; Stiles, 1978; Faegri and van der Pijl, 1978). Examples of morphological coadaptations between bees and bee flowers are also numerous. Bee flowers are mechanically strong, often with floral "lips" which provide a surface upon which bees can land and maintain a foothold. The petals of these flowers are brightly colored, generally yellow or blue, and the flowers are frequently fragrant. Bees are known to have a keen sense of odor, and are physically very strong insects, allowing them to gain entrance into the semi-closed bee flowers (Free and Butler, 1959; Baker, 1963; Beattie, 1971; Alford, 1975; Faegri and van der Pijl, 1978). Similar coadaptations exist for other groups of animals (e.g., bats, flies, butterflies, beetles) and the flowers they typically pollinate (Baker, 1961; Gregory, 1963; Percival, 1965; Thien, 1974; Howell, 1977; Faegri and van der Pijl, 1978).

Many studies stress the "reciprocal pattern in which flowers exploit the behavioral repertoire of insects, and the insects exploit the genetic parameters of the expression of floral form" (Macior, 1974, p. 760). It is of adaptive value for both the animals and the plants if the pollinators are able to readily react to possible changes in food abundance, weather variables and numbers of other plant and animal species present in the habitat. The interaction between plants and "behaviorally plastic" pollinators has received much attention in recent

years. Heinrich (1979a) has described the phenomenon he calls "majoring" and "minoring" in bumblebees, by which the bees forage on the flower species of greatest nectar abundance and yet periodically sample flowers of other species, thereby monitoring resource abundance in all species. Much recent work has been done on the directionality of bee movement in relation to local nectar abundance. Pyke (1978a) and Heinrich (1979b) have found that bees foraging in a rewarding flower patch tend to change directions on successive flights between flowers, while those in a nectar depleted patch tend to fly in only one direction, more quickly taking them out of the patch presently being foraged. Pyke (1978a) has also determined that there is a strong negative relationship between the distance of departing flight and the presumed rewards the bees had obtained.

That honeybees shift foraging behavior in response to changes in food resources is widely known. Several authors have studied the "dance language" of honeybee foragers returning to the hive from the field (von Frisch, 1971; Lindauer, 1971; Michener, 1974). Through this dance the foragers are thought to communicate to other workers the distance, direction from the hive and quality of currently attractive nectar flows. Honeybees are known to prefer highly concentrated nectar, and will switch from a nectar source of low concentration to one of a higher concentration (Vansell et al., 1942; Butler, 1945). Honeybees are relatively flower "constant" in that, during each foraging trip from the hive, they tend to visit flowers of only one species. They are believed to be more constant than bumblebees (Michener, 1974; Grant, 1950), yet, when nectar resource levels

reach low levels this high selectivity is greatly reduced (Filmer, 1941; Grant, 1949).

The foraging behavior of hummingbirds and sunbirds has also been studied in some detail. It has been found that, in general, the time spent foraging by these birds is roughly proportional to the energy obtained from the flowers being foraged (Wolf, 1975). Though Baker (1961) and Grant (1949) report that hummingbirds display very low flower fidelity, several authors have found individual hummingbirds to "major" on particular flower species (Wolf and Hainsworth, 1971; Feinsinger, 1976; Stiles, 1978). It is accepted, however, that the foraging behavior of nectarivorous birds is more adaptable and opportunistic than that of many insect pollinators (Stiles, 1978). Hummingbirds prefer high nectar concentrations to lower concentrations (Hainsworth and Wolf, 1976), and forage from inflorescences with many flowers; for example, they avoid Ipomopsis aggregata inflorescences with less than seven flowers even though these inflorescences occur with a frequency of approximately 25% (Pyke, 1978b). A study by Gill and Wolf (1975) showed that larger sunbirds in a community of seven sunbird species preferentially forage from closed mistletoe flowers. As the proportion of closed flowers declines through the day the birds increasingly add previously avoided open flowers to their diet.

Studies into the "behavioral plasticity" of the plants in the plant-pollinator relationship are not common. Several authors believe that interspecific competition for pollinators has resulted in asynchronous blooming of plant species occuring

in the same habitat (Mosquin, 1971; Pojar, 1974; Heithaus, 1974; Stiles, 1975; Frankie, 1975; Heinrich, 1975b, 1976b; Waser, 1978). Yet shifts in a plant species' blooming time occurs on an evolutionary time scale and does not allow plants to react to daily or even hourly changes in pollinator abundance and behavior. Flowers do show daily cycles of nectar productivity (Park, 1929; Vansell et al., 1942; Butler, 1945; Baker, 1961; Feinsinger, 1978; Corbet, 1978), but this has not been shown to be a plant response to pollinators.

Several authors have observed that as sampling frequency increases, the production of nectar increases as well (Raw, 1953; Mel'nichenko, 1963; Kurina, 1974; Feinsinger, 1978). This result indicates that natural pollinators, through the use of floral nectar resources, may themselves increase the rate of nectar production in flowers. If this is true, it means that plants change their rate of production in response to pollinator use, and perhaps, therefore, to current pollinator density in the habitat. This would indicate a behavioral plasticity on a time scale previously unsuspected in plants.

However, much more work needs to be done on the exact nature and extent of this productivity response in the plant kingdom. It is also necessary to study this response as it occurs in a community context, where the plants live with and respond to daily and seasonal changes in pollinator abundance and behavior, weather variables, soil moisture content and the presence of competing plant species. Such studies may allow increased insight into the evolutionary significance of nectar productivity.

Salmonberry (Rubus spectabilis, Pursh) flowers secrete
nectar and through this attract pollinators (Fig. 1). The
following study investigated possible changes in salmonberry
nectar secretion as a response to shifts in pollinator
visitation frequency. At the same time, shifts in bee foraging
behavior were investigated as a possible response to variations
in floral nectar resources. The ultimate goal of this study has
been to fit the responses of both components together to allow
increased understanding of the plant-pollinator relationship.

The plant-pollinator system selected for this study was
chosen primarily for ease of study. Throughout much of their
flowering season, salmonberry plants produce large numbers of
flowers. It is possible to sample the flowers for available
nectar using simple micropipette techniques, and the plants can
be found along forest roads, allowing easy access. Though pollen
is also produced by the flowers and is utilized by bumblebees
(Alford, 1975), several authors believe that pollen is
"collected coincidentally with nectar" (Inouye, 1977, p. 253),
that pollen is continuously plentiful enough to meet colony
needs and that nectar is the resource which may limit bumblebee
colony growth (Heinrich, 1975a). The same assumption has been
made, sometimes implicitly, throughout this study, though
whether it is an assumption which has a factual basis deserves
further study. Bumblebees are desirable study animals since one
can safely assume that colony workers fly for no other reason
than to forage for food, and they forage relatively unhindered
by the presence of observers (Pyke, 1978a).

Fig. 1: Salmonberry flowers and bumblebee foragers.
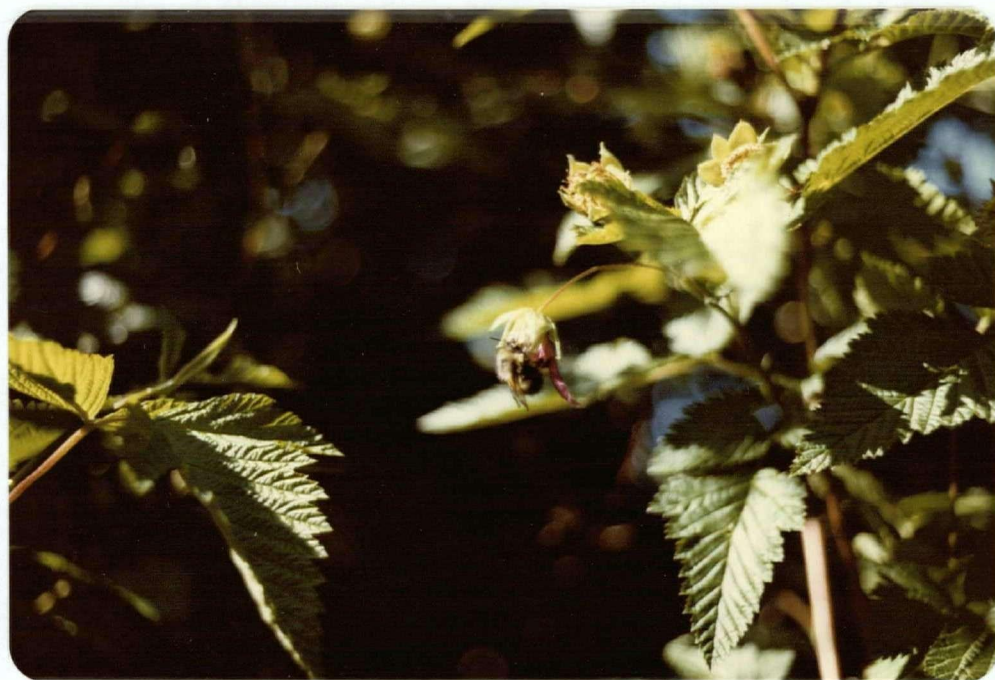
II. FLOWER PRODUCTIVITY

a.) Introduction

The purpose of this study was primarily to investigate the effects of bumblebee foraging frequencies upon salmonberry nectar productivity, measured as calories/hour. To be able to account for the variability in productivity due to sampling rate alone, several other variables were simultaneously monitored; these included flower age, level of insolation, relative humidity, time of day and date of sampling. The effect of these individual variables upon nectar productivity were also analyzed.

Several authors have noted that as sampling frequency increases the production of nectar also increases (Raw, 1953; Mel'nichenko, 1963; Kurina, 1974; Feinsinger, 1978). This response is considered to be adaptive for the plants since they need not shunt energy into nectar production when pollinators are not present, and as pollinator demand increases, can then offer resources in proportion to demand. It is necessary to offer the right amount of reward to the pollinators to keep them moving from flower to flower within the same plant species in an effort to collect needed food resources; too much reward and pollinators simply gorge themselves and cease to travel amongst the flowers (hence cease to be effective pollinators), too little and they become discouraged with the species upon which they are currently foraging and switch to another (Heinrich, 1975a). By being able to track pollinator demand plant species can then continuously offer the appropriate amount.

A seemingly reasonable method of determining the amounts of nectar harvested by foraging insects involves comparing standing crop levels in flowers open to forager use with levels in isolated flowers (see e.g., Heinrich, 1976a). Yet if foragers are acting to increase the rates of nectar production, this method would consistently underestimate true quantities of nectar harvested by pollinators more active than the reseacher.

It seemed likely that the findings of other authors should hold for salmonberry, that as sampling frequency increases the calories/hour offered by the flowers should also increase.

B.) Methods

Study site: The study was conducted at the UBC Research Forest located near Haney, B.C. The 5157 hectare forest is dominated by stands of Douglas fir, western hemlock and western redcedar. The actual study sites were located along K30, the road just north of Marion Lake, and along H20, the Eunice Lake road (see map, Fig. 2). Elevations of the sites were, respectively, 330 meters and 480 meters.

The two sites were very similar in terms of species present. The sides of the roads were dominated by long rows of salmonberry intermixed with stands of thimbleberry (Rubus parviflorus). Other flowering species were present in the area (e.g., violets, dandelions), many of which have been described as highly attractive to bees in other areas (Mosquin, 1971). Yet, in my study areas salmonberry was the species of bee

Fig. 2:   Map of the University of British Columbia
          Reasearch Forest, showing study sites at
          Marion and Eunice Lakes

North

Pitt Lake
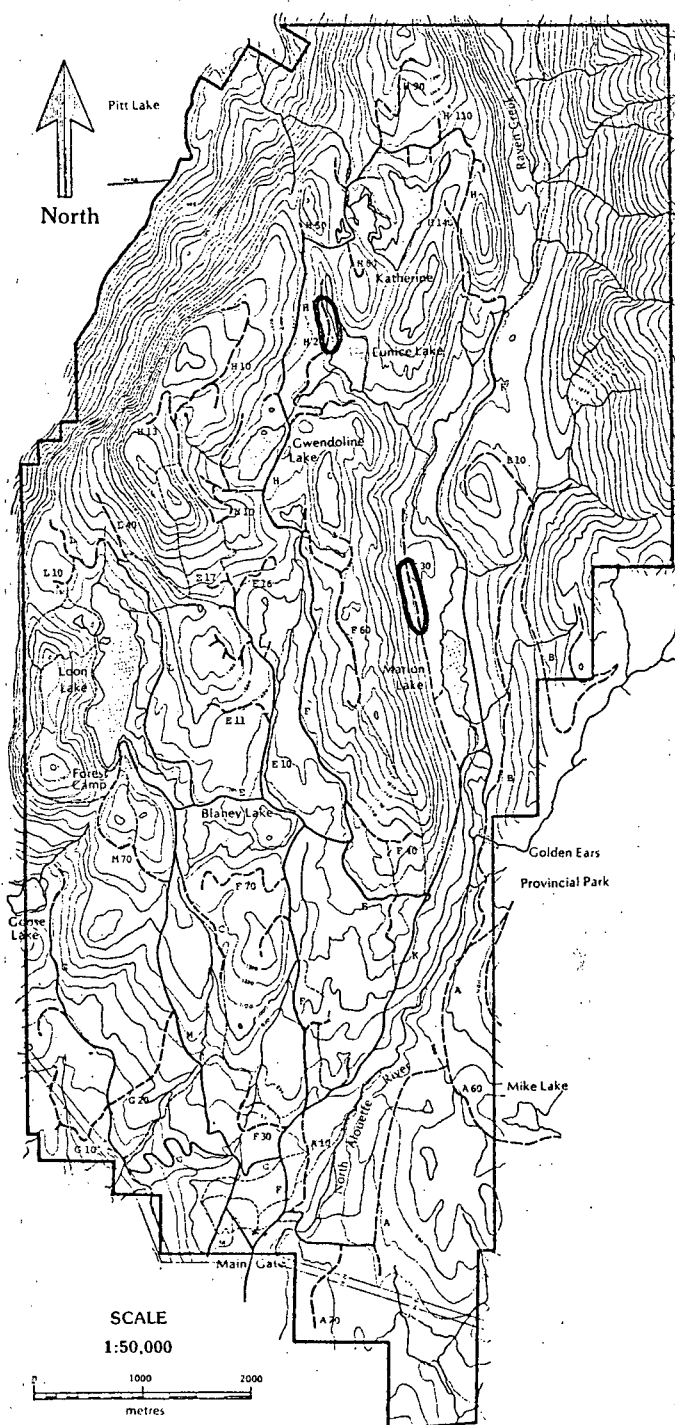
THE UNIVERSITY OF BRITISH COLUMBIA

RESEARCH FOREST

MAPLE RIDGE, B.C.

Director: Professor J. Walters, R.P.F.
Address: U.B.C. Research Forest
R.R.2
Maple Ridge, B.C.
V2X 7E7
Phone: 463-8148

WELCOME TO THE RESEARCH FOREST

This experimental forest is dedicated to research, education, and demonstration in the forest sciences.

You are invited to walk around the Forest — no vehicles, horses, or bicycles are permitted. We ask that you respect the prime function of the Forest and do not tamper with research installations.

- No fishing or hunting is allowed because of research projects concerning stream ecology and wildlife
- Dogs are not permitted as they hinder research into blacktail deer
- We do not allow camping or fires, our neighbour to the east, the Golden Ears Provincial Park, provides these facilities
- The Forest Camp at the south end of Loon Lake is closed to the public. Please stay out of this area.

PLEASE TAKE YOUR LITTER HOME WITH YOU

Legend

- main road
- branch road
- building
- trail

- contours at 100' intervals
- restricted area (no public access)
- powerline

Katherine

Cunice Lake

Gwendoline Lake

Loon Lake

Forest Camp

Blaney Lake

Goose Lake

Marion Lake

Golden Ears

Provincial Park

Mike Lake

North Alouette River

Main Gate

SCALE

1:50,000

0   1000   2000

metres

preference, with species such as violets and dandelions receiving no observed visits from bumblebees. Only near the end of the salmonberry flowering season did attractive species such as thimbleberry begin to flower.

Bumblebees were by far the most frequent salmonberry flower visitors at the study sites, these being predominantly _Bombus sitkensis_, Nylander, though occasionally individuals of _B. melanopygous_ and _B. mixtus_ were seen. "Flower flies" (_Criorhina luna_) were common, but were far less numerous than _B. sitkensis_ and each fly visited far fewer flowers than did each _B. sitkensis_ individual per unit time. A few hummingbirds were present in the areas, but it was rare to see them foraging at salmonberry flowers. Present in great abundance were small rove beetles of the genus _Eusphalerum_, which, though they flew infrequently, did carry pollen on their bodies (Barber, 1976), and may thus have been effective pollinators.

The following study took place between May 3 and June 28, 1979. Several authors have used nectar collected from the honeystomachs of bees to analyse flower nectar concentration (e.g., Butler, 1945), yet this method would have been far too cumbersome for the present study. Pipetting nectar from flowers was used instead, the assumption being made that pipetting techniques adequately simulated the possible effects of bumblebee foraging upon nectar production. Samples of 10 flowers were used due to the need to collect nectar samples as quickly as possible; I found that extracting nectar from 10 flowers and measuring its volume and concentration required 40 min to 60 min to complete. Each flower was arbitrarily chosen except for the

requirement that it be at least 2 "plants" distant (approx. 3 meters) from other flowers in the same or other sampling groups. Salmonberry plants reproduce vegetatively by means of rhizomes under the soil, thus it is difficult to tell if an above ground "plant" is truly separate from a neighboring plant. Barber (1976, p.60) states that "the ability of salmonberry to reproduce vegetatively is responsible for the local perpetuation of colonies". Yet he also states that, "seedlings are sometimes found growing on peat, rotten logs and stumps, mineral soil and along roadsides" (Barber, 1976, p.60). It seems likely that salmonberry plants growing along the roadsides of the study sites originated from many seedlings which germinated following local disturbance. Thus, I felt that the above requirement would help assure that flowers sampled would be on separate plants.

Small bags constructed of Nitex netting (mesh opening, 0.2 mm) were used to exclude all animals from flowers under study, including beetles of the genus Eusphalerum. Nectar was removed from the flowers using Drummond "microcaps", disposable micropipettes. Each flower was drained first with a 25 ul tube followed by a 10 ul tube. Tubes were carefully manipulated to gather all nectar possible without causing extensive damage to floral nectaries. Sampling frequencies were selected after observing frequencies of bumblebee visits to patches of salmonberry flowers early in the season. During three observation sessions, each flower in a patch was visited by a bee an average of every 0.67 hr, 1.3 hr and 1.2 hr. Samplings with pipettes were thus set at 2 hours, 4 hours, 6 hours and 8 hours, instead of 12 hours, 24 hours and 36 hours as used by Raw

(1953). Due to the need to collect approximately 10 flowers in each sample, sampling could not be much more frequent, yet I felt that the selected frequencies reflect biological reality more closely than do previous studies.

For ease of recording and reporting, sampling frequency data are expressed in terms of the time elapsed between group samplings. This value is the denominator of the frequency expression, 1 sample/x hours, thus the time elapsed between samples is inversely proportional to the sampling frequency. Also recorded were the volume of nectar obtained from each flower and the % sugars present in the nectar, measured using a Fisher Instruments hand refractometer. Depending upon the sampling rates assigned each group, flowers could be sampled up to 3 or 4 times a day. Fresh groups of flowers were chosen each morning due to the possibility of flower damage resulting from sampling techniques.

Nectar volume and % sugars were converted to calories/hour as follows (Robert Montgomerie, personal communication). It was assumed here that nectar is composed primarily of the disaccharide sucrose and its components, glucose and fructose, though other substances are known to be present in very low concentrations (Baker and Baker, 1975). The mg sucrose/ul solution corresponding to each refractometer reading was obtained from Weast (1976). Multiplying this value by the measured ul of sample, then further multiplying by the constant 3.7 calories/mg of sucrose (Heinrich and Raven, 1972), yields the number of calories available from each flower. Dividing this by the time elapsed between samplings then yields

the calories/hour for each flower.

To determine flower age, a structural feature of the flower was needed as an accurate indicator. From previous observations, I felt that the diameter of the androecium (anther ring) would make a suitable indicator due to its ease of measurement as well as the apparent increasing of the diameter with age. On April 25, 20 unopened flower buds were tagged along approximately 1/2 mile of the rarely used forest road, G10. For 4 days thereafter measurements of each androecium diameter were made using a small calipers (Fig. 3). For those cases in which the anther ring was acircular, the measurement was made along the dimension judged to be the average. The androecium diameter was recorded for each flower measured for productivity.

