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## COMPETITION BETWEEN HUMMINGBIRDS AND INSECTS FOR THE NECTAR OF TWO SPECIES OF SHRUBS

JAMES H. BROWN, ASTRID KODRIC-BROWN,  
THOMAS G. WHITHAM, AND HEDLEY W. BOND

**ABSTRACT.**—The nectars of two species of shrubs, *Ribes pinetorum* and *Chilopsis linearis*, were limited food resources that were utilized by both hummingbirds and insects. Both shrub species had bimodal patterns of daily nectar secretion with peaks in morning and afternoon. *Ribes pinetorum*, blooming at high altitude, was visited frequently by hummingbirds because its timing of nectar secretion coincided with periods of low temperature when insects were inactive. Sufficient nectar accumulated in flowers to make hummingbird foraging economical in early morning and late afternoon, but not at midday when insects were foraging and had lowered nectar levels. *Chilopsis linearis*, blooming at lower elevations where low temperatures did not inhibit insect activity, attracted increasing numbers of bumblebees which depleted nectar levels and virtually excluded hummingbirds. The present study provides another example of competition between vertebrates and insects, and suggests that this interaction between distantly related taxa may play a significant role in plant-pollinator coevolution as well as in community ecology.

Although many species of flowering plants have coevolved highly specific relationships with animal pollinators (Faegri and van der Pijl, 1971; Grant and Grant, 1965, 1968; Proctor and Yeo, 1972; van der Pijl and Dodson, 1967). Others are relative generalists. They may be pollinated by several animal taxa which forage for their nectar or pollen. Animals may compete for these food resources. Competition for floral rewards between individuals of closely related species is well documented and is thought to play a major role in the organization of guilds of nectar-feeding animals (e.g., Feinsinger, 1976; Heinrich, 1976; Inouye, 1978; Gill, 1978; Gill and Wolf, 1975; Kodric-Brown and Brown, 1978; and many others). Several recent studies have suggested that organisms in different classes and phyla compete for food and other resources (e.g., Brown and Davidson, 1977; Reichman, 1979). Since two classes of vertebrates (birds and mammals) and several orders of insects (Hymenoptera, Lepidoptera, Diptera, and Coleoptera) commonly feed on nectar or pollen and serve as pollinators, competition between these distantly related taxa may play a significant role in the ecological relationships among these flower visitors and in the coevolution of plants and their pollinators (Carpenter, 1979; Kodric-Brown and Brown, 1979).

In the present paper we assess competition between hummingbirds and bees for the nectar of two Southwestern shrubs, *Ribes pinetorum* Greene (Saxifragaceae), orange gooseberry, and *Chilopsis linearis* (Cav.) Sweet, (Bignoniaceae), desert willow.

**METHODS.**—*Study Sites.*—The field work was done in the vicinity of the Chiricahua Mountains of southeastern Arizona. *Ribes pinetorum* was studied from 10-23 May 1974 at Rustler Park, 16.7 km W Portal, Cochise Co., Arizona, 2610 m. The study population consisted of 10 dense shrubs, each 2 to 3 m in diameter, distributed over an area of approximately 0.1 ha. Plants were growing adjacent to a spring in a clearing in mixed coniferous forest.



*Chilopsis linearis* was studied from 16-27 May 1974, 7.2 km N Portal, Cochise Co., Arizona, 1400 m. Approximately 25 individual plants, each 3 to 5 m tall, were distributed for a distance of 200 m along the edges of a normally dry wash. The surrounding habitat was desert scrub, dominated by mesquite, *Prosopis velutina* Woot., and creosotebush, *Larrea tridentata* (DC.) Cov.

*Measurements of Nectar Production and Availability.*—Nectar production was measured by enclosing branches with approximately 20 flowers in each of six or more 2-mm mesh nylon bags. The bags excluded all potential pollinators but interfered minimally with air movement and light penetration. After flowers had been bagged overnight or for 2-h periods during the day, nectar was collected and measured in 1 or 20  $\mu$ l Drummond micropipettes. Procedures differed somewhat for the two species. Nectar could be collected from flowers of *R. pinetorum* accurately and repeatedly without damage to the flowers. As a result the same flowers were sampled at successive 2-h intervals throughout the day and were emptied prior to being bagged. Flowers of *C. linearis* had to be destroyed in order to measure precisely their nectar content. Consequently it was necessary to correct measured values of accumulated nectar in bagged flowers for the quantity present when the flowers were bagged. To do this, we measured accumulated nectar in flowers which had been bagged either overnight or for 2-h periods during the day. We also measured amounts of nectar in unbagged, control flowers on the same shrub at the time of bagging; these latter values were subtracted from those of the bagged flowers to calculate the quantity of nectar secreted. Twenty-four-hour nectar production was estimated by adding 2-h samples. In this way errors due to evaporation or dependence of secretion on the amount of accumulated nectar were minimized.