Insolation was continuously monitored each day using an actinograph manufactured by Weather Measure Corporation of Sacramento, Calif. Insolation data collected during productivity studies is expressed as average "levels" per hour of nectar production. These figures, when multipied by the instrument constant (k=0.405), yield the more standard units, cal/cm^2/min, though raw levels were used for the analysis in this study. Relative humidity was measured 2 or 3 times daily using a standard sling psychrometer supplied by Taylor Instrument Company of Rochester, N.Y. Time of day was recorded for each sample; data were then transformed into "hours after sunrise", a more biologically meaningful measurement. A census of flowers was taken each week, which consisted of simply walking three 9 meter transects laid out upon the road, each transect separated by 3 meters, and counting all flowers seen along one side of the

Fig. 3:　Using a calipers to determine the androecium diameter of a salmonberry flower (petals not shown).
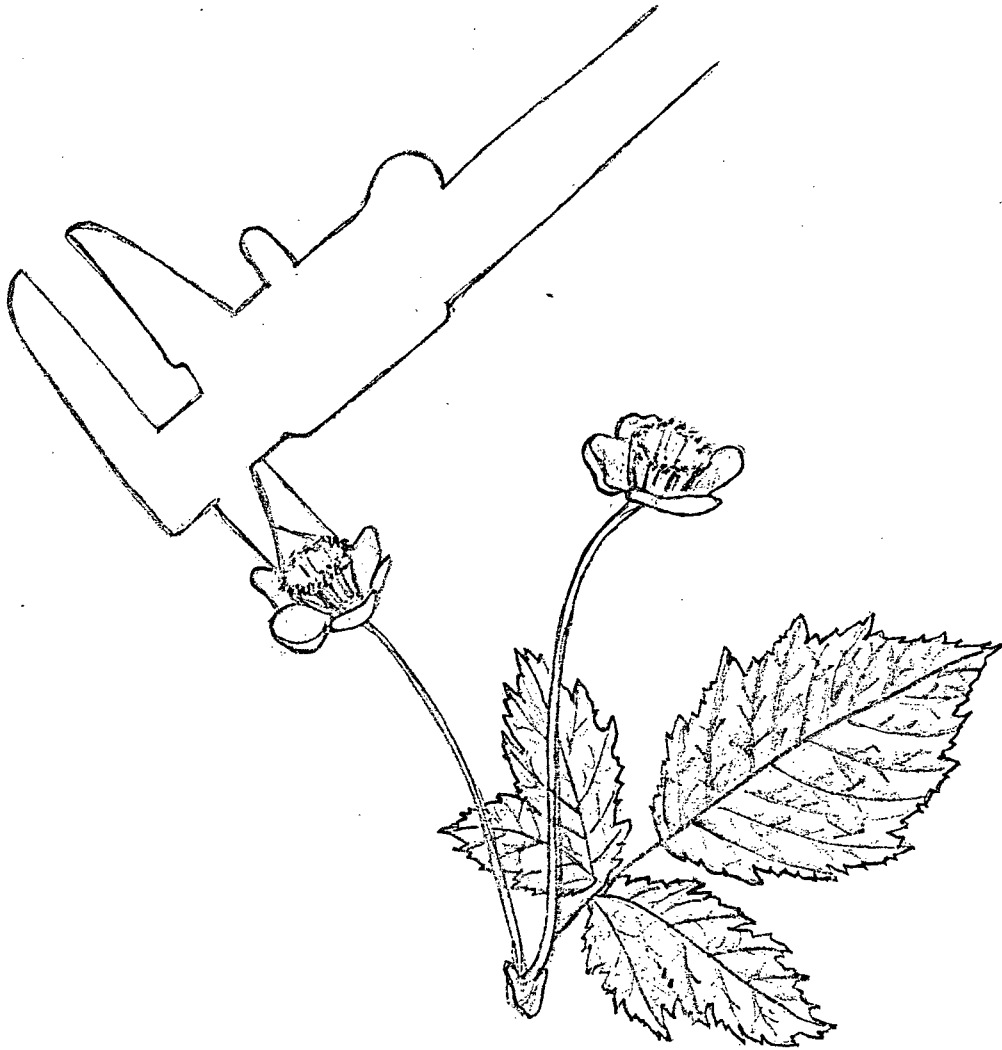
road.

C.) Results

A peak in numbers of flowers at the study site occurred on May 15 (Fig. 4), with a drastic decline occurring on May 28. The rise cn June 5 represents a shift in study areas to Eunice Lake. Flower numbers here slowly declined in late June, and salmonberry flowers could no longer be found in the forest area at this time.

Androecium diameter data were adjusted to reflect the actual age of the flowers, not merely the number of days since tagging. When choosing a bud, it is impossible to know its true age pricr to opening. Thus, buds included in the sample were probably not all identical ages. For the graph in Fig. 5, a bud, on the day it first opens, is considered as 1 day old, prior to that it is considered as 0 days old. Androecium diameter is highly correlated with flower age (r=.8389, p<.001).

Table I lists basic statistics for the variables, cal/hr, % sugars and ul nectar/hr, while a frequency histogram for the variable, cal/hr, is shown in Fig. 6. The average flower secreted 0.81 ul nectar/hr which was composed of 23% sugar, thus making available 0.67 cal/hr. These values are somewhat misleading since they are based on data collected using several sampling rates, which may have influenced nectar productivity. A pooling of data was necessary here since little information is available for any cne sampling rate used during the study.

A model using a stepwise regression procedure, adding

Fig. 4: Relationship between date and the mean number
        of salmonberry flowers counted per meter in
        1979. Bars indicate one ± standard deviation
        of each sample mean.

Marion Lake
Site

Eunice Lake
Site

20

16

flowers/meter

12

8

4

0

May 1   May 13   May 25   June 6   June 18   June 30

Date
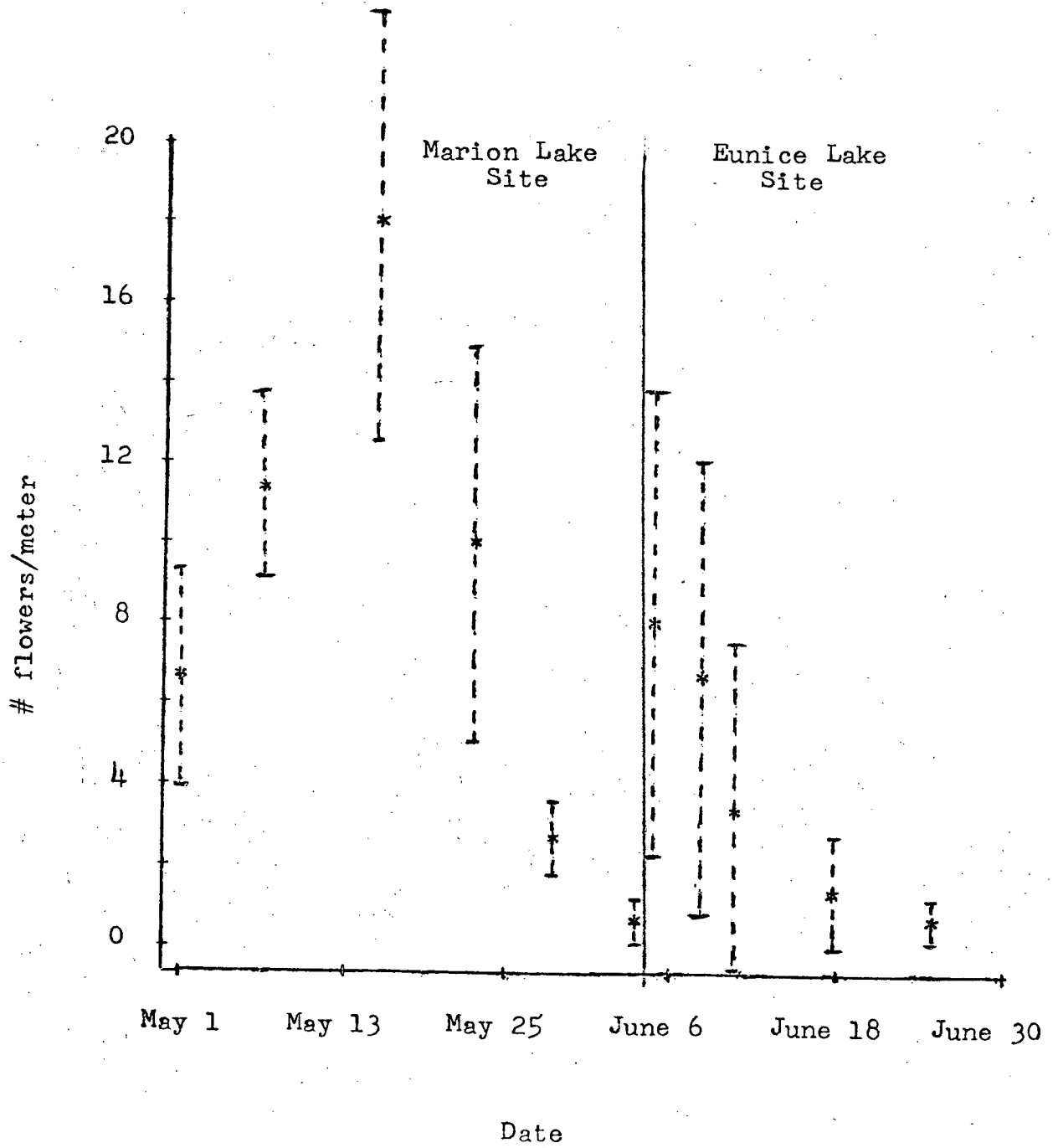
Fig. 5:   Regression of androecium diameter and age of
           salmonberry flowers.
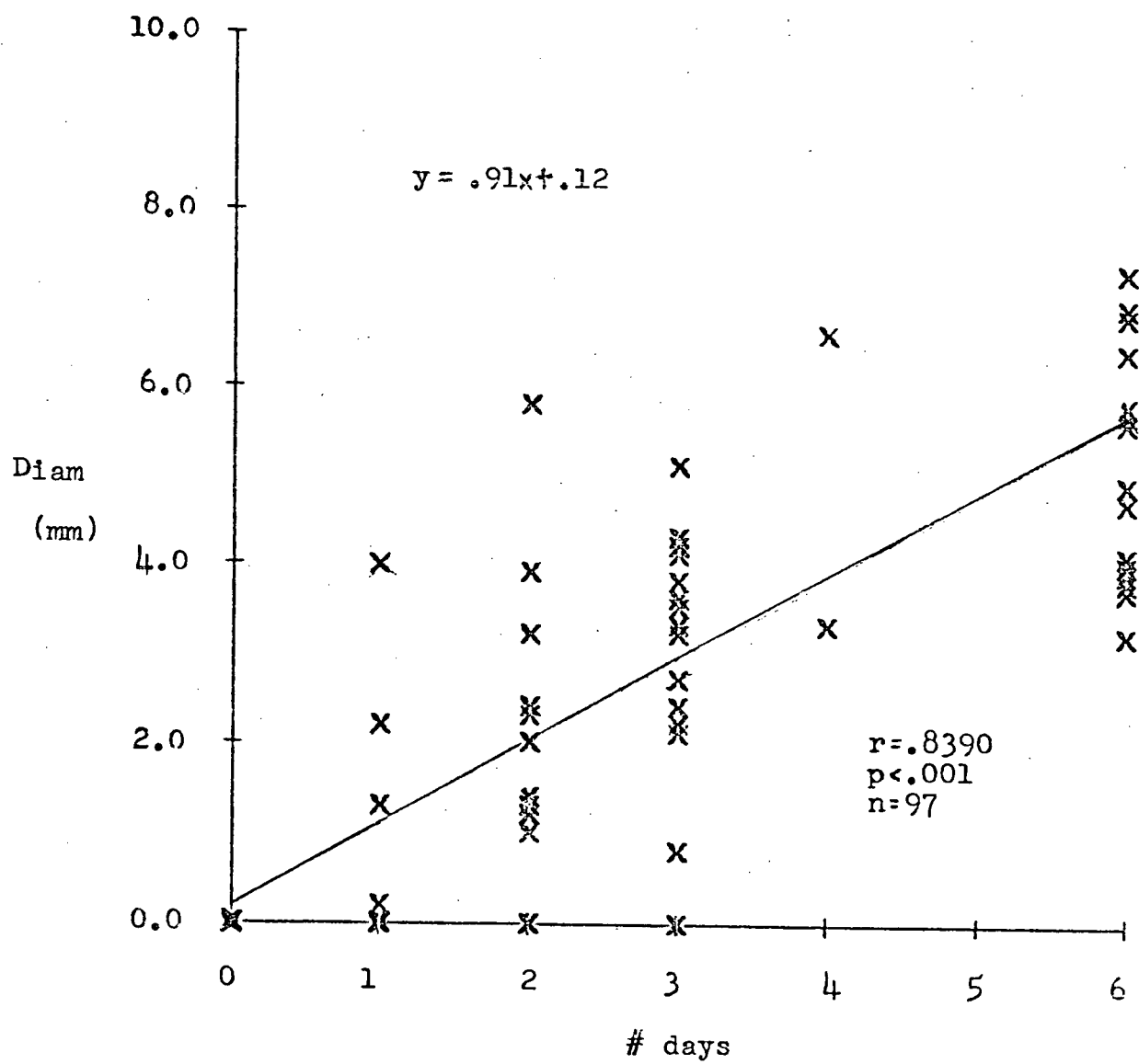
Table I: Basic statistics for the nectar production of
all salmonberry flowers sampled.

Table II: Basic statistics for the nectar production of
the four most productive salmonberry flowers
sampled at each episode.

Table I

	N	Min	Max	Mean	Std Dev	95% CI
cal/hr	779	0	13.31	0.67	0.98	0.60 0.74
% sugars	557	2.7	84.0	23.5	10.4	22.6 24.4
ul nectar/hr	786	0	15.00	0.81	1.23	0.73 0.90

Table II

	N	Min	Max	Mean	Std Dev	95% CI
cal/hr	334	0	13.31	1.08	1.26	0.94 1.22
% sugars	258	10.0	49.0	23.6	9.0	22.5 24.7
ul nectar/hr	334	0	15.0	1.26	1.57	1.09 1.43

Fig. 6: Histograms showing frequency distributions
of productivity values.

    a) For all salmonberry flowers sampled,
each $X=9$ observations.

    b) For more productive flowers sampled at
each episode, each $X=3$ observations.

Frequency of Observations (each X=9)

```
0.           357  +XXXYXXXAXYXYXXXXXXXXXXX XXXXXXXXXXXXXXXXXY
 .50000      166  +XXXXXAXAXYXYXYXXXXX
1.0000        77  +XXXXXXXXXX
1.5000        71  +XXXXXXXX                              (a )
2.0000        44  +XXXXX
2.5000        22  +XXX
3.0000         9  +X
3.5000         3  +X
4.0000         2  +X
4.5000         2  +X
5.0000         1  +X
5.5000         0  +
6.0000         0  +
6.5000         1  +X
7.0000         0  +
7.5000         0  +
8.0000         1  +X
8.5000         0  +
9.0000         0  +
9.5000         0  +
10.000         0  +
10.500         0  +
11.000         0  +
11.500         0  +
12.000         0  +
12.500         0  +
13.000         0  +
13.500         1  +X
14.000         0  +
```

Frequency of Observations (each X=3)

```
0.            85  +XXXXXXXXXXXXXXXXXXXXXXXXXXXXX
 .50000       84  +XXXXXXXXXXXXXXXXXXXXXXXXXXXXX
1.0000        50  +XXXXXXXXXXXXXXXXX
1.5000        44  +XXXXXXXXXXXXXXX                       (b )
2.0000        30  +XXXXXXXXXX
2.5000        21  +XXXXXXX
3.0000         9  +XXX
3.5000         3  +X
4.0000         2  +X
4.5000         2  +X
5.0000         1  +X
5.5000         0  +
6.0000         0  +
6.5000         1  +X
7.0000         0  +
7.5000         0  +
8.0000         1  +X
8.5000         0  +
9.0000         0  +
9.5000         0  +
10.000         0  +
10.500         0  +
11.000         0  +
11.500         0  +
12.000         0  +
12.500         0  +
13.000         0  +
13.500         1  +X
14.000         0  +
```

Calories/Hour (midpoints of intervals)

variables into the model as long as they accounted for variability remaining from previously introduced variables, was constructed for productivity (cal/hr) and is presented in Table III. The data used for the model and for all subsequent analyses (unless otherwise noted) were transformed by taking the natural logarithm (ln) of the data. For many analyses performed, including the multiple regression model, this transformation resulted in higher correlation coefficients than did the original values or alternative transformations. A variable was included in the model if the "t" statistic associated with it is significant at $p < .05$. Variables selected in the productivity model include the time elapsed between samples as well as date, androecium diameter, number of flowers/meter, relative humidity and the hours after sunrise at which each sampling was done. The model accounts for 37% of productivity variability, including each flower in each group of 10 sampled, for all sampling frequencies.

To investigate the possibility that these results were offset by "defective" flowers, (those which secreted nectar well below the mean due to characteristics not determined in this study), the data were reanalyzed using only the 4 most highly productive flowers in each sample group. Some basic statistics and a histogram for these flowers are provided in Table II and Fig. 6. Mean productivity for these flowers was 1.08 cal/hr. A test to determine the significance of the difference between the mean of these "productive" flowers and that of all flowers sampled (Table IV) shows that the two groups did secrete significantly different amounts of nectar, (at a significance

Table III: Stepwise regression model built for the variable,
             ln calories/hour, for all salmonberry flowers.

             a) Variables selected for the model.
             b) Variables not selected.
             c) Steps in model construction.

ANALYSIS AT STEP 9 FOR 19.V19 N= 708 OUT OF 1182

SOURCE	DF	SUM OF SQRS	MEAN SQUARE	F-STAT	SIGNIF
REGRESSION	9	46.903	5.2115	46.060	.0000
ERROR	698	78.976	.11315		
TOTAL	707	125.88			

MULTIPLE R= .61042 R-SQR= .37261 SE= .33637

a)

VARIABLE	PARTIAL	COEFFICIENT	STD ERROR	T-STAT	SIGNIF	
CONSTANT		22.276	3.6327	6.1320	.0000	
1.V1	.09680	.16797 -1	.65374 -2	2.5694	.0104	date
5.V5	-.10378	-.14828	.53788 -1	-2.7567	.0060	diameter
10.V10	.23096	.82819 -1	.13212 -1	6.2687	.0000	rel. humidity
11.V11	.20602	.29574 -2	.53169 -3	5.5623	.0000	# flowers/meter
14.V14	-.14221	-.83959	.22120	-3.7956	.0002	ln date
15.V15	-.11968	-.23381	.73412 -1	-3.1849	.0015	ln hours after sunrise
16.V16	.33573	.41066	.43612 -1	9.4163	.0000	ln time elapsed between samples
18.V18	.08002	.23379	.11023	2.1209	.0343	ln diameter
23.V23	-.21194	-6.0474	1.0555	-5.7295	.0000	ln rel. humidity

b)

REMAINING	PARTIAL	SIGNIF	
2.V2	.01580	.6767	hours after sunrise
3.V3	-.03386	.3714	time elapsed between samples
4.V4	.02718	.4731	sunshine
17.V17	.01850	.6253	ln sunshine
24.V24	.06152	.1041	ln # flowers/meter

REGRESSION OF 19.V19 USING FORWARD SELECTION

c)

STEP	R-SQR	STD ERROR	# VAR	VARIABLE		PARTIAL	SIGNIF
1	.18816	.38046	1	14.V14	IN	-.43377	.0000
2	.26866	.36151	2	16.V16	IN	.31372	.0000
3	.31379	.35028	3	10.V10	IN	.24997	.0000
4	.32519	.34761	4	15.V15	IN	-.12886	.0006
5	.33315	.34580	5	23.V23	IN	-.10862	.0039
6	.35501	.34033	6	11.V11	IN	.18105	.0000
7	.36338	.33835	7	5.V5	IN	-.11393	.0025
8	.36856	.33721	8	1.V1	IN	.09025	.0168
9	.37261	.33637	9	18.V18	IN	.08002	.0343

Table IV: Test of the difference between the means of two
flower populations: all flowers sampled and
the four more productive flowers sampled at
each episode.

For productivity data, the sample means are proportional to the variances. Therefore, a square root transformation has been performed on all data used for the following tests, as recommended by Ostle and Mensing (1965).

Part 1:   Test of equal variances of the two populations $\sigma_1^2 = \sigma_2^2$, an assumption of the test in part 2.   Using .05 significance level.

using $\dfrac{s_1^2}{s_2^2} = F_{(n_1-1),(n_2-1)}$

$s_1 = 0.56$ $s_1^2 = 0.31$
$s_2 = 0.54$ $s_2^2 = 0.29$

$$\frac{s_1^2}{s_2^2} = \frac{0.31}{0.29} = 1.07$$

$F_{(334-1),(779-1)} =$ $F_{(333,778)(.025)} \cong$ 0.88 $0.88 < 1.07 < 1.13$
                   $F_{(333,778)(.975)} \cong$ 1.13

so must accept that $\sigma_1^2 = \sigma_2^2$.

Part 2: Difference between the means of two flower
populations.

$$using \quad (u_1 - u_2) = (\bar{x}_1 - \bar{x}_2) \pm ts_{(\bar{x}_1 - \bar{x}_2)}$$

where $\bar{x}_1$ = sample mean of population 1 = 0.87
$\bar{x}_2$ = sample mean of population 2 = 0.61

$$s^2_{(\bar{x}_1 - \bar{x}_2)} = s^2 p/n_1 + s^2 p/n_2$$

$$s^2 p = \frac{(n_1 - 1)s^2_1 + (n_2 - 1)s^2_2}{(n_1 - 1) + (n_2 - 1)} = \frac{(333)(0.31) + (778)(0.29)}{333 + 778}$$

$$= 0.30$$

$s^2_{(\bar{x}_1 - \bar{x}_2)} = 0.30/334 + 0.30/779 = 0.00128$
$s_{(\bar{x}_1 - \bar{x}_2)} = 0.036$

For 95% confidence limits, $t_{(.975, 1111 df)} = 1.962$

so $(u_1 - u_2) = (0.87 - 0.61) \pm (1.962)(0.04)$
$= 0.26 \pm 0.08$
or 0.34 and 0.18

level of .05 for determination of the "t" statistic). A regression model constructed for these more productive flowers is presented in Table V. Many of the same variables are included here as in the first model, yet here the model accounts for 54% of productivity variability. Hence, for each sample of 10 flowers there was a subset of flowers which produced nectar at rates significantly higher than the other flowers, and whose productivity is more predictable using the variables measured in this study.

A striking seasonal effect can be seen in productivity data, and it is particularly for this reason that discussion of a "mean" productivity value is misleading. As Fig. 7 shows, calories offered gradually decreased as the summer progressed; a seasonal mean does not reflect differences between what was offered during different days and weeks. A high correlation exists between cal/hr of all flowers sampled and date (r=-.4280, p<.001), and date was the first variable selected as being of significant explanatory value in the seasonal regression model (Table III). Cal/hr secreted by the four most productive flowers of a group is even more highly correlated with date (r=-.5667, p<.001).

To gauge the effects of the time elapsed between samples ("TEBS") upon nectar productivity (cal/hr), a scattergram of the data is provided in Fig. 8. As TEBS increased, cal/hr increased as well, though a great deal of variability can be observed (r=.1012, p<.01 for all flowers, and r=.1362, p<.02 for more productive flowers). To view this relationship independent of the strong seasonal effects, Fig. 9 illustrates the residuals of

Table V: Stepwise regression model built for the variable,
ln calories/hour, for the four most productive
salmonberry flowers sampled at each episode.

a) Variables selected for the model.
b) Variables not selected.
c) Steps in model construction.

ANALYSIS AT STEP 6 FCR 19.V19 N= 300 OUT OF 334

SOURCE	DF	SUM OF SQRS	MEAN SCUARE	F-STAT	SIGNIF
REGRESSICN	6	34.732	5.7887	58.740	.0000
ERROR	293	28.875	.98549 −1		
TOTAL	2SS	63.6U7			

MULTIPLE R= .73895   R-SQR= .54604   SE= .31392

a)

VARIABLE	PARTIAL	COEFFICIENT	STD EFROR	T-STAT	SIGNIF	
CONSTANT		17.425	4.6668	3.7338	.0002	
1.V1	-.35460	-.11178 −1	.17220 −2	-6.4915	.0000	date
10.V10	.24276	.75436 −1	.17610 −1	4.2836	.0000	rel. humidity
11.V11	.22537	.26278 −2	.66363 −3	3.9597	.0001	# flowers/meter
15.V15	-.20522	-.37242	.10376	-3.5893	.0004	ln hours after sunrise
16.V16	.44271	.52049	.61586 −1	8.4514	.0000	ln time elapsed between samples
23.V23	-.21205	-5.1602	1.3893	-3.7142	.0002	ln rel. humidity

b)

REMAINING	PARTIAL	SIGNIF	
2.V2	.03321	.5706	hours after sunrise
3.V3	-.05439	.5570	time elapsed between samples
4.V4	-.04691	.4229	sunshine
5.V5	.03335	.5689	diameter
14.V14	-.06238	.2864	ln date
17.V17	-.05501	.3472	ln sunshine
18.V18	.04710	.4211	ln diameter
24.V24	.05657	.3338	ln # flowers/meter

REGRESSION OF 19.V19 LSING FORWARD SELECTICN

c)

STEP	R-SQR	STD ERROR	# VAR	VARIAELE		PARTIAL	SIGNIF
1	.32933	.37835	1	1.V1	IN	-.57387	.0000
2	.43144	.34855	2	16.V16	IN	.39020	.0000
3	.48727	.33193	3	1C.V1C	IN	.31335	.0000
4	.51528	.32329	4	15.V15	IN	-.23374	.0000
5	.52467	.32068	5	11.V11	IN	.13919	.0166
6	.54604	.31392	6	23.V23	IN	-.21205	.0002

Fig. 7: Scatter plot of date and salmonberry flower productivity (ln calories/hour).

ln(calories/hour + 1.0)

r=-.4280
p<.001
n=779

Date
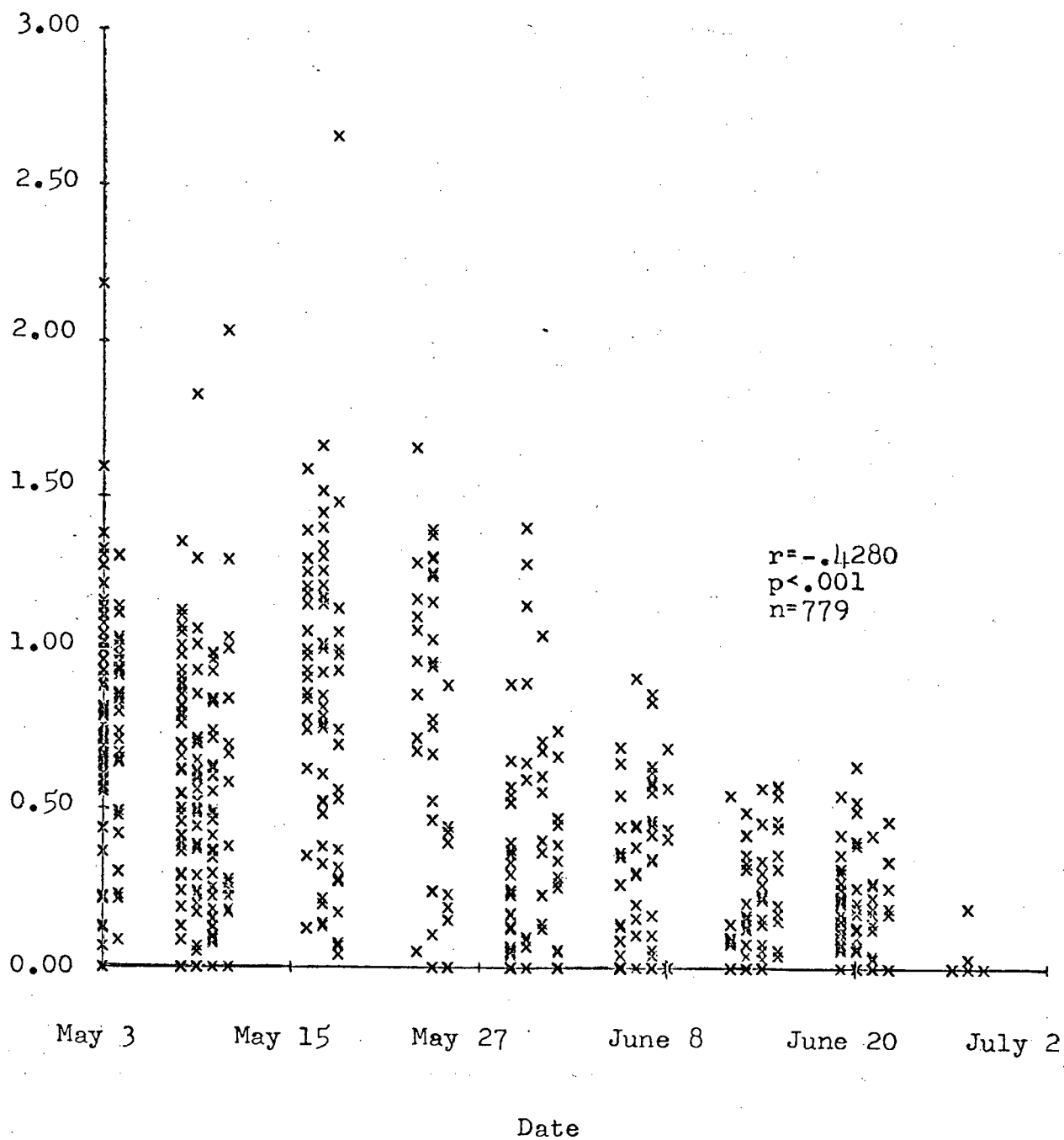
Fig. 8: Effect of the time elapsed between samples on
         salmonberry flower productivity (ln calories/hr).

ln(calories/hour + 1.0)

r=.1012
p<.01
n=779

Time Elapsed Between Samples (hours)
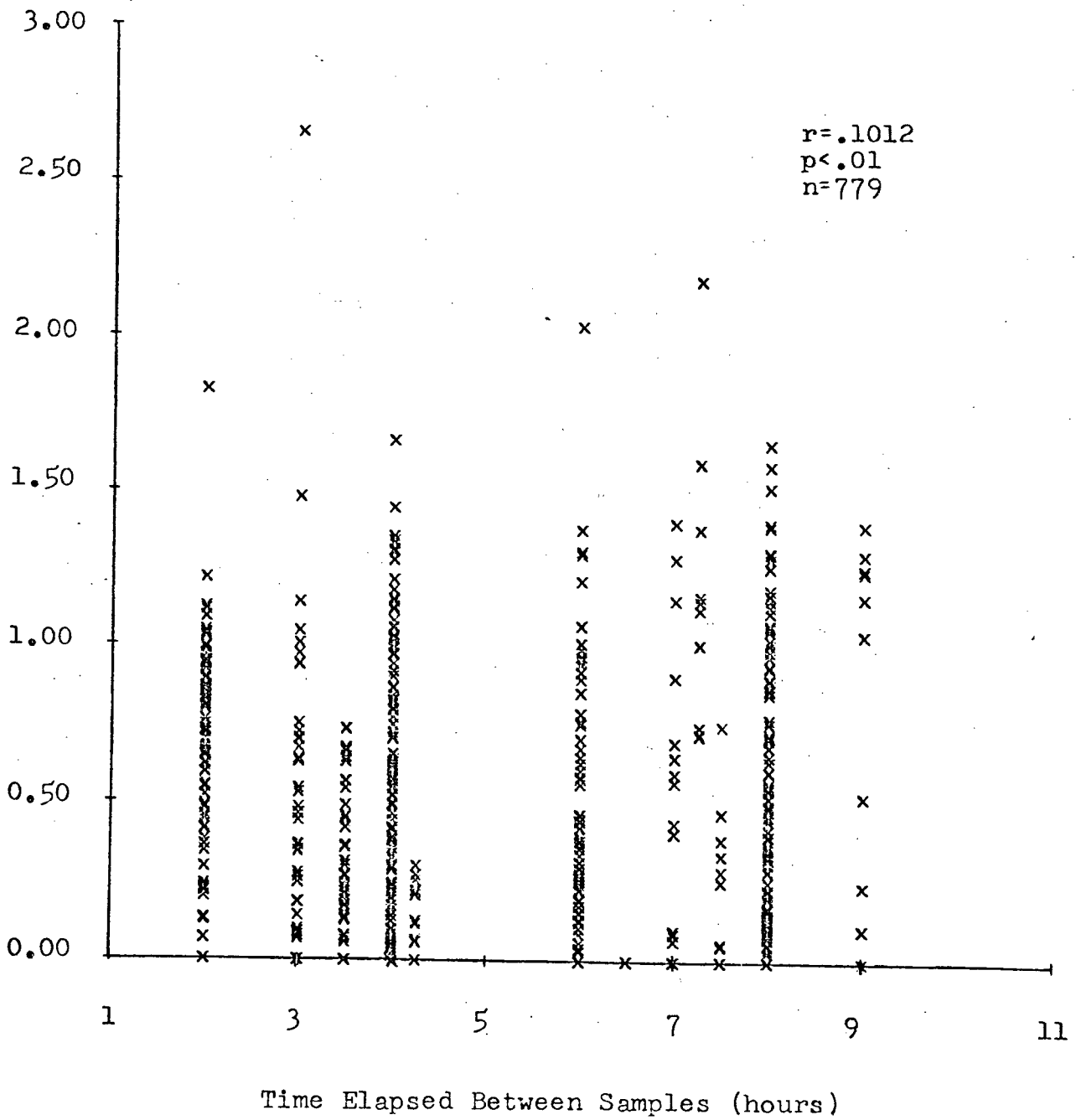
Fig. 9: Effect of the time elapsed between samples on
         productivity (ln calories/hour) in the four
         most productive salmonberry flowers sampled
         at each episode, independent of seasonal effects.

Residuals of regression of
ln(calories/hour+1.0) on date

Time Elapsed Between Samples (hours)
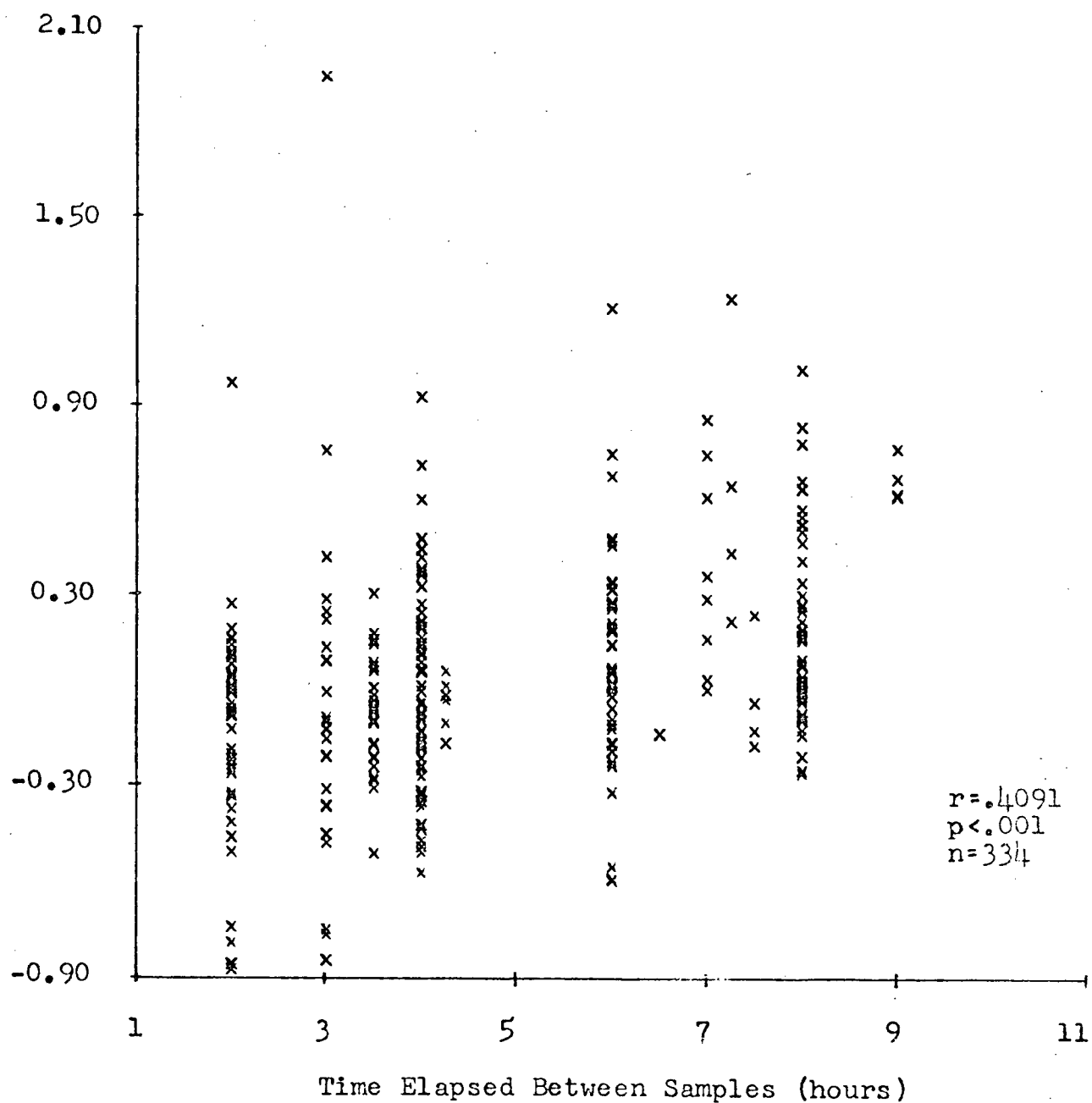
the regression of cal/hr on date plotted against TEBS for the more productive flowers. The significant positive correlation (r=.4091, p<.001) clearly shows that as TEBS increased, nectar productivity also increased. Of course, the fact that TEBS is included in the multiple regression model demonstrates that sampling frequency explains a significant amount of productivity variability independent of all other variables included in the model.

The seasonal model for all flowers sampled includes androecium diameter as being significantly related to nectar production. Independent of seasonal effects, smaller diameter flowers showed a slight tendency to secrete calories of nectar at higher rates than did larger diameter flowers (r=-.0750, p<.05). It is interesting to note that androecium diameter is not included in the regression model for the more productive flower data.

As relative humidity decreased throughout the season there was a significant decrease in productivity (r=.3599, p<.001), and the relationship is stronger if one considers data for only the productive flowers (r=.4024, p<.001, Fig. 10). Relative humidity is included in the regression models for productivity (Tables III and V), and, of course, significantly correlates with productivity independently of date (r=.2152, p<.001 for all flowers, and r=.2046, p<.001 for productive flowers). The relationship between sunshine and cal/hr throughout the season was significantly negative (r=-.2482, p<.001 for productive flowers). Yet, independent of seasonal effects, no relationship existed between calories produced and sunshine.

Fig. 10: Scatter plot of relative humidity and productivity
(ln calories/hr) in the four most productive
flowers sampled at each episode.
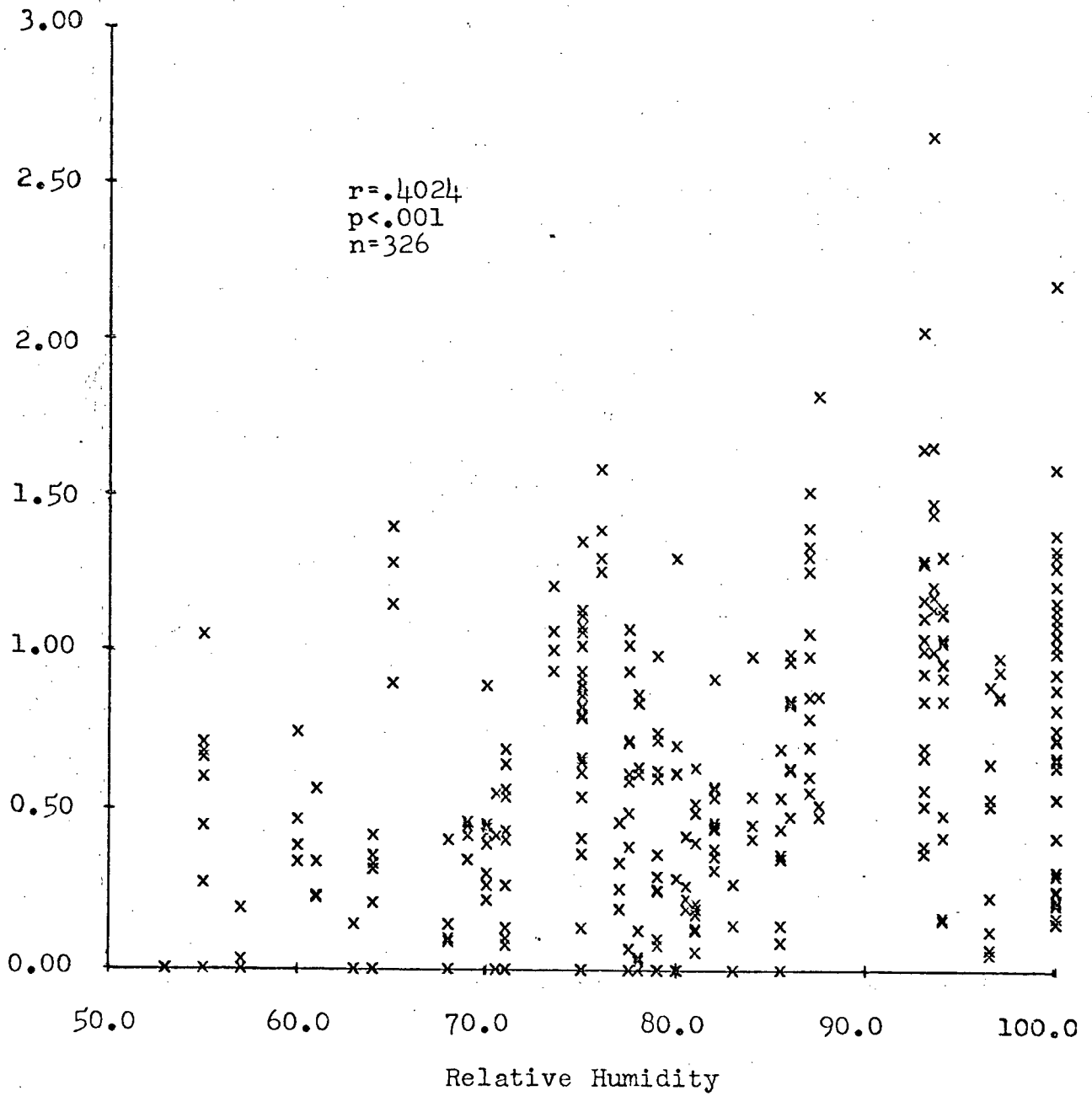
The time at which the samples were taken, expressed as hours after sunrise (HAS), is included in both regression models. The correlation between HAS and productivity (cal/hr) is significant (r=-.1155, p<.05), however, with date effects removed the correlation is no longer statistically significant.

Relationships between the variables, cal/hr, ul nectar/hr, and % sugars are of interest. The sampling date correlates inversely with ul nectar/hr, and positively with % sugars, (respectively, r=-.6189, p<.001, and r=.2197, p<.001 for productive flowers). Thus, as the season progressed, salmonberry flowers produced lower volumes of a more highly concentrated nectar. Seasonally, as TEBS increased the % sugar within the nectar increased (r=.2495, p<.001 for all flowers and r=.4348, p<.001 for productive flowers). The relationship is stronger when date effects are removed, (for all flowers, r=.3436, p<.001, Fig. 11). Throughout the season, ul nectar/hr is not significantly correlated with TEBS, yet when seasonal effects are removed there is a significant positive relationship (r=.2317, p<.001, Fig. 12, for productive flowers), indicating that increases both in volume and sugar concentration were responsible for the increasing of cal/hr with increased TEBS.

On the other hand, with an increase in flower androecium diameter there was an increase in % sugars but a decrease in ul nectar/hr (for all flowers, respectively, r=.3293, p<.001 and r=-.2469, p<.001), and the same patterns can be observed independent of date, (r=.1736, p<.001 and r=-.1083, p<.01). Here, as well as for cal/hr, data from the more productive

Fig. 11: Effect of the time elapsed between samples on
% sugar secreted by salmonberry flowers,
independent of seasonal effects.