The quantity of nectar contained in large samples (usually >80) of flowers, termed nectar availability (standing crop), was sampled at 2-h intervals throughout the day for both species. Concentration of nectar was measured in terms of equivalent concentrations of sucrose by refractometry. As the number of *R. pinetorum* flowers declined during the study, the number of flowers in bloom was quantified by counting blossoms in selected 1 m<sup>2</sup> areas on the surface of shrubs each day.

*Pollinator Censuses.*—At each site hummingbirds and insects were censused for a 5-min period every 30 min from 0600-2000 h on the same days that we measured nectar secretion and availability. Hummingbirds were censused by walking a standardized path through the entire study area and counting all individuals observed. Hummingbirds also were censused at artificial feeders at two sites (meadow and forest) within 300 m of the *R. pinetorum* study site. Six feeders that continuously supplied 25% sugar water were set out on 18 May after our intensive work on *R. pinetorum* had been completed. On 23 May visits of hummingbirds to these feeders were recorded for 30-min periods each hour throughout the day.

Individual insects visiting flowers were censused by counting total numbers that occurred in standardized observation areas (1 m<sup>3</sup>) at four different shrubs during a 5-min census each half hour. Feeding rates of insects and hummingbirds on *R. pinetorum* and of bumblebees and carpenter bees on *C. linearis* were measured by counting the number of flowers visited during timed feeding bouts. All species of insects which commonly visited the flowers were collected, examined for pollen, and identified from collections at the Southwest Research Station of the American Museum of Natural History. Foraging hummingbirds were observed carefully at close range through binoculars and were captured in mist nets and sampled for pollen. Coincident with day-long studies of nectar production and animal visits, air temperature in the shade was measured at half-hour intervals with a mercury thermometer.

*Sampling Effort.*—The data presented in this paper represent the concentrated efforts of six individuals. Most of our effort was devoted to obtaining detailed information on daily patterns of nectar secretion, nectar availability, and nectarivore foraging. We sampled each shrub species intensively for two complete 24-h periods. Except in one case, we bagged flowers in the evening (2000 h) and sampled nectar and censused animals on the following day from dawn (0600 h or earlier) to dusk (2000 h). One 24-h sample period for *R. pinetorum* extended from 1300 h on one day (11 May) to the same time the following day (12 May). Sample sizes were large and statistically reliable (see Figs. 1-5 and their legends). Data for the 2 days were extremely similar for each plant species. In order to avoid redundancy and save space, we have presented data for only 1 day each in Figures 1, 3, and 4, and used 3-point running averages to smooth out variation in nectarivore densities due to sampling error. However, we used raw, unaveraged data for both days in Tables 2 and 3 and Figures 2 and 5. In addition, Whitham (1977 and unpublished data) obtained many more data on daily patterns of nectar availability and bumblebee foraging for *C. linearis* in other years, which confirm the pattern presented here.



TABLE 1.—Important characteristics of the flowers of the two species.

	<i>Ribes pinetorum</i>	<i>Chilopsis linearis</i>
Shape	radially symmetrical with reflexed petals	bilaterally symmetrical; decurved bilabiate corolla; protruding ventral petals
Color	bright red yellow anthers	pale lavender with red and yellow guide lines within tube
Odor	none	sweet fragrance
Position of anthers and stigma	central and exerted	dorsal and enclosed within tube
Arrangement on plant	signly, in pairs, or triplets in terminal leaf axis	crowded terminal racemes
Length of floral tube	3 to 4 mm	16 to 20 mm
Nectar concentration <sup>a</sup>	22.6	24.3
24-h nectar secretion <sup>b</sup>	5.5 $\mu$ l	3.5 $\mu$ l

<sup>a</sup>Values represent equivalent percent sucrose as measured by refractometry; on samples from more than 50 flowers on each species.

<sup>b</sup>Based on total secretion of many flowers overnight and for successive 2-h periods during the day (see Figs. 2 and 5, and the text).

**RESULTS AND DISCUSSION.**—Table 1 summarizes some important characteristics of the flowers of the two plant species, including morphology, attractants, and nectar. The two kinds of flowers differ in many respects, but both are visited by significant numbers of hummingbirds and insects. This creates the potential for interspecific competition among the diverse taxa of animals that use the nectar of these flowers as a food resource.

*Ribes pinetorum*.—We studied *R. pinetorum* near the end of its flowering season. The number of flowers in bloom was declining from day to day, and there was a corresponding decline in the densities of all major kinds of nectar-feeding animals (Table 2). This correlation between flower availability and nectarivore density is the first evidence that nectar of this species was a limited resource.