Residuals of regression of
ln(% sugars + 1.0) on date

r=.3436
p<.001
n=557

Time Elapsed Between Samples (hours)
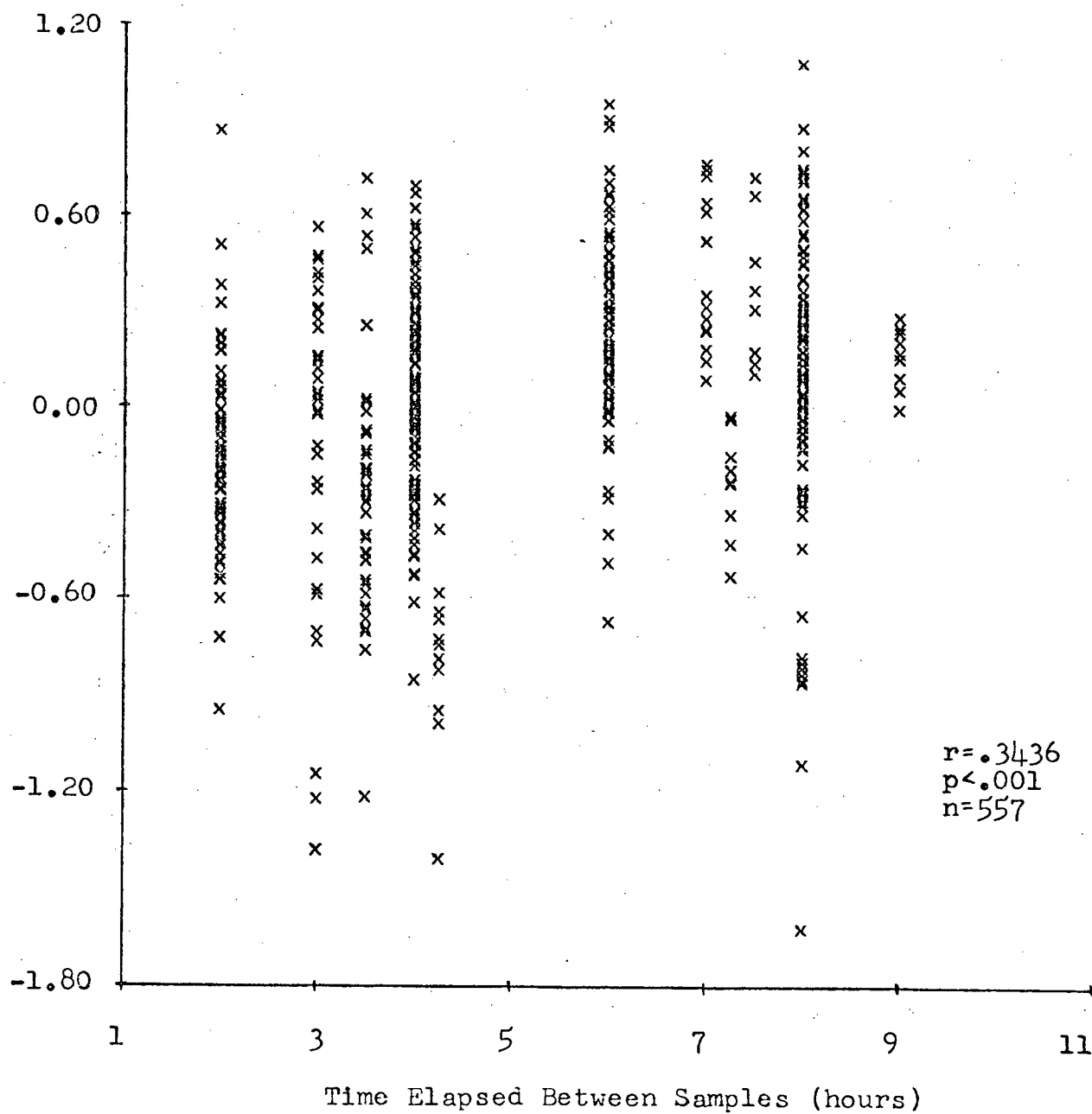
Fig. 12: Effect of the time elapsed between samples on
ln ul nectar/hour secreted by the four most
productive flowers sampled at each episode,
independent of seasonal effects.

Residuals of regression of
ln(ul nectar/hour + 1.0) on date

r=.2317
p<.001
n=333

Time Elapsed Between Samples (hours)
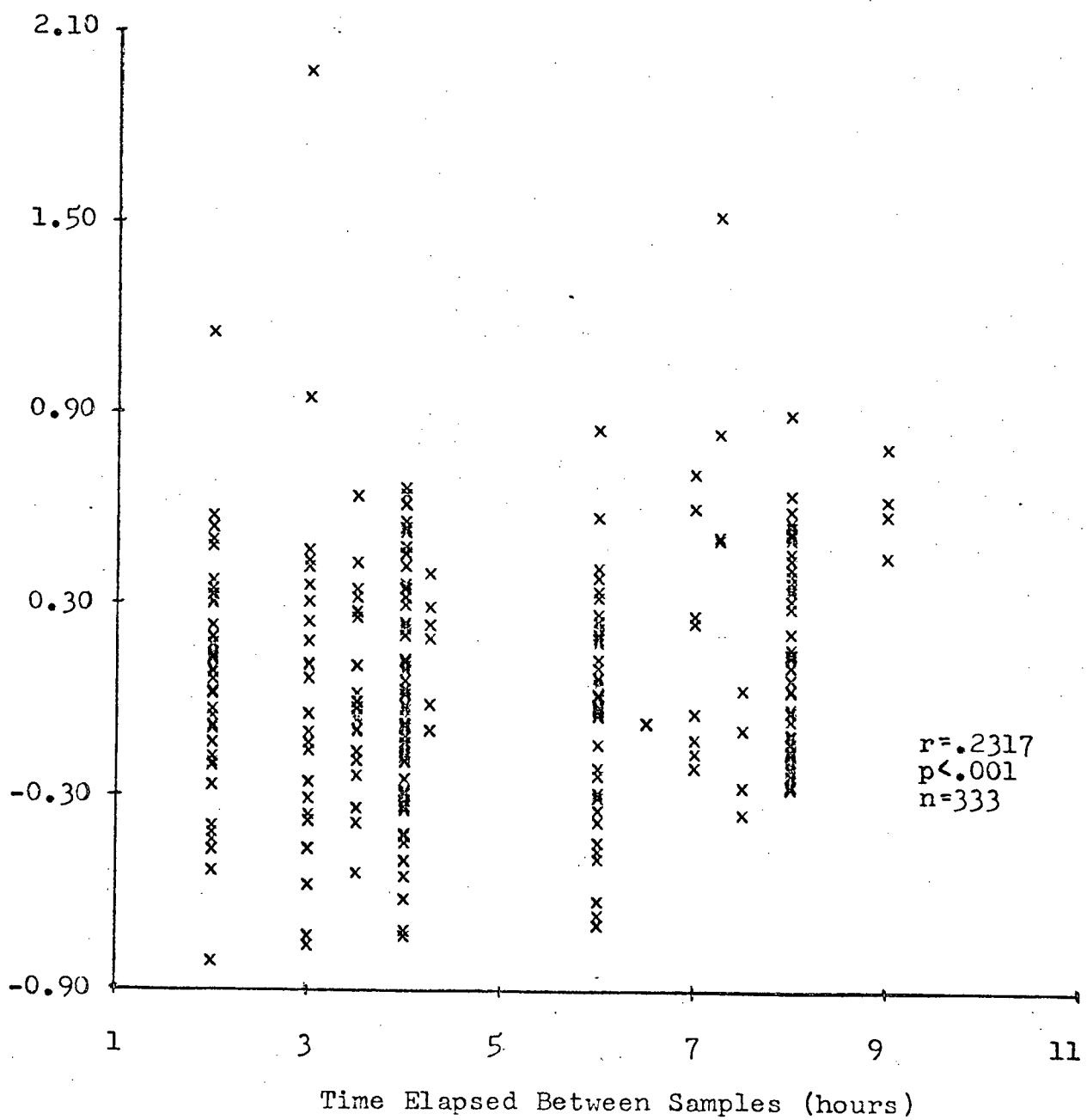
flowers show weaker correlations, particularly for ul nectar/hour.

Nectar volumes decreased as relative humidity decreased throughout the season, (r=.4865, p<.001 for more productive flowers), yet % sugar increased with sunshine levels (r=.5671, p<.001). Without the effects of date the same patterns are evident (for all flowers, respectively, r=.3637, p<.001 and r=.5491, p<.001, Figs. 13 and 14).

D.) Discussion

Though no previous information is available for salmonberry, Szklanowska (1972) found that raspberries (Rubus idaeus) produce 27 mg sugar/day, while blackberries (Rubus fruticosus) produce 15 mg sugar/day, or, respectively, 7.68 cal/hr and 4.27 cal/hr, assuming a "day" to consist of 13 hours. His measurements were made under optimum conditions for nectar secretion, which Szklanowska reports as being sunny, moderately humid days following cool nights. Whitney (1978) recorded a raspberry production value of 4 mg sugar/day, or 1.14 cal/hr, which may represent an average value over an entire season or simply a single measurement made under sub-optimal conditions. Measurements made in this study place the mean of salmonberry nectar secretion at 1.08 cal/hr for the more productive flowers. This reflects many days in the flowering season of salmonberry, not all representing optimum conditions. May 18 was the day of highest production, the average for the most productive flowers on that day being 3.24 cal/hr, with .95 confidence limits being

Fig. 13: Scatter plot of relative humidity and ln
ul nectar/hour secreted by salmonberry,
independent of seasonal effects.

Residuals of regression of
ln(ul nectar/hr + 1.0) on date

r=.3637
p<.001
n=766

Relative Humidity
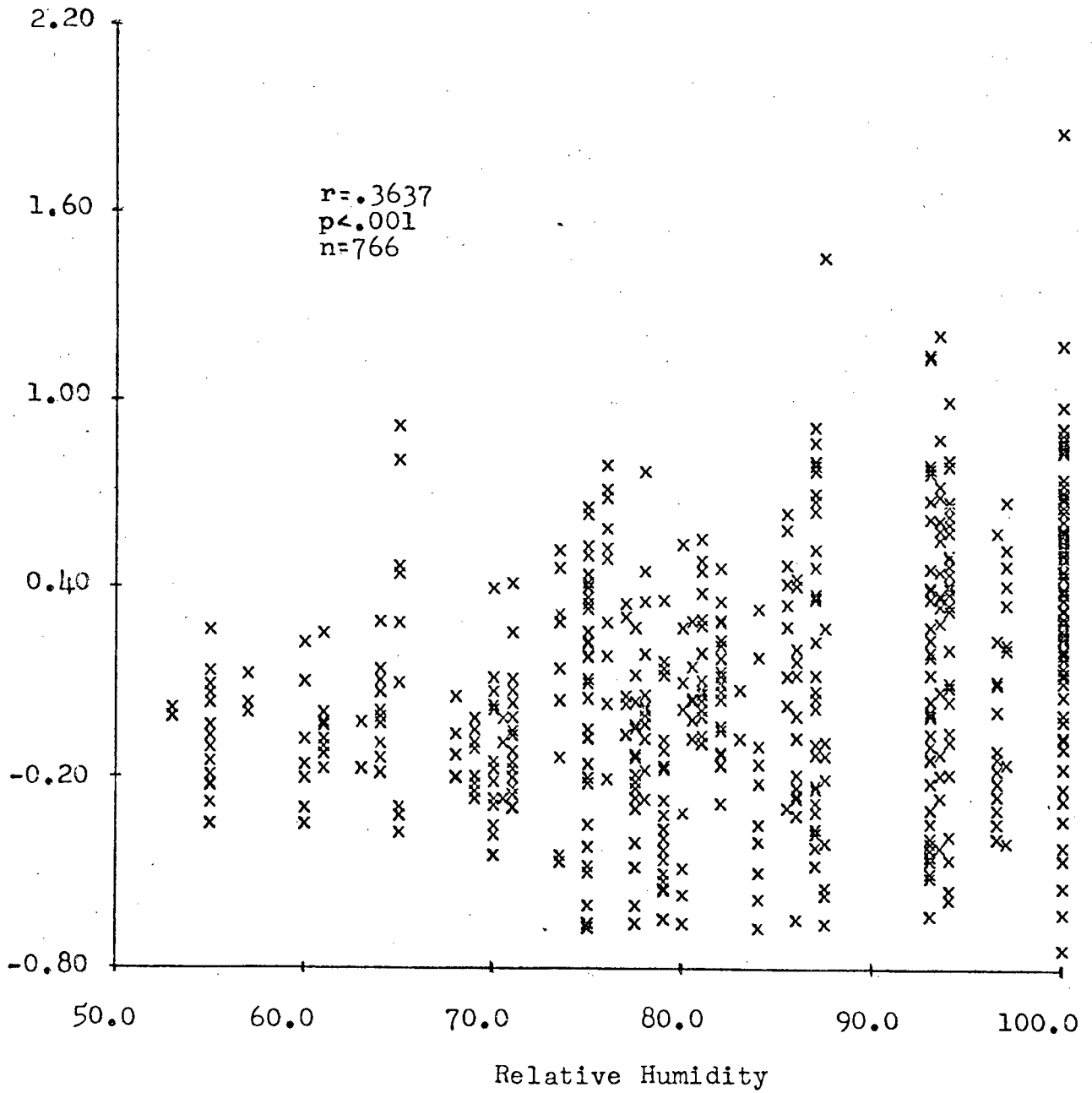
Fig. 14:   Effect of sunshine levels on ln % sugar
           secreted by salmonberry flowers, independent
           of seasonal effects.

Residuals of regression of
ln(% sugars + 1.0) on date


r=.5491
p<.001
n=523

Sunshine Levels/hr of Production
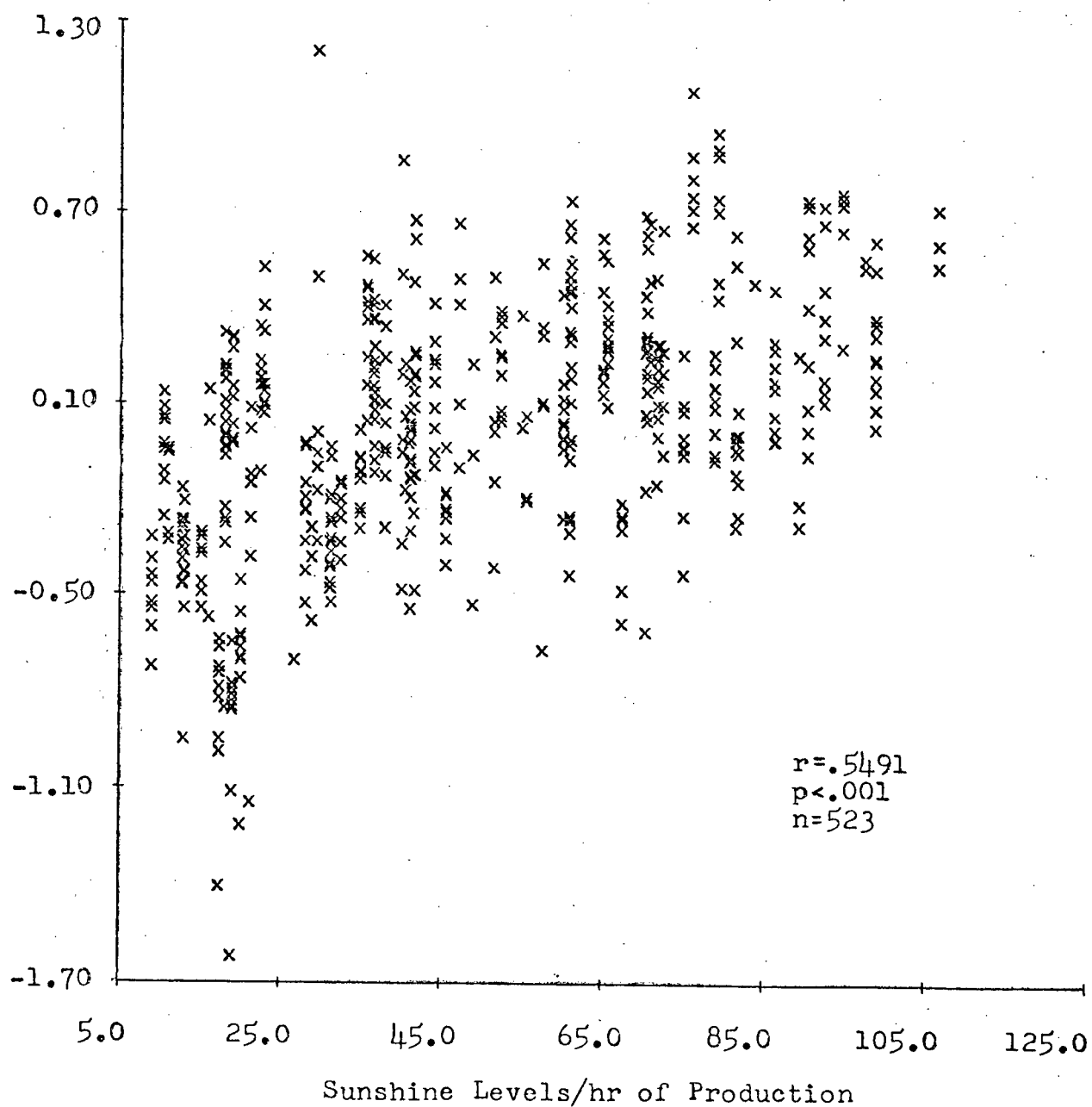
set at 0-6.71 cal/hr. Apparently, salmonberry produces at approximately the same levels as do other species of Rubus.

The extreme variation in salmonberry nectar productivity on seasonal and daily time scales is striking, and may have drastic consequences on insect foragers. Production strongly decreases as the season progresses, shifting from daily averages of 2.07 cal/hr, 2.45 cal/hr and 3.24 cal/hr (May 16,17,18), down to daily averages later in the season of .31 cal/hr, .32 cal/hr and .08 cal/hr (June 21,22,27). This decrease in cal/hr closely reflects a corresponding decrease in nectar volumes secreted throughout the salmonberry flowering season. The concentration of sugars in the nectar increases at the same time, yet the increase is not enough to offset the decline in calories offered resulting from declines in volumes secreted.

Production within single days, (that is, independent of date), is also highly variable, with a trend for increased caloric production early in the day, when relative humidity levels are highest, that drops off steadily as sunshine levels increase. This again reflects trends in volumes of nectar secreted; as the day passes the plants produce smaller amounts of nectar while the concentration of the nectar increases. This could mean that the nectar is actually secreted at higher concentrations, or that it is secreted at concentrations similar to those early in the day and rapidly evaporated to higher levels. This pattern has been observed by several authors working on various plant species (Butler, 1945; Percival, 1965; Feinsinger, 1978; Corbet, 1978), and helps to account for several of the correlations noted previously, for example, that

production (cal/hr) correlates positively with relative humidity. Seasonally, the cool, rainy days typical of spring in the forest give way gradually to the warm, sunny days of summer. Thus, relative humidity and sunshine levels are highly correlated with productivity seasonally.

Corbet (1978) discusses possible adaptive values of such a pattern of daily nectar secretion:

Let us instead regard flowers as sophisticated gadgets for dispensing nectar at the right concentration at the right time. If there is a degree of concentration specificity among pollinators, there will be a selective advantage for flowers whose morphology and secretory periodicities interact with the local climate in such a way as to increase the likelihood that the nectar will be at an appropriate concentration at a time of day when a suitable pollinator is active (Corbet, 1978, p.27).

Yet why must the flowers secrete large amounts of dilute nectar early in the morning to allow evaporation to bring it to "appropriate" concentrations rather than simply secrete nectar at the proper concentration at the time the pollinators are active? It seems likely that air and possibly soil moisture levels are responsible for timing of nectar secretion, secretion being highest when plants have high levels of surplus moisture available. Huber (1956) has found that for several plant species, the nectar has the same composition as the phloem sap, and that for plants which have nectaries supplied by a large amount of xylem, production is reduced by deficient soil

moisture and is increased with an increase of moisture. He has found, further, that the amount of sugar secreted is sensitive to changes in transpiration rate. To view secretion apart from possible environmental constraints upon the plants seems unrealistic.

According to Shuel (1955), increased insolation results in increased nectar secretion (mg sugar/unit time) in white clover. Percival (1965, p.97) writes that,

> species differ in their response to insolation. In Cuba the finest nectar plant, the white 'Campanula' (*Ipomoea sidaefolia*) secretes best during hot days with bright sunshine, but in another Cuban plant, the Coral Vine (*Antigonon leptopus*), strong insolation diminishes the flow as the day wears on, and flow is continuous on cloudy days.

Fahn (1949) discovered that in one location in Palestine, *Tecomaria capensis* shows a clear rise in dry weight of nectar available with a drop in temperature. In this study I found that salmonberry produces more total mg sugar in generally cooler conditions; as insolation increases only percentage sugar increases while volume secreted greatly diminishes.

Shuel (1955) speculated that the increase he observed in productivity with increased insolation is due to an increase in photosynthesis. Barber (1976) found that salmonberry does display an increase in photosynthesis with increased insolation, yet he did not investigate patterns of nectar productivity in his study. It may be that the increase in nectar concentration observed in this study is due not only to high rates of

evaporation but also to an actual increase in concentration of the liquid secreted due to higher rates of photosynthesis, along with increasingly unfavorable moisture conditions for nectar secretion.

The plants may secrete more calories during the spring and early morning hours due to a favorable moisture balance, yet these times are also cool and therefore active pollinators are operating at heavy caloric cost. Increased caloric output by the plants may be necessary to allow the insects active during these times to forage with even a small net energy gain (Heinrich, 1975a; Reader, 1977).

The negative correlation between androecium diameter and nectar productivity (cal/hr) is quite weak yet significant. Since androecium diameter correlates so strongly with flower age, tentative conclusions can be made concerning floral age and floral productivity. G.W. Wood has explored this question and writes:

> In some plants, the old flowers secrete more nectar than the young ones, in others, the reverse relationship exists; some plants may have a high nectar yield in the old flowers but have a similar quantity of sugar to the young flowers. In blueberry, both nectar volume and nectar sugar content per clone increase through much of the bloom period. Therefore, if we assume a direct relationship between yield of nectar or nectar sugar and bee visitation, present evidence would show that the blueberry is more attractive to nectar gathering insects towards the

latter part of the bloom period (Wood, 1961, p.1039).
For salmonberry, the younger flowers seem to be the most productive, in terms of cal/hr, since they put out the greatest amounts of highly concentrated nectar. Older flowers put out less nectar but at an apparently higher concentration, thus weakening the relationship between cal/hr and age. This does not necessarily mean that older flowers actually secrete higher concentrations of nectar, but simply that they secrete small amounts which may undergo more rapid evaporation due to the increased surface area/volume of the smaller drops. The increased androecium diameter of older flowers as opposed to younger flowers doubtless aids in the more rapid evaporation of the small amounts present. Percival (1965) discusses the increase of % sugar secreted as blossoms of orange trees age, claiming that "its attraction for insects does not diminish" (p.92).

It seemed possible that the strong, negative correlation between productivity and date was due to the fact that as the season progresses the average age of flowers available increases $(r=.3257, p<.001)$. Yet, the regression models discussed previously include both flower diameter and date as significant variables, and the residuals of the regression of cal/hr on diameter are signigicantly correlated with date (Fig. 15, $r=-.3861, p<.001)$. These facts lead to the conclusion that flowers of all ages produce at lower rates with the passing of summer, perhaps due to decreased soil moisture, or perhaps due to the shunting of energy to fruit production as increasing numbers of flowers on each plant are fertilized. Some authors might even

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Fig. 15: Scatter plot of productivity (ln calories/hr)
and date, independent of androecium diameter
effects.

Residuals of regression of ln(calories/hr+ 1.0) on diameter

r=-.3861
p<.001
n=779

Date
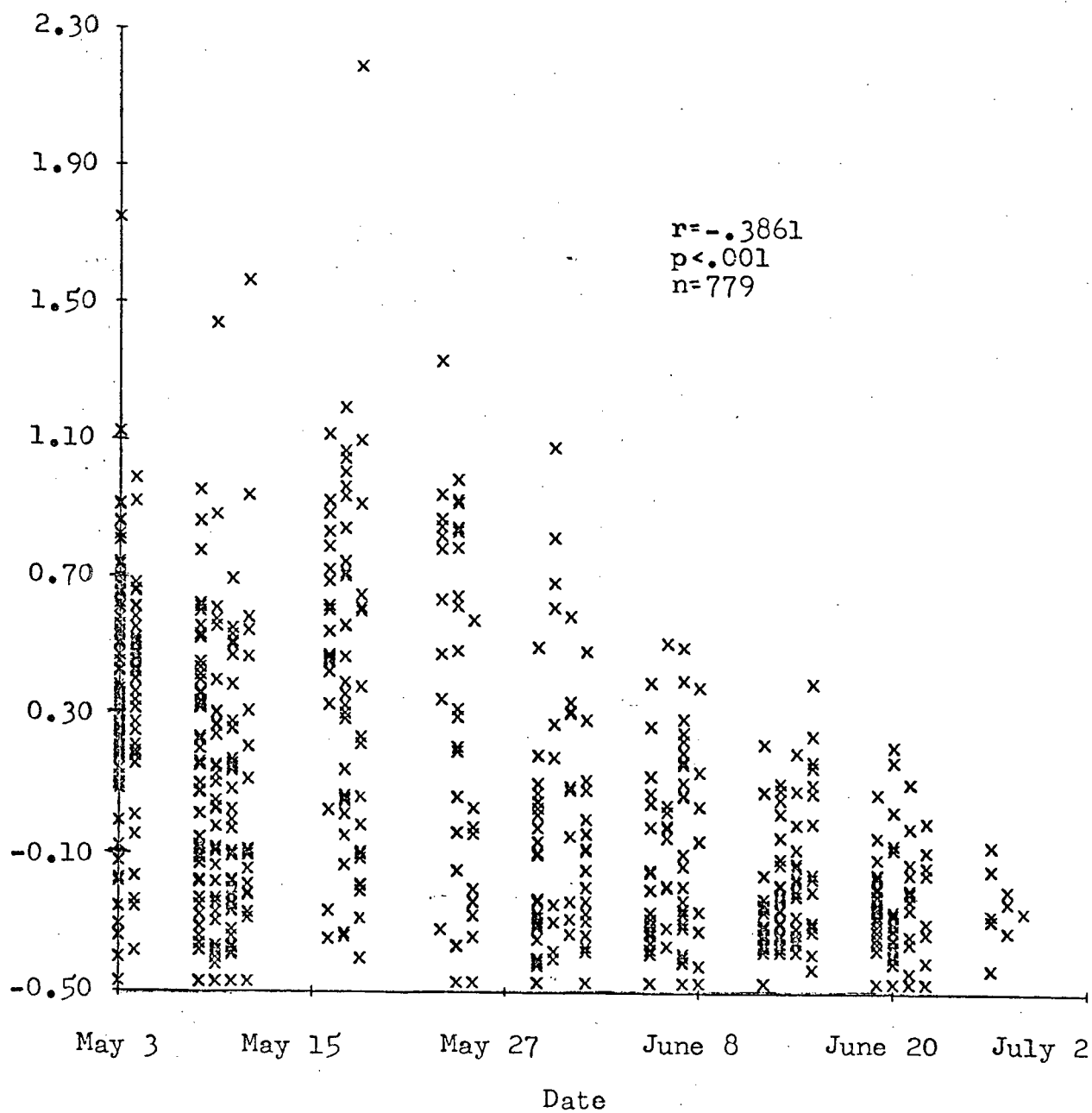
maintain that plants are gradually cutting back production to guarantee consistent, efficient, pollinator activity in higher air temperatures.

The fact that the most productive flowers show no correlation between flower diameter and productivity may be due to several factors. It may be that a very large sample size is necessary for the rather weak relationship to become apparent, or it may mean that the productivity of these flowers is uniformly high, regardless of diameter.

Feinsinger (1978) has discovered the existence of "bonanza" flowers on individuals of several tropical plant species. The present study has shown that rather highly productive flowers may exist in salmonberry as well; at least, at each sampling some flowers are producing at levels well above lower producing flowers. Many authors have noted the high heterogeneity which characterizes nectar production in plants (Heinrich, 1975a; Feinsinger, 1978), arguing that it encourages efficient pollination. Once unproductive salmonberry flowers are removed from consideration, relationships between productivity and date, sampling frequency, as well as climatic variables are stronger, indicating that many flowers are unproductive due to variables not measured in this study (e.g., flower height, distance from flower to main stem, microclimatic effects at individual flower sites, and possibly properties inherent within each flower in addition to flower age).

The present study shows that sampling frequency has a significant impact upon productivity, yet surprisingly, the effect is just the opposite of previous findings. Here, as

sampling frequency decreases nectar volume and nectar sugar concentration increase, thus increasing cal/hr offered. The increase in % sugar is not surprising, since flowers sampled infrequently have nectar exposed longer to evaporation. Yet even with evaporation effects the volume/hour increases. This result is especially intriguing when one is reminded that Raw (1953) obtained the opposite result with two species of Rubus (R. idaeus and R. fruticosus). One explanation of the adaptive value of the flower response found here is in terms of plant competition for pollinators. Given the fact that bumblebees have the ability to select between flowers (discussed in Chapter III), it is reasonable to assume that they discriminate on the basis of nectar standing crop. Plants having flowers being utilized by very few pollinators might be expected to increase their nectar production rates in an effort by each plant to attract the few pollinators in the area, whereas plants with flowers which are being used at a very high rate would individually benefit by keeping production rates low. Many pollinators in the area, competing amongst themselves for floral nectar, virtually guarantee that every flower will be visited. This argument could also explain why the model built for nectar productivity included the variable, number of flowers/meter, as having explanatory value independent of date. Increased numbers of flowers in the research area would presumably result in increased plant competition for the available pollinators.

Pollination biologists frequently call upon competition to help explain certain observed traits in both plants and their pollinators. The bright colors of showy alpine flowers have been

explained by invoking plant competition for the few pollinators which are active in alpine conditions (Pojar, 1974), and such plant competition has been used to explain observations of asynchronous blooming periods of flowering plants in the same geographical area (Mosquin, 1971; Heithaus, 1974; Heinrich, 1976b). On the other hand, competition among pollinators for foraging sites has been used to explain variation in tongue lengths of bumblebees (Heinrich, 1976a; Inouye, 1977), differing sizes of bumblebees (Morse, 1978), and temporal differences in activity between pollinator species (Linsley et al., 1973). The results presented here indicate that plant competition for pollinators may be occurring only during certain periods in the day and during certain days or weeks of a blooming season. During other periods it may be the case that the pollinators are forced into a competitive situation for floral resources. This apparent shift in competition has also been discussed by Mosquin (1971).

An alternative explanation for the observation that cal/hr decreases with sampling frequency involves the finding that, as fertilization occurs, nectar productivity decreases dramatically (Shuel, 1978). The present study involved the removal of nectar from flowers up to four times a day. Though the glass micropipettes used could not have transferred much pollen, the many entries into the flowers could in some way have simulated normal pollination, perhaps even the removal of nectar signalling the flower that pollination had indeed occurred. Thus, competition between flowers may not need to be invoked as an explanation for the difference in production between flowers

sampled infrequently and those sampled often. It is worth noting that under the competition explanation, flowers which are not being used raise production levels, while under the second it is flowers which are being frequently utilized which then decrease productivity.

I do not believe that the pipetting techniques used here damaged the flowers. Early in the season several flowers were sampled 3 or 4 times throughout a 2 or 3 day period. Although the volumes secreted decreased as the day progressed, the next morning there were present levels of nectar lower than levels measured the previous morning, yet not low enough to indicate that damage had occurred to the nectaries. Rather, I believe the lower levels were due to advancing flower age, a full day being a significant time unit in the life of a flower which lasts only 5-7 days.

To further investigate the possibility of fertilization and/or floral damage confounding the results, several of the analyses previously discussed were performed on data gathered from flowers sampled only once. This means that flowers included in the analyses were all entered twice, once for initial nectar removal and again for final nectar sampling. With the effects of date removed, the time elapsed between samples is significantly correlated with productivity ($r=.1410$, $p<.002$, $n=510$). With the effects of sunshine, relative humidity and date removed there is still a significant, positive correlation ($r=.1176$, $p<.02$, $n=450$). Thus, the decrease in productivity with increased sampling frequency was not due to flower damage or to increased fertilization.

It should be emphasized that the present study was
conducted in the field, where productivity is under the
influence of many factors which vary independently (Percival,
1965). Many of these were not measured in this study, such as
flower height, plant height, number of flowers per plant, etc.
The variables which were measured may not have accurately
reflected conditions realized by each flower on each salmonberry
plant. Sunshine levels were measured with an actinograph placed
on a logging road, yet many plants and flowers experienced very
different sunshine conditions if shaded sometime during the day.
Relative humidity was similarly measured in the middle of a
road, yet the relative humidity value of importance to the
plants should be that of the air surrounding the plant, and the
relative humidity value of importance to values of nectar volume
and concentration should be that of the air inside each flower.
Even though these sources of error surely increased the
variation in nectar productivity measured during this study, it
is encouraging that the regression models presented earlier can
account for 54% of production variability. To substantiate the
claim made here, that high sampling frequency has a negative
impact upon productivity, salmonberry plants should be raised
under otherwise constant laboratory conditions while the
relationship is again explored. The strongest conclusion one can
make here is that a negative relationship is definitely
indicated.

III. FORAGING BEHAVIOR

a.) Introduction

A growing number of studies clearly demonstrate that as food resources become scarce, animals cease to forage in a specialized manner and increasingly accept a broader range of food items available. Werner and Hall (1974) found that bluegill sunfish will feed upon only larger sizes of Daphnia as long as food abundance remains high. With limited abundance the fish utilize a wider range of prey sizes. Similarly, Krebs et al.(1977) found that great tits were non-selective at low prey encounter rates while at higher rates the birds selected only larger sized prey. Smith et al.(1978) obtained the apparently opposite result, that as food became scarce on the Galapagos Islands, each species of Darwin's finch selected a narrower range of food items. However, as the authors admit, the fact that food resources changed qualitatively during their study makes difficult a comparison with the studies previously mentioned.

The purpose of this study was to assess changes in bumblebee foraging behavior accompanying shifts in the floral nectar rewards offered, various environmental factors, and date. Bee foraging behavior examined in this study included the number of foragers encountered at various flower patches per unit time, the percentage of flowers actually used after being approached by the bees, and the average androecium diameter of flowers used by the bees.

In cool, rainy conditions bumblebees, being exothermic,

would not be expected to fly frequently, since flight in cooler conditions is energetically very costly (Heinrich, 1975a). However, if a colony were short of stored nectar, bumblebees should fly more frequently in inclement conditions than if an abundance were present (Alford, 1975); indeed, bumblebees have been observed foraging in even near-freezing temperatures (Heinrich and Raven, 1972). Several authors believe that, in the presence of an abundance of stored nectar, bumblebee workers do not fly under even the best weather conditions (Heinrich, 1979a; Alford, 1975). I suspected that strong correlations would be found between numbers of bees foraging and sunshine levels, temperature and relative humidity. Yet, it was also hypothesized that, assuming that bumblebees seek to maximize their net energy gain (Pyke, 1978), a strong, positive correlation should exist between number of bees foraging and nectar standing crop.

Bumblebees do not utilize all flowers upon which they land, and they do not land upon all flowers they approach. Upon approach, they may "decide" to forage from a flower or to avoid it altogether. Faegri and van der Pijl (1978) write that bees have a very keen sense of odor. Kauffeld and Sorensen (1971) thought that honeybees initially select flowers by color, but that at closer distances honeybees are guided by aroma. In a series of experiments, von Frisch (1971) trained honeybees to feed on sugar solution placed inside a small cardboard box. The box also contained a fragrant flower or a few drops of scented oil. The bees were then offered an array of clean boxes, none of which contained sugar solution, but one contained the scent used for training. The bees would alight and enter only the scented

box. When offered an array of boxes, one of which was scented
and another brightly colored, the bees flew towards the colored
box. Yet they hesitated about an inch from the box entrance and
began to fly about the entrances of the other boxes. They
entered only the scented box. It seems reasonable to assume
that, through an ability to differentiate aroma intensities,
bumblebees should choose flowers which yield the greatest
amounts of nectar standing crop. Yet the bees can afford to be
so choosy only when there is a surplus of nectar available in
relation to colony demands. Once nectar becomes a scarce
resource bees should utilize virtually all flowers they
approach, since even slight amounts of nectar present would be
worth harvesting. In general, as resources become limiting bees
should gradually choose to forage from a greater fraction of the
flowers they investigate. This situation is roughly analogous to
that in which predators choose smaller prey items as the total
number of prey declines.

Assuming that a certain range of flower ages is most
productive (Wood, 1961), I further hypothesized that while
nectar was plentiful the bees would be observed to prefer
flowers of a certain age, and therefore, of a certain androecium
diameter (Chapter II). As nectar reward conditions decline
through the salmonberry season bees would utilize a wider range
of flowers.

B.) Methods

The study was conducted between May 3 and June 28, 1979.

Bumblebees were observed at various times of day throughout the season foraging on patches of salmonberry flowers, each observation session lasting 10 minutes, as in Free (1955) and Kauffeld and Sorensen (1971). Other authors have used 15 minute sessions (Parrish and Bazzaz, 1978), yet I felt that 15 minute sessions would result in high variability due to weather changes during the session.

The patches observed were located along the margins of old logging roads (K30 and H20, UBC Research Forest). Since it was rare to find clearly distinct patches of flowers, patches often had to be chosen by simply marking off an easily observable area of a large number of flowers. Typically, a fresh observation patch was chosen once a week. Each morning, before observations were made, each flower in a patch received a numbered tag, its androecium diameter was measured and a record of its general condition was made. Since bumblebees are very perceptive of new objects in their environment, simple tags were constructed out of masking tape in an effort to avoid colored ribbons which may have been overly attractive to bees. A few observations made on untagged patches confirmed the belief that the tags themselves were not attracting bees into tagged patches.

During 10 minute sessions the number of bees entering a patch was noted, and for each bee it was recorded which flowers were investigated and which flowers were actually utilized. A bee "foraged" if it actually landed upon a flower. Any deviation in flight towards a flower which was not then landed upon was defined as "investigated". The ratio used in the following analyses was calculated by dividing the total number of flowers

used by all the bees entering the patch during a session by the total number of flowers investigated. The observation of a simple change in diameters used by the bees would not be convincing, since this could be due to a change in androecium diameters of flowers present. For this reason, the ratio, average androecium diameter used/average androecium diameter present, was investigated. As was done in productivity studies, sunshine levels during the days of this study were continuously monitored, and relative humidity was measured 2-4 times a day. Temperature was also recorded once an hour while observations were being conducted.

Levels of nectar standing crop available were measured at various times of day throughout the season. 10 flowers were included in each standing crop sample, each flower being drained of nectar present using first a 25 ul micropipette followed by a 10 ul micropipette. Each volume was analyzed for % sugar with a hand refractometer. Calories of nectar present could then be calculated using values of volume and % sugar, as described in the previous chapter.

C.) Results

There was a significant positive relationship between productivity and nectar standing crop over the season (r=.4481, p<.001). As the season progressed, the standing crop fell dramatically (Fig. 16, r=-.4477, p<.001), and seasonally, standing crop decreased as relative humidity decreased and decreased with increased sunshine levels (r=.2024, p<.001 and

Fig. 16:   Scatter plot of nectar standing crop (calories/flower)
in salmonberry flowers and date.

Calories/Flower

r=-.4477
p<.001
n=902
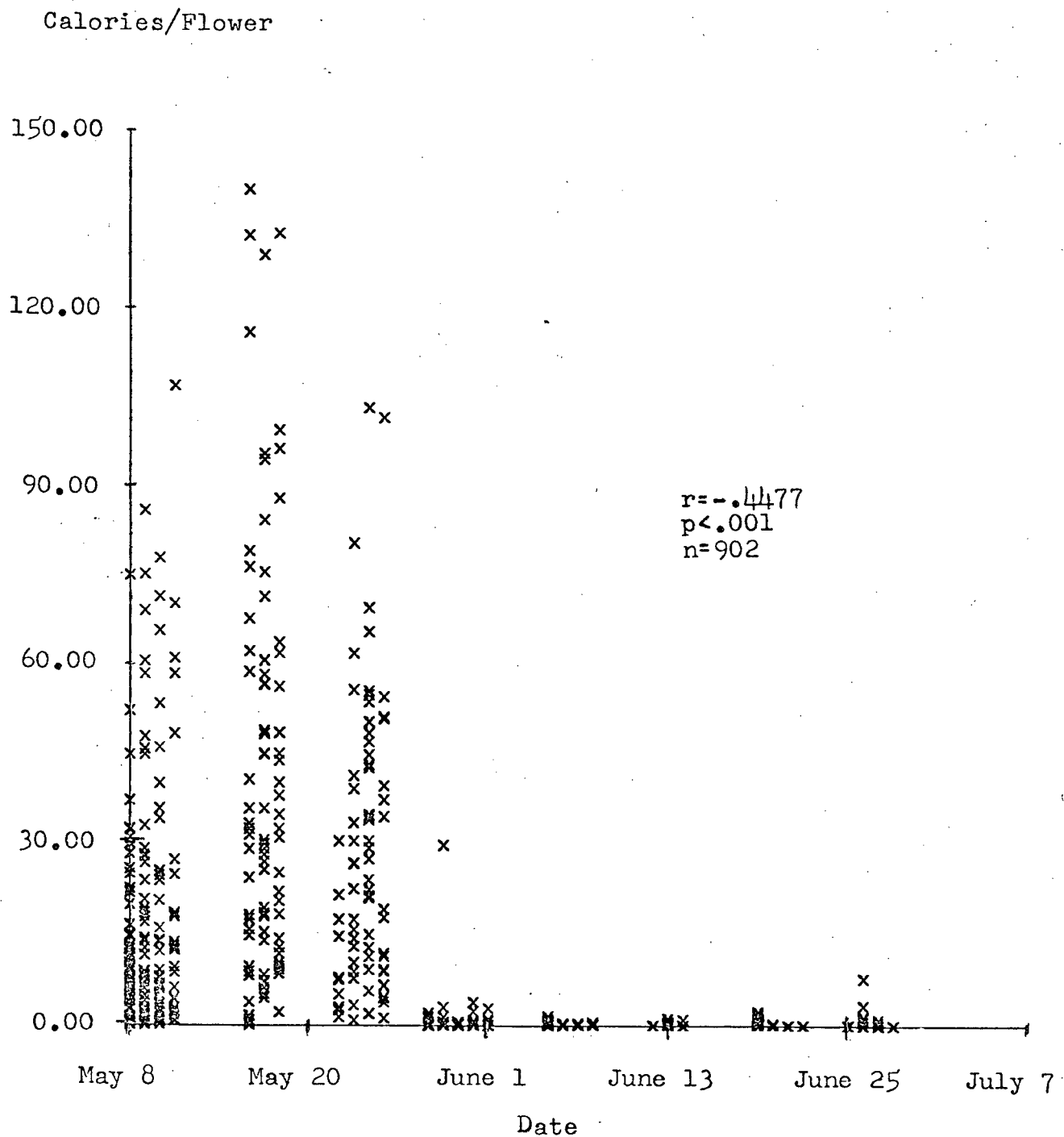
r=-.1525, p<.001). Fig. 17 presents the residuals of the regression of standing crop on date plotted against productivity. Independent of date, as flower nectar productivity increased there was a corresponding increase in nectar standing crop (r=.2955, p<.001).

A stepwise regression model of numbers of bee foragers per 10 minutes per flower ("bee density") throughout the season includes the following variables as being significant: date, sunshine levels and the standing crop of nectar in nearby flowers (Table VI), the standing crop values representing the averages of each group of 10 flowers sampled. These variables together accounted for approximately 54% of the variation in bee density. Date alone accounts for by far the majority of variation (45%), and a scattergram of bee density vs. date is provided in Fig. 18 (r=.6585, p<.001).

"Throughout the season" is defined here as including the dates May 3 to June 8. Correlations made which include dates after June 8 are not so strong as when these dates are excluded, this being due, I'm convinced, to the blooming at this time of other plant species with flowers which are attractive to the bees. A close examination of the graph of bee density and dates through June 28 (Fig. 19) show a point, June 8, after which the bees decreased in number. This was the date when patches of blueberry (Vaccinium spp.) and thimbleberry (Rubus parviflorus) were beginning to bloom in the research area, species highly attractive to bumblebees.

From Fig. 20 one could conclude that as sunshine levels increased through the season, bee density increased as well

Fig. 17: Scatter plot of nectar standing crop (calories/flower) and productivity (calories/hour) in nearby salmonberry flowers, independent of seasonal effects.

Residuals of regression of
calories/flower on date

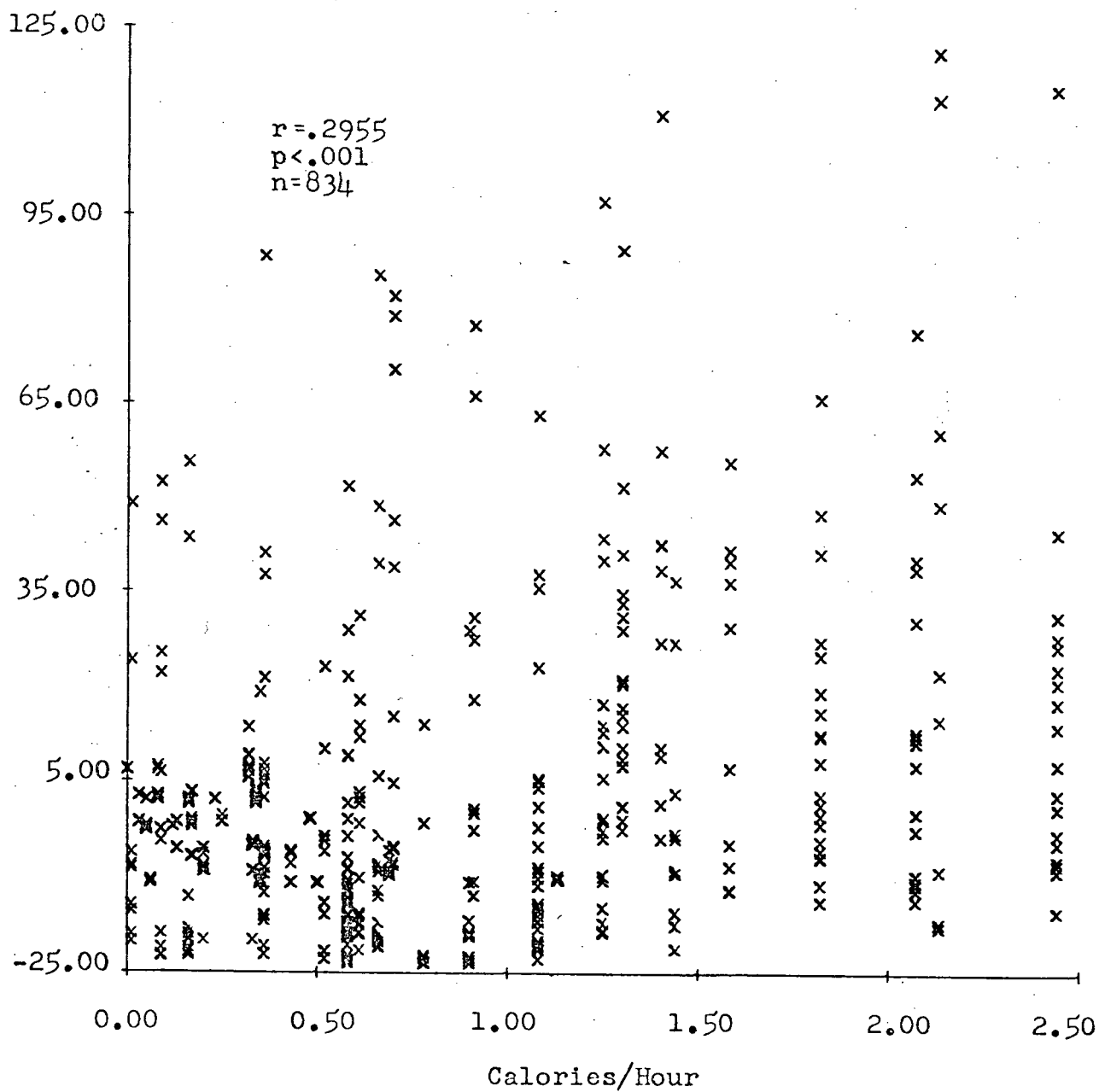r=.2955
p<.001
n=834

Calories/Hour

Table VI: Stepwise regression model built for the variable,
            ln number of bees/10 min x flower ("bee density").

            a) Variables selected for the model.
            b) Variables not selected.
            c) Steps in model construction.

ANALYSIS AT STEP 4 FOR 53.V53   N= 404 OUT OF 561

SOURCE	DF	SUM OF SQRS	MEAN SQUARE	F-STAT	SIGNIF
REGRESSION	4	1.5102	.37754	118.84	.0000
ERROR	399	1.2675	.31768 -2		
TOTAL	403	2.7777			

MULTIPLE R= .73734   R-SQR= .54367   SE= .56363 -1

	VARIABLE	PARTIAL	COEFFICIENT	STD ERROR	T-STAT	SIGNIF	
	CONSTANT		.99094	.22835	4.3396	.0000	
a)	1.V1	.26270	.16269 -1	.29914 -2	5.4384	.0000	date
	4.V4	.18903	.11496 -2	.29898 -3	3.8452	.0001	sunshine
	24.V24	-.21944	-.42333	.94223 -1	-4.4929	.0000	ln date
	31.V31	-.17084	-.11077 -1	.31981 -2	-3.4635	.0006	ln standing crop

	REMAINING	PARTIAL	SIGNIF	
	3.V3	-.02705	.5896	hours after sunrise
	5.V5	.08557	.0874	temperature
b)	6.V6	.00754	.8805	rel. humidity
	8.V8	.09267	.0641	standing crop
	26.V26	-.02606	.6033	ln hours after sunrise
	27.V27	.02483	.6206	ln sunshine
	28.V28	.08034	.1086	ln temperature
	29.V29	.00718	.8862	ln rel. humidity

REGRESSION OF 53.V53 USING FORWARD SELECTION

	STEP	R-SQR	STD ERROR	# VAR	VARIABLE		PARTIAL	SIGNIF
	1	.45441	.61399 -1	1	1.V1	IN	.67410	.0000
c)	2	.51367	.58041 -1	2	24.V24	IN	-.32956	.0000
	3	.52995	.57132 -1	3	4.V4	IN	.18299	.0002
	4	.54367	.56363 -1	4	31.V31	IN	-.17084	.0006

Fig. 18:   Scatter plot of number of bees/10 min x flw
           (bee density) and date.

ln(1.0 + #bees/10 min x flower)

r=.6585
p<.001
n=561
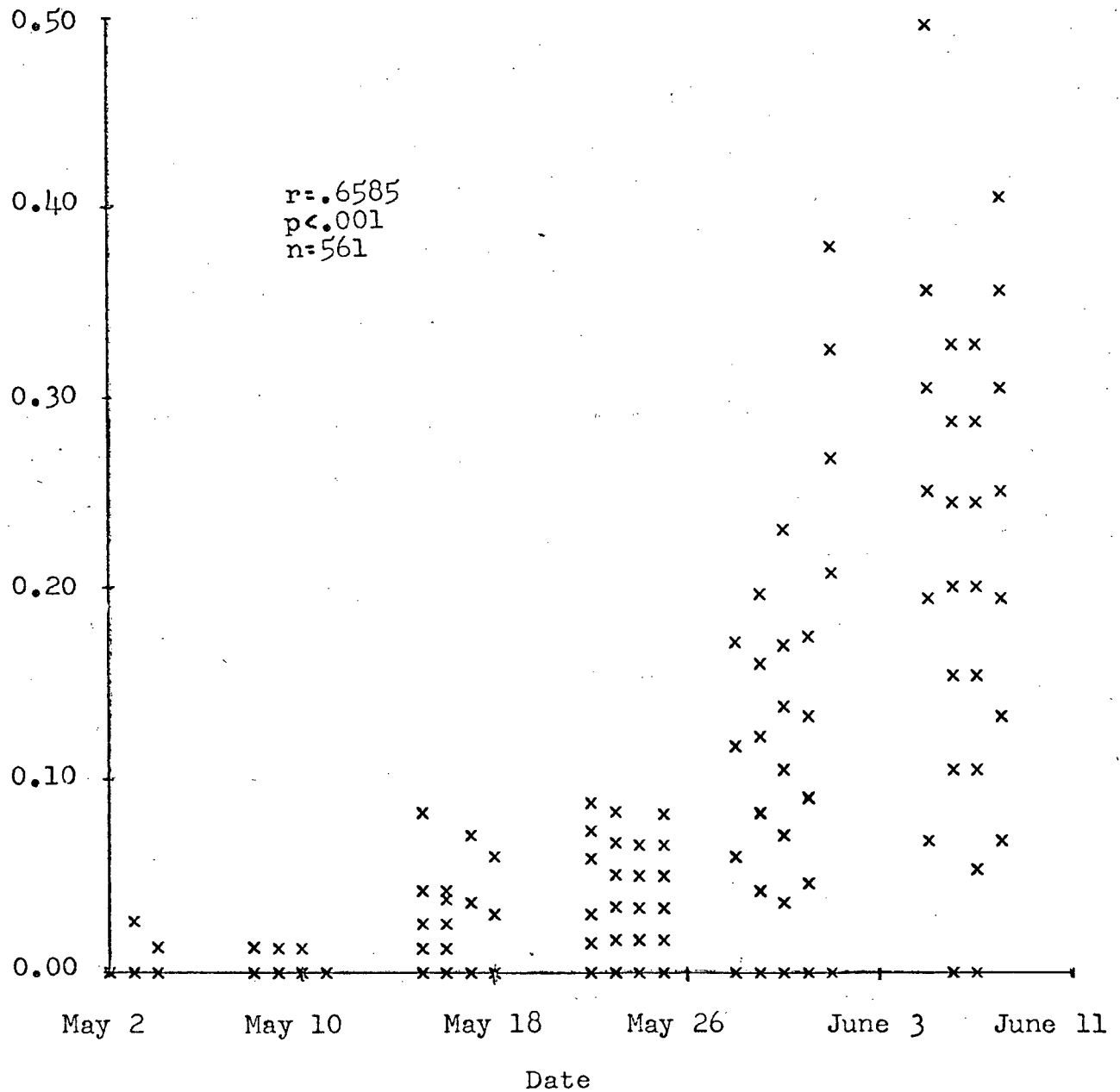
Date

Fig. 19: Scatter plot of number of bees/10 min x flw
          (bee density) and date, including data gathered
          throughout the entire salmonberry season.
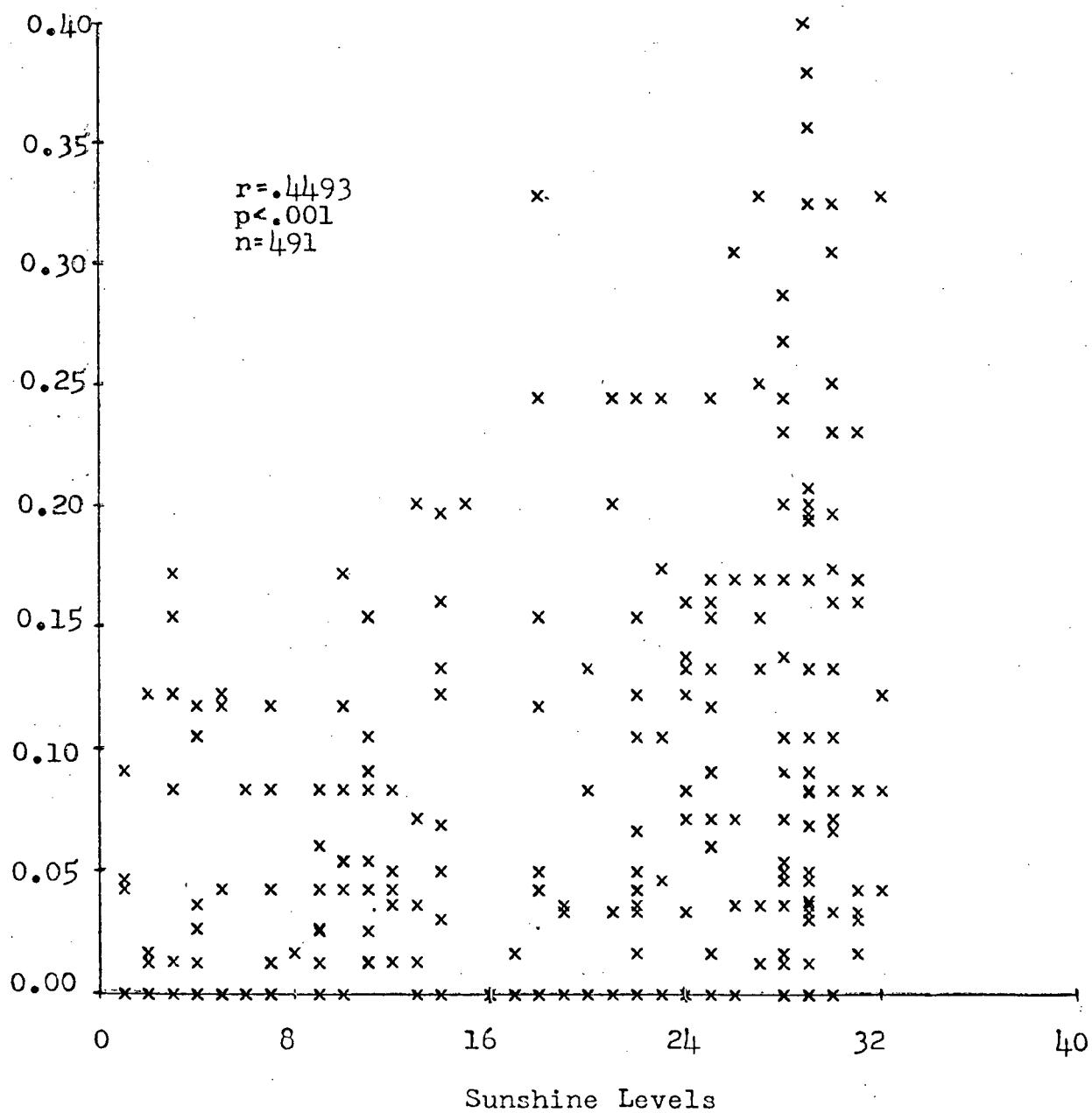
ln(1.0 + #bees/10 min x flower)

Date
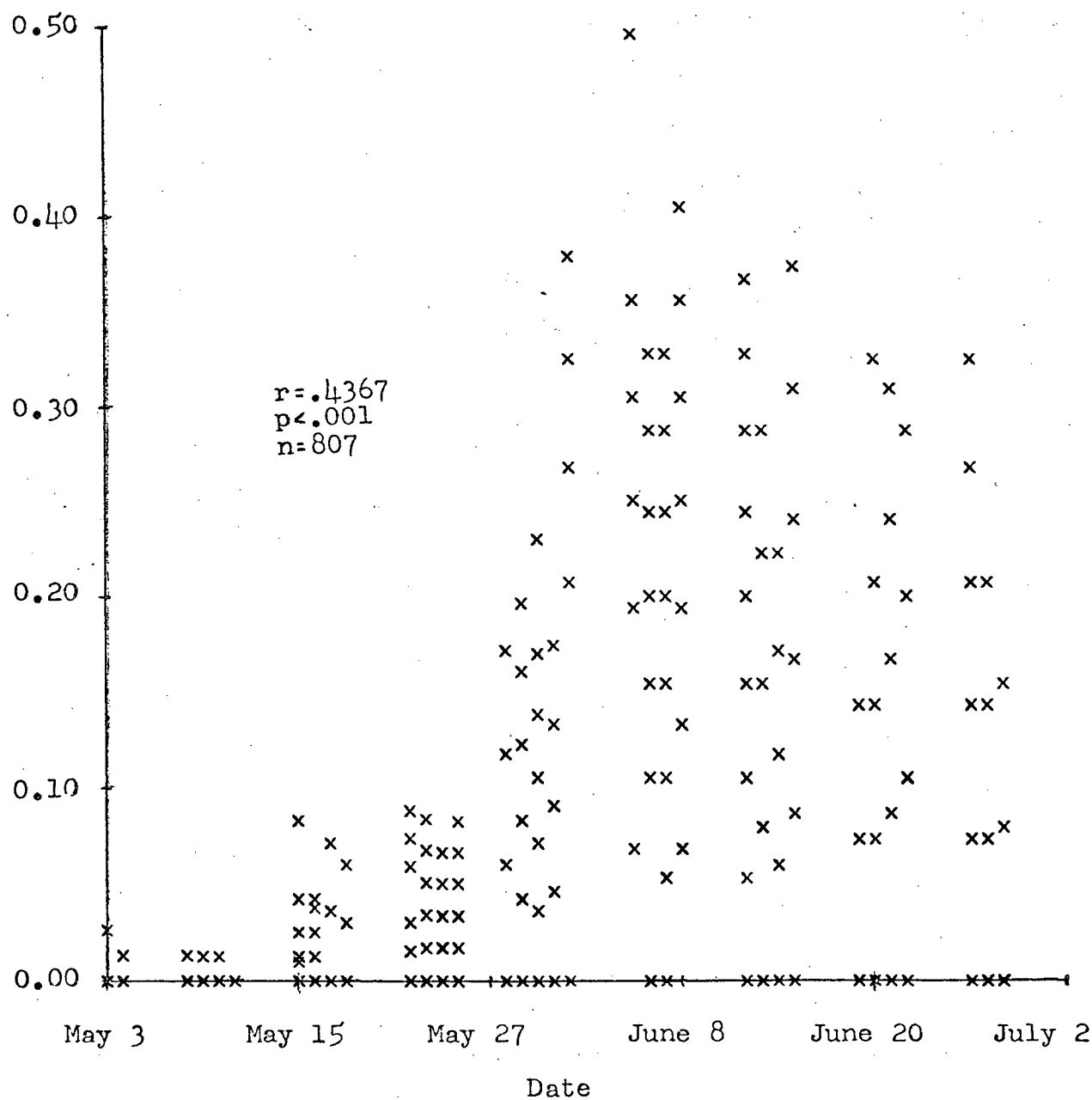
Fig. 20: Effect of sunshine levels on number of bees/10 min x flw (bee density).

ln(1.0 + #bees/10 min x flower)

r=.4493
p<.001
n=491

Sunshine Levels

(r=.4493, p<.001). There is, however, a great deal of variability in the data, activity values were often quite low at even the higher ranges of sunshine levels. Although the level of sunshine is included in the stepwise regression model as providing significant explanatory value independent of date effects, its contribution is not very great. Seasonally, bee density increased as relative humidity declined (r=-.1174, p<.01). To view this relationship independently of date, the correlation between the residuals of a regression of bee density on date and relative humidity values was examined. The correlation (r=-.1266) is significant with p<.01. Temperature correlates positively with bee density throughout the season (r=.2990, p<.001), but is not correlated significantly once date effects are removed (r=.0545, p>.05). I would conclude from these results that as sunshine and temperature levels increased and relative humidity decreased during the course of the season, there was a strong increase in bee density, yet with the seasonal effect removed there was only a very weak tendency for an increase in forager numbers with these environmental factors.

As bee density increased throughout the season nectar standing crop declined (r=-.5731, p<.001). Nectar standing crop (average calories/flower per sample of 10 flowers) is included in the regression model as explaining a significant percentage of the variation in bee density independently of date (Table VI). As is the case for sunshine levels, however, the percentage it does explain is very low, the correlation coefficient between the residuals of regression of bee numbers on date and standing crop being -.0973 (p<.05). Analysis on data

gathered only before noon shows standing crop to be more highly correlated with bee numbers, again, independent of date (Fig. 21, r=-.2185, p<.001).

It is interesting to note that flower density had a very strong relationship with bee density throughout the season (r= -.4497, p<.001), yet when the effect of date was removed there was not a significant correlation between bee density and flower density (r=-.0053). It is also interesting to notice that on May 28 there was a large surge in bee density, just as there was a drastic decrease in nectar standing crop available per flower (Figs. 16 and 18).

The regression model constructed for the variable, number of flowers used/number of flowers investigated, ("# used/# inv") is presented in Table VII. Variables chosen as significant account for only 13% of variability in the data, however, many relationships exist which are of interest. # used/# inv increased significantly as the season progressed (r=.1973, p<.001), yet this significance is most likely due to the great number of data points involved (n=316, Fig. 22). With date effects removed, there is no relationship between sunshine levels and # used/# inv, nor between bee density and the latter variable. Independent of date, there is a significant negative correlation between # used/# inv and temperature (Fig. 23, r= -.2327, p<.001), and a rather weak, positive correlation with relative humidity (r=.1279, p<.05). Apparently, there was a decline in # used/# inv as temperature increased and the air became drier during the course of a day. Though # used/# inv increased with declining standing crop over the season (r=

Fig. 21: Scatter plot of nectar standing crop (calories/flower)
and number of bees/10 min x flw (bee density),
independent of seasonal effects. Includes data
gathered before noon.

Residuals of regression of
ln(1.0 + #bees/10 min x flower) on date
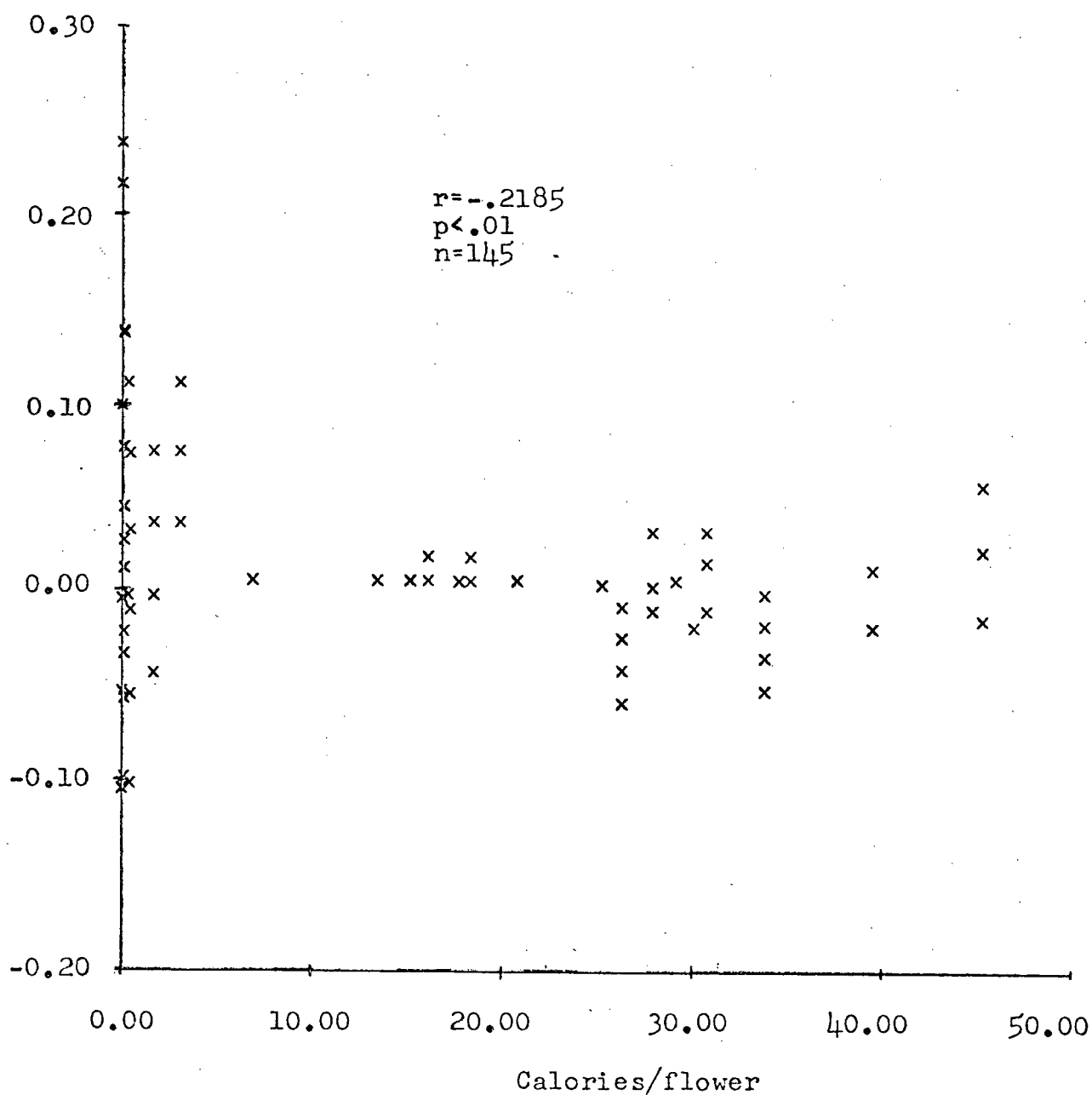

r=-.2185
p<.01
n=145

Calories/flower

Table VII: Stepwise regression model built for the variable,
ln number of flowers used/number of flowers
investigated ("# used/# inv").

a) Variables selected for the model.
b) Variables not selected.
c) Steps in model construction.

ANALYSIS AT STEP 3 FOR 35.V35   N= 249 OUT OF 561

SOURCE	DF	SUM OF SQRS	MEAN SQUARE	F-STAT	SIGNIF
REGRESSION	3	4.7181	1.5727	11.844	.0000
ERROR	245	32.534	.13279		
TOTAL	248	37.252			

MULTIPLE R= .35589   R-SQR= .12665   SE= .36440

a)

VARIABLE	PARTIAL	COEFFICIENT	STD ERROR	T-STAT	SIGNIF	
CONSTANT		-28.660	14.326	-2.0005	.0465	
5.V5	-.14673	-.18727	.80657 -1	-2.3217	.0211	temperature
28.V28	.13497	9.9456	4.6646	2.1321	.0340	ln temperature
31.V31	-.26471	-.66069 -1	.15377 -1	-4.2966	.0000	ln standing crop

b)

REMAINING	PARTIAL	SIGNIF	
1.V1	-.03033	.6359	date
3.V3	-.10098	.1141	hours after sunrise
4.V4	.01773	.7820	sunshine
6.V6	-.03535	.5811	rel. humidity
8.V8	-.02197	.7317	standing crop
24.V24	-.08967	.1609	ln date
26.V26	-.07060	.2700	ln hours after sunrise
27.V27	.05474	.3927	ln sunshine
29.V29	-.03057	.6333	ln rel. humidity
52.V52	-.09057	.1567	bee density
53.V53	-.09292	.1462	ln bee density

REGRESSION OF 35.V35 USING FORWARD SELECTION

c)

STEP	R-SQR	STD ERROR	# VAR	VARIABLE		PARTIAL	SIGNIF
1	.05920	.37668	1	31.V31	IN	-.24331	.0001
2	.11045	.36702	2	5.V5	IN	-.23340	.0002
3	.12665	.36440	3	28.V28	IN	.13497	.0340

Fig. 22: Scatter plot of number of flowers used per number of flowers investigated (# used/# inv) and date.

ln(#flws used/#flws investigated + 1.0)

r=.1973
p<.001
n=316

2.00

1.75

1.50

1.25

1.00

0.75

0.50

0.25

0.00

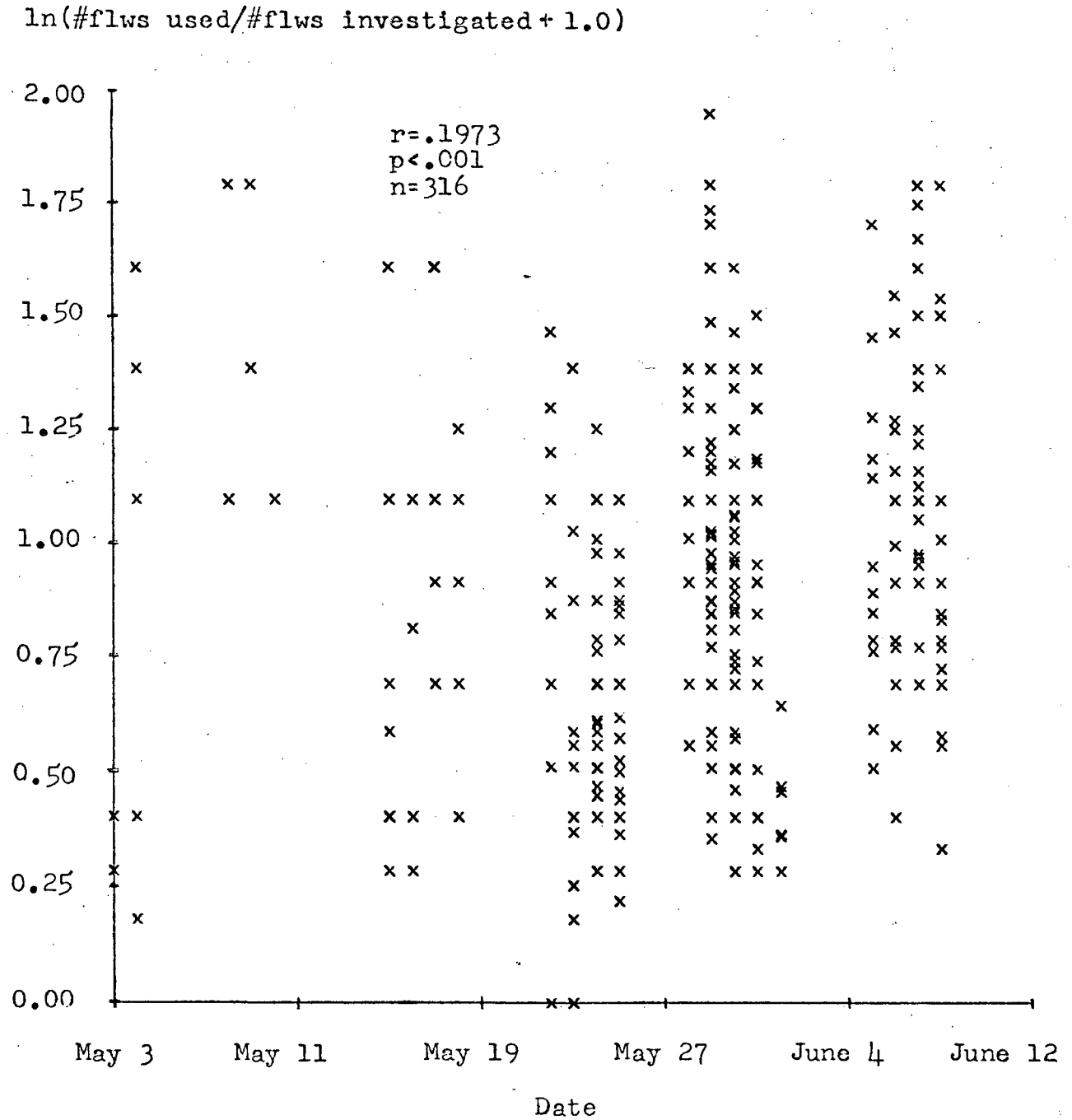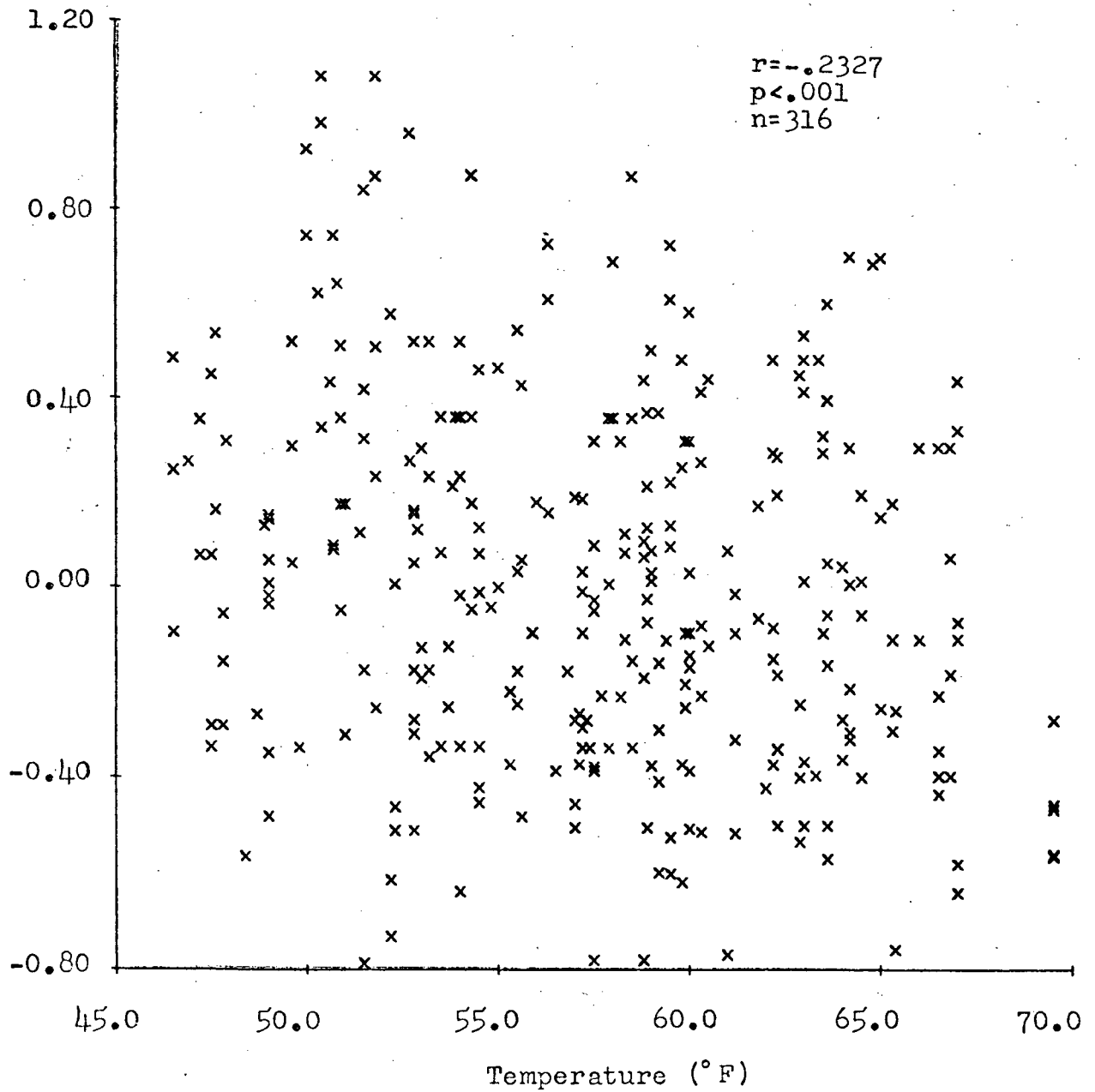May 3   May 11   May 19   May 27   June 4   June 12

Date

Fig. 23: Scatter plot of temperature and the number of
flowers used/number of flowers investigated
(# used/# inv), independent of seasonal effects.

Residuals of regression of
ln(#flws used/#flws investigated +1.0) on date

r=-.2327
p<.001
n=316

Temperature (°F)

-.2928, p<.001), there was not a significant relationship between
the two variables independent of seasonal effects (r=-.1051,
p>.05).

Several of these relationships are stronger during the
morning hours, yet, without seasonal effects, the same patterns
are evident. Temperature and # used/# inv are still negatively
correlated (r=-.2479, p<.05), while the latter variable is
negatively correlated with bee density (r=-.1670), though the
relationship is not significant (p>.05). These correlations seem
to indicate that bee density and # used/# inv were acting in
opposition, though this conclusion must remain extremely
tentative due to the lack of consistent relationships between
the variables just examined. It is interesting to note that the
variable, # flowers used/bee, did increase as the season
progressed and the levels of standing crop fell (Fig. 24,
r=.5733, p<.001).

The regression model for average androecium diameter
used/average androecium diameter present ("diam used/diam
present") is shown in Table VIII, where sunshine, temperature
and nectar standing crop were chosen as significant variables,
together accounting for 39% of variability in all data, and 49%
of variability in data gathered only before noon. For all data,
diam used/diam present increased as the season progressed
(Fig. 25, r=.2960, p<.001). Diam used/diam present increased
with increasing bee density (r=.2835, p<.001), and increased
with declining standing crop levels (r=-.5338, p<.001).
Independent of seasonal effects, there was no relationship
between bee density and diam used/diam present (r=.0662, p>.05),

Fig. 24: Scatter plot of number of flowers used/bee and date.

ln(2.0 + #flowers used/bee)
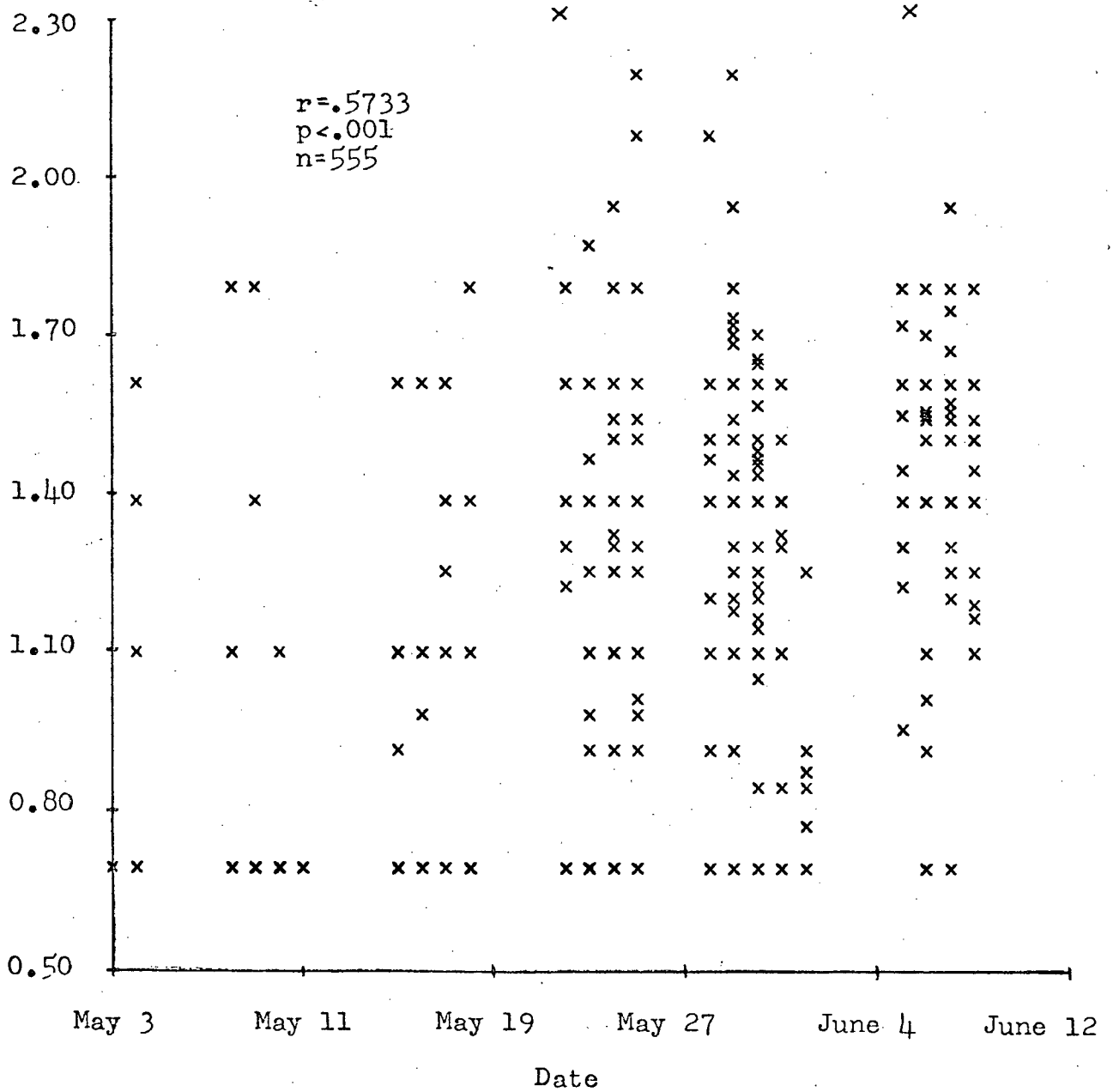
Date

Table VIII: Stepwise regression model built for the variable,
               ln average androecium diameter used/average
               androecium diameter present.

               a) Variables selected for the model.
               b) Variables not selected.
               c) Steps in model construction.

ANALYSIS AT STEP 4 FOR 50.V50   N= 226 OUT OF 561

SOURCE	DF	SUM OF SQRS	MEAN SQUARE	F-STAT	SIGNIF
REGRESSION	4	3.5465	.88662	35.942	.0000
ERROR	221	5.4516	.24668 -1		
TOTAL	225	8.9981			

MULTIPLE R= .62780   R-SQR= .39414   SE= .15706

a)

VARIABLE	PARTIAL	COEFFICIENT	STD ERROR	T-STAT	SIGNIF	
CONSTANT		-15.922	6.3934	-2.4904	.0135	
4.V4	.13908	.26208 -2	.12553 -2	2.0878	.0380	sunshine
5.V5	-.19362	-.10544	.35939 -1	-2.9338	.0037	temperature
28.V28	.17714	5.5682	2.0811	2.6756	.0080	ln temperature
31.V31	-.56418	-.73562 -1	.72417 -2	-10.158	.0000	ln standing crop

b)

REMAINING	PARTIAL	SIGNIF	
1.V1	-.06954	.3023	date
3.V3	-.06319	.3487	hours after sunrise
6.V6	-.10941	.1040	rel. humidity
8.V8	.08864	.1882	standing crop
24.V24	-.06561	.3305	ln date
26.V26	-.05700	.3980	ln hours after sunrise
27.V27	.01107	.8697	ln sunrise
29.V29	-.10781	.1092	ln rel. humidity
52.V52	.01860	.7829	bee density
53.V53	.02581	.7022	ln bee density
12.V12	.03896	.5636	# used/# inv
35.V35	.07613	.2587	ln # used/# inv

REGRESSION OF 50.V50 USING FORWARD SELECTION

c)

STEP	R-SQR	STD ERROR	# VAR	VARIABLE		PARTIAL	SIGNIF
1	.31453	.16594	1	31.V31	IN	-.56083	.0000
2	.36126	.16054	2	5.V5	IN	-.26111	.0001
3	.38219	.15824	3	28.V28	IN	.18099	.0066
4	.39414	.15706	4	4.V4	IN	.13908	.0380

Fig. 25: Scatter plot of average androecium diameters
used/average diameters present and date.

ln(diam used/diam present + 1.0)

r=.2960
p<.001
n=278

Date
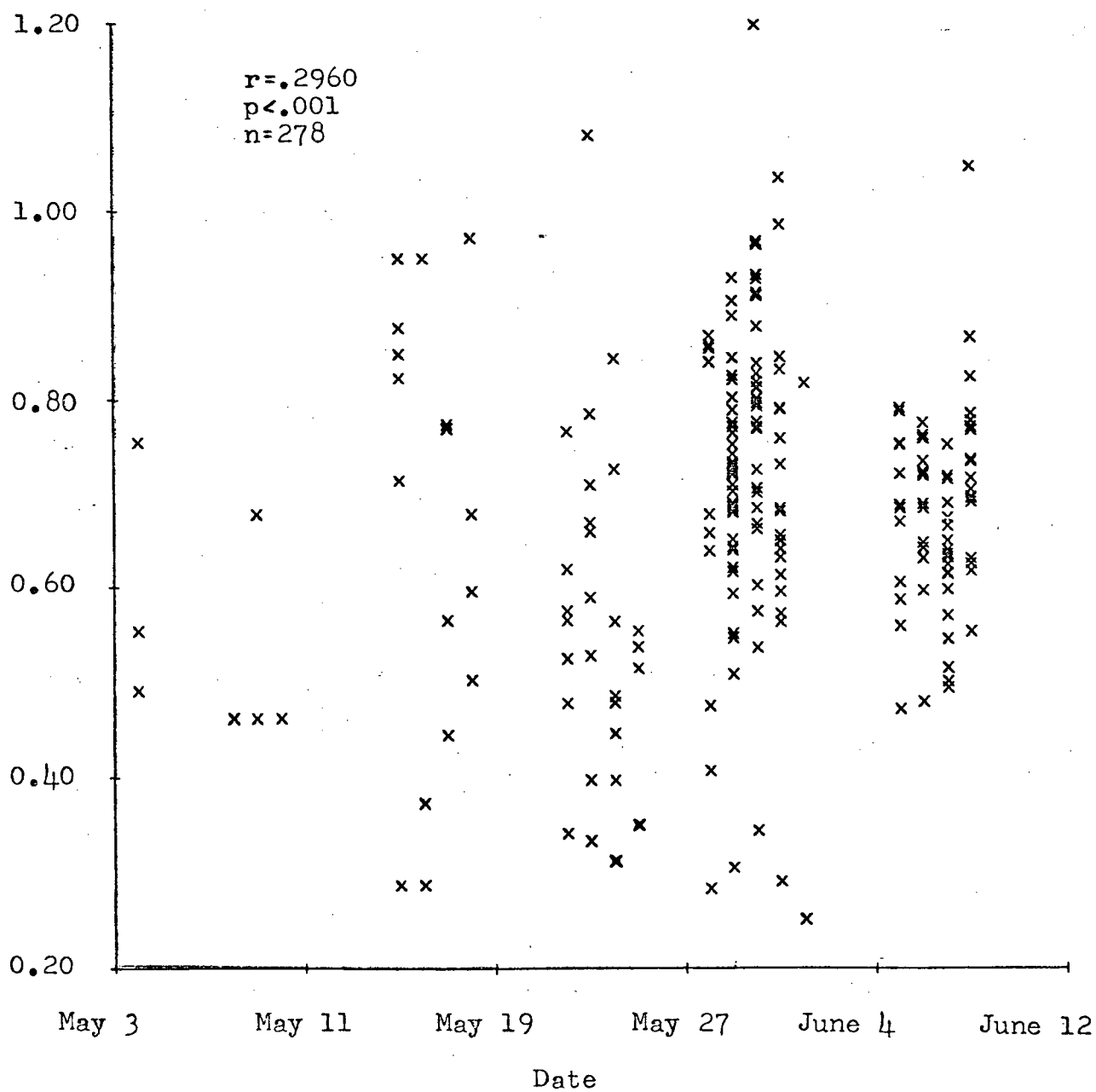
but the latter variable did show an increase with declining
standing crop levels (Fig. 26, r=-.3190, p<.001). Data collected
before noon still show diam used/diam present to be negatively
correlated with standing crop (r=-.2998, p<.01), and a weak,
positive relationship exists between the former variable and bee
density (r=.2222, p<.052). Thus, as bee density increased and
nectar standing crop levels decreased, the bees foraged from
increasingly larger diameter flowers relative to the size of
flowers present.

D.) Discussion

From the data just presented it seems clear that
B. sitkensis do modify foraging behavior to meet changing food
resource conditions throughout each day during the salmonberry
flowering season, this behavior being the average androecium
diameter of flowers used by the bees during a session. The data
further indicate that the ratio of the average number of flowers
foraged by the bumblebees during an observation session to the
average number of flowers investigated may also be changing as
food conditions vary.

When nectar resources are at high levels relatively few
bumblebees forage per flower, this situation occurring during
the early morning hours of a typical day when productivity is
highest. Standing crop levels are also high early in the
flowering season as opposed to later days, while number of
foragers is rather low early in the season. During each day, as
bee numbers build, the standing crop in each flower decreases,

Fig. 26: Scatter plot of nectar standing crop (calories/flower)
          and androecium diameter used/androecium diameter
          present, independent of seasonal effects.

Residuals of regression of
ln(diam used/diam present + 1.0) on date

Calories/flower

r=-.3190
p<.001
n=269
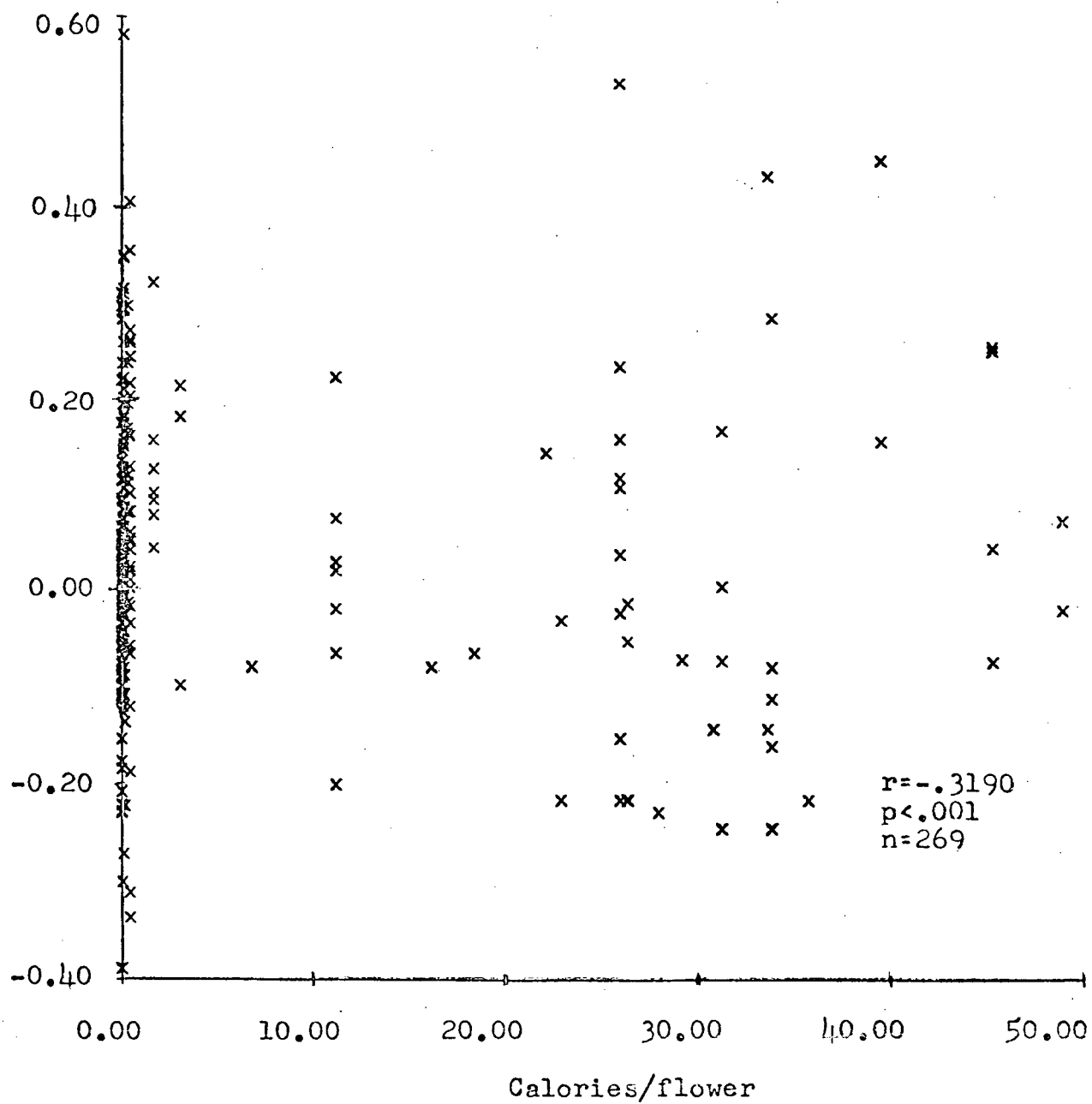
presumably due to the removal of the nectar by the insects. Previous authors have found that bee forager numbers reach a peak about midmorning, or 10-11:00 (Free, 1955; Alford, 1975), and Corbet (1978) describes this same negative relationship between bee numbers and calories available. Nectar is not replaced since flower productivity reaches a peak in the early morning and steadily decreases as the day proceeds (Chapter II). Similarly, forager numbers steadily build as the summer proceeds; this, and the fact that productivity peaks in early summer and then gradually declines (Chapter II), keeps standing crop levels quite low later in the season. After May 27, the numbers of salmonberry flowers decreased drastically, abruptly increasing the numbers of bee foragers per flower. The increased number of foragers seem to have suddenly cut standing crop levels to a very small fraction of previous levels.

Corbet (1978) argues that insects may forage for floral nectar just at the time of day when the increasing vapor pressure deficit evaporates the liquid to the concentration appropriate for the insect's caloric demands. Standing crop data gathered during this study show that the minimum concentration values for most days do not reach excessively low levels. The lowest concentration values recorded during each day early in the season averaged approximately 18-20%, with daily mean values being around 21-27%. Honeybees in California ignore orange blossom nectar early in the morning, when it contains only 16% sugar. They switch to orange nectar in the afternoon when the nectar concentrates to 30% sugar through evaporation (Vansell, Watkins and Bishop, 1942). Jamieson and Austin (1956) found that

honeybees are able to distinguish between sucrose solutions of 40 and 50%. The differences between salmonberry nectar concentrations in the morning and midmorning do not seem great enough to support Corbet's belief. The fact that bumblebee foragers are not so active in the early morning indicates, I believe, that factors other than calories available are determining insect foraging behavior, the obvious candidates being weather variables.

The caloric cost of flight is decreased at relatively high temperatures (Heinrich, 1975a). Thus I feel that, in this study, bumblebee foragers increase in numbers as the day proceeds due to increasing air temperatures, and not due primarily to any property of the nectar rewards alone. According to this explanation, bees must make foraging decisions based on opposing demands placed upon them by weather conditions and by flower productivity patterns. While Corbet's main point that daily patterns of floral rewards must be investigated before pollinator activity can be adequately understood is certainly appreciated, trying to explain bumblebee forager numbers simply on the basis of floral rewards may be misleading.

It is reasonable to claim that the decrease in standing crop through the day is due to increasing numbers of nectar foragers and decreasing nectar productivity, yet it is difficult to know if there is any increase in forager numbers due, in turn, to the low levels of standing crop. It is believed that bumblebee colonies send out greater numbers of foragers when food resources are scarce as opposed to plentiful times when surplus nectar is stored in the hive (Alford, 1975). Thus this

effect could have influenced the increase in forager numbers observed through the day in this study.

As the season advances, productivity in salmonberry flowers declines (chapter II), standing crop levels also decline, yet bumblebee forager numbers continually increase. Since bumblebee colonies do increase in numbers throughout the early summer, it is again difficult to know whether the seasonal increase in forager numbers observed is a response to the decreasing levels of nectar available, or due to the seasonal buildup in colony numbers, or both. So this question could be explored in more detail, an attempt was made to entice emerging queens to use buried nest boxes. Unfortunately, this attempt met with no success. It does seem that seasonally, as is the case for each day, bumblebees do not forage during the periods when levels of nectar offered are greatest. This is, again, probably not due to intrinsic properties of the nectar, but is due to the fact that queens do not emerge from their winter torpor to found colonies until climatic conditions reach adequate levels, and, after colony initiation, it takes a certain amount of time to build up colony numbers. Thus, neither daily nor seasonally are the bees able to take advantage of peaks in nectar productivity (cal/hr).

As forager numbers increase and standing crop levels decrease daily and seasonally, bees approach and utilize flowers with a wider spectrum of androecium diameters, whereas when numbers are low they forage from flowers with smaller androecium diameters, (or, they use younger flowers). This adds weight to the conclusion discussed in the previous chapter that nectar productivity is greatest in young flowers and gradually falls as

the flowers age. The data indicate that, as forager numbers increase, (and nectar levels decrease), the bees may be actually utilizing a smaller fraction of the flowers that they approach. This finding is exactly opposite to that previously predicted.

That the actual number of foragers correlates with the latter behaviors does not, I believe, indicate that increased bee traffic in the patch directly causes the bees to alter these behaviors. Even on busier afternoons, a maximum of only 9 bees appeared per 10 minutes, and it was extremely rare for any direct interactions to occur between them. It is also highly unlikely that weather factors directly influence changes in these behaviors, since correlations between these variables are often not impressive if they exist at all.

The answer as to what directly causes changes in # used/# inv and diam used/diam present most likely lies in the nectar standing crop available to the foragers. Calories/flower correlates well with average diam used/average diam present, and is chosen in regression models for it and for # used/# inv. According to this explanation, as bee density increases, the nectar standing crop declines in preferred flowers, which consequently influences the bees to diversify the flower ages they accept. They also, apparently, forage from an ever smaller fraction of the flowers they approach, possibly because many more flowers become empty of floral rewards sufficient to sustain bee usage.

The prediction made earlier, that the bees should utilize more of the flowers they approach as nectar rewards decline still makes sense as long as there is enough reward in the

flowers used to allow bees to make even a small net energy profit. There presumably does exist a level of nectar at which the bees can no longer afford to forage upon certain flowers, and it is at this point that bees begin to again avoid many flowers they approach, as they did when resources were quite plentiful. Even though standing crop levels were monitored throughout this study, pipette techniques were far too crude to investigate this nectar level at which the bees began to avoid unprofitable flowers. Often bees could be observed foraging from flowers I had previously "emptied" using pipettes. Thus I believe this point of unprofitability lay beyond my measurement capability.

The fact that # flowers used/bee increases as the season progresses indicates that each individual bee is working harder as standing crop conditions decline. This helps to explain the observation that bumblebees take the time to carefully investigate new objects in their environment during the early weeks of spring, while paying little attention to them later in the summer.

It is also interesting that many of the relationships previously discussed are more highly correlated when observations made during only the morning hours are considered. Since it is likely that the bees have depleted any stored food resources during the night (Alford, 1975), each bee would presumably be strongly motivated to gather food once the air temperature allows cost efficient flight. Each bee would forage in approximately the same manner since each faces similar food and weather conditions. As the hours pass, however, each bee

accumulates different amounts of food, (levels of nectar standing crop being quite heterogeneous), and so can deviate to a greater extent from the foraging behavior of other bees. By early afternoon, therefore, differences in foraging histories of each bee lead to a great deal of variability in foraging behavior. It may be the case as well that, in the afternoon, nectar standing crop levels are so low that many bumblebees can no longer forage efficiently regardless of the number of flowers they utilize. Thus they may rest for several hours or for the rest of the day. Alternatively, the bees could be shifting their activities to another part of the forest where the rewards are more attractive through the afternoon, bumblebees being often highly mobile (Adrian Belshaw, personal communication). These explanations would perhaps account for the fact that even though sunshine levels are high, there are often very few bees observed foraging.

The findings here correspond nicely with studies by Heinrich (1979a) and Whitham (1977) on bumblebee foraging behavior as it shifts in relation to food resources. Heinrich found that, as food resources become scarce through high bumblebee competition, bumblebees extend their foraging activities to plant species rarely used when resources are at higher levels. Whitham found that, as resources become scarce, the bees actually forage from _Chilopsis_ in a different manner than when times are good, increasingly using "groove nectar" as well as the preferred "pool nectar". The present study shows that as food levels decline bumblebees expand the range of acceptable flower "individuals", increasingly using older

flowers which produce less nectar than previously preferred younger flowers. As shown in the previous bumblebee studies, bumblebees increasingly become "generalists" in their foraging activities, a result consistent with current ecological theory (Pyke et al., 1977).

Unlike other studies, however, no relationship could be found in this study between numbers of bee foragers and flower density. Waddington (1976) found flower density to be an excellent predictor of halictid bee density , and Thomson (1978) found a similar increase in flower visitors with an increase in flower density. However, these studies were conducted in meadows, whereas the present study was conducted on flowers which grew along a road. After foraging one flower, a bee in a meadow should have a larger arc from which to choose another flower or patch of flowers than should a bee foraging along a road. This is true not only because salmonberry plants along a road occur in a narrow width and the flowers are located predominantly on the outer edges of plants, but also because bumblebees tend to forage at a rather constant height above the ground. Thus, bees along a road need to pass through less dense areas to arrive at a flower-rich area.

IV. CONCLUSIONS

In this study the following results were obtained:

1.) there exists a strong correlation between the androecium diameter of salmonberry flowers and flower age.

2.) there exists high heterogeneity among flowers in nectar productivity. Four out of ten flowers sampled secreted nectar at significantly higher rates than the remaining six.

3.) nectar productivity in salmonberry flowers declined as the flowering season progressed. Productivity was high when relative humidity was high and decreased as levels of sunshine increased through the day and through the season. Productivity was highest in young flowers and declined with increasing flower age.

4.) a decline in sampling frequency brought about a corresponding decline in nectar productivity. As the time elapsed between samples increased, floral productivity increased as well.

5.) bumblebee density correlates better with various weather varicus weather and productivity variables early in the day, as opposed to during the afternoon. This is presumably because it was only in the morning that the bees experienced uniform energy conditions.

6.) with an overall decline in available nectar, the bees increasingly selected older flowers from which to forage. They also may have been avoiding increasingly greater numbers of flowers they approached. These flowers were presumably empty of

nectar levels sufficient to maintain foraging.

7.) there was no relationship between bee density and flower density.

Though pipettes were used to study the effects of sampling frequency, it was assumed that pipetting techniques adequately simulate the effects of bee foraging on the flowers. If this assumption is valid, then bumblebees do have the capacity to alter the rates of nectar productivity while nectar levels in flowers simultaneously influence bumblebee foraging behavior. During the course of a single day, nectar productivity is highest during the cool, morning hours when bee foragers are infrequent. Productivity also peaks early in the flowering season, when a bee colony still consists of only one queen and perhaps a few workers. It may be the case that productivity is highest at these times due not only to moisture effects but also to the lack of foragers at this time, which influences the flowers to secrete nectar at higher rates. Though I believe that moisture factors are of primary importance, the possible impact of actual forager use on productivity at these times should be further investigated.

The bees increase in density as air temperature increases, other authors finding that they reach maximum levels at 1000-1100 hr. That they peak during the midmorning hours, rather than in the afternoon, suggests that productivity does partially determine the time at which the bees forage. The opposing effects of these factors should be explored in more detail, perhaps using simulation models of energy flow between flowers and bees. As the bees increase in density, both daily and

seasonally, they increasingly select older flowers and seem to avoid flowers with insufficient nectar rewards, thus perhaps stimulating empty flowers to produce at a higher rate. This conclusion concerning avoidance of certain flowers approached is based on inconsistent evidence, and thus should be explored in more detail in a laboratory setting where confounding factors can be adequately controlled.

As mentioned in Chapter II, plants may be competing for pollinators early in the season and early in the mornings. The increase in productivity with decreased sampling frequency may be a physiological adaptation to enhance a plant's competitive ability. Studies should be done to discover if salmonberry plants are actually engaged in mutual competition at this time. Many flowers should be removed from the study sites and the seed set examined in the remaining flowers. Competition between plants would then be indicated if the reproductive output actually did increase.

The data indicate that, later in the season, and later in the day, the bees are competing for nectar resources, since it is during these times that measured nectar levels are low and bees accept a wider diversity of flower ages. Bumblebees at my sites rarely interacted directly, possible competition occurring instead through exploitation of nectar resources. Future studies should be done involving the removal of several local bee colonies to observe the effects on the reproductive output of the remaining colonies. It should be a simple matter to count the number of queens and drones produced per colony near the end of the summer, yet it would be a huge task to even find the nest

sites at my study areas.

Mosquin (1971) is the only study of which I am aware in the pollination ecology literature which, through an examination of actual plant-pollinator community characteristics, discusses the possibility that competition may be shifting from the animal component to the plant component as the summer proceeds. Other studies have implied that, if resources become limiting in a habitat, it is only one component of the relationship which suffers. In the alpine, it is plants which compete for a few pollinators (Pojar, 1974), while Heinrich argues that in the bogs of Maine it is nectar resources which are sometimes limiting, possibly leading to "resource partitioning" in bumblebees (Heinrich, 1976a).

However, if it is natural selection which brings about the high degree of morphological and behavioral fit observed between plants and their pollinators, it is far more likely that, in any given habitat, competition for limited resources should be occurring amongst the plants for pollinators, alternating with periods of competition amongst the pollinators for plants. I have documented here circumstantial evidence that this is occurring at my study sites.

The shift in a pollinator scarce community to a nectar scarce community may not be gradual. A very sudden plunge in nectar standing crop is visible in Fig. 19, corresponding to a drop in number of flowers per meter in the habitat (Fig. 21). This sudden loss of flowers may have resulted in a suddenly very different world from a bumblebee's point of view.

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