Daily patterns of animal visitation to flowers of *R. pinetorum* were related to two primary factors: availability of nectar and ambient temperature (Figs. 1 and 2, Table 3). Flowers of this species secreted nectar in a bimodal pattern with peaks in early morning and late afternoon (Fig. 1). The quantity of nectar actually present (available) in flowers represents a standing crop that reflects two opposing rate processes: secretion by the flower and removal by nectar-feeders. The bimodal pattern of nectar availability closely followed

TABLE 2.—Numbers of flowers and animal visitors of *R. pinetorum* over a 24-hr period at the end of the blooming season.

	12 May	13 May
Flowers per m <sup>2</sup> of bush surface <sup>a</sup>	45.8	23.3
Honeybees <sup>b</sup>	25.3	13.6
Other insects <sup>b</sup>	27.1	7.1
Broad-tailed Hummingbirds <sup>c</sup>	36	24
Rivoli's Hummingbirds <sup>c</sup>	3	0

<sup>a</sup>Values represent the average counts of four 1 m<sup>2</sup> sample plots.

<sup>b</sup>Values represent the average number of insects counted during those census periods (16 on 12 May, and 10 on 13 May) during which the air temperature in the shade exceeded 18°C.

<sup>c</sup>Values represent the total number of hummingbirds censused at the *R. pinetorum* during the day.

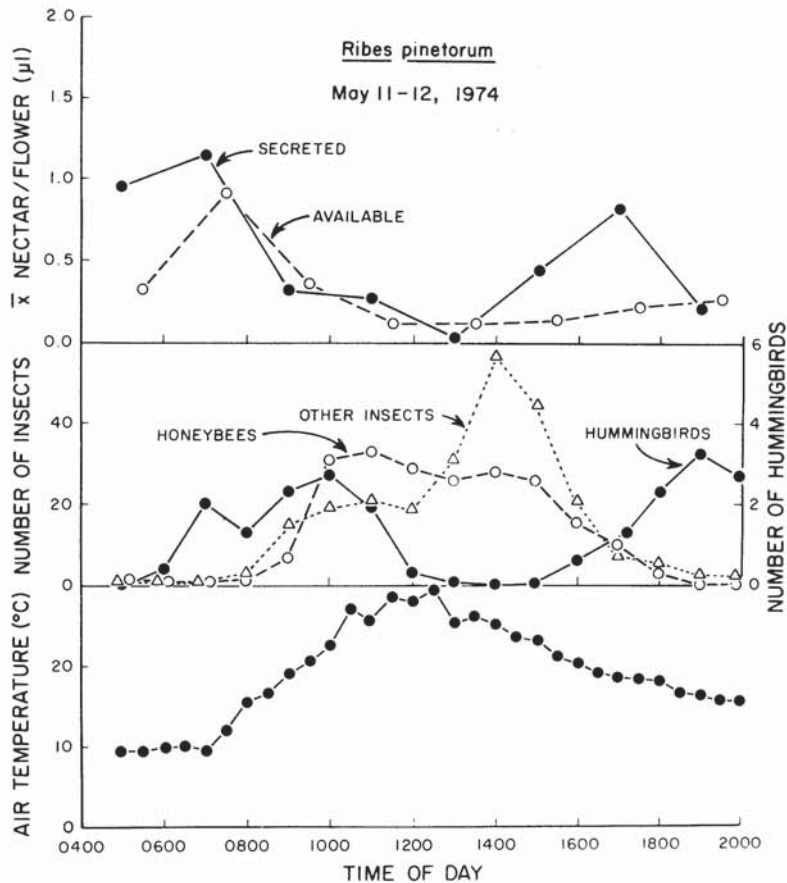


FIG. 1.—Patterns of nectar secretion and availability, animal visits, and ambient temperature for *R. pinetorum* on 11-12 May 1974. Plotted values for nectar quantities represent means of samples of 40 to 250 flowers and for animal visits represent three point running averages of census numbers. The first value for nectar secretion represents the amount produced overnight (since 2000), and subsequent values represent amounts produced during the previous 2-h period. Standard errors in nectar production and availability are  $0.26 \mu\text{l}$  when nectar levels are high,  $<0.1 \mu\text{l}$  when they are low.

the pattern of nectar secretion with only a small time lag (Figs. 1 and 2), indicating that nectar was harvested almost as rapidly as it was secreted. This point is underscored by frequency distributions of nectar quantities among flowers at different times of day (Fig. 3). Even during the morning and afternoon periods when flowers were most actively secreting nectar and some contained substantial quantities, a large proportion were empty or nearly so because of recent foraging.

Because nectar is a limited resource which is depleted almost as soon as it becomes available, we might expect a close correlation between nectar availability and rate of animal visitation. We observed such a relationship for hummingbirds, but not for insects. Hummingbirds visited flowers frequently in early morning and late afternoon when standing crops of nectar were high, but they were absent at midday when little nectar was available (Figs. 1 and 2). This pattern was substantiated by multiple regression analysis, which tested for the contributions of three factors (temperature, nectar standing crop, and number of insects) in accounting for the variance in hum-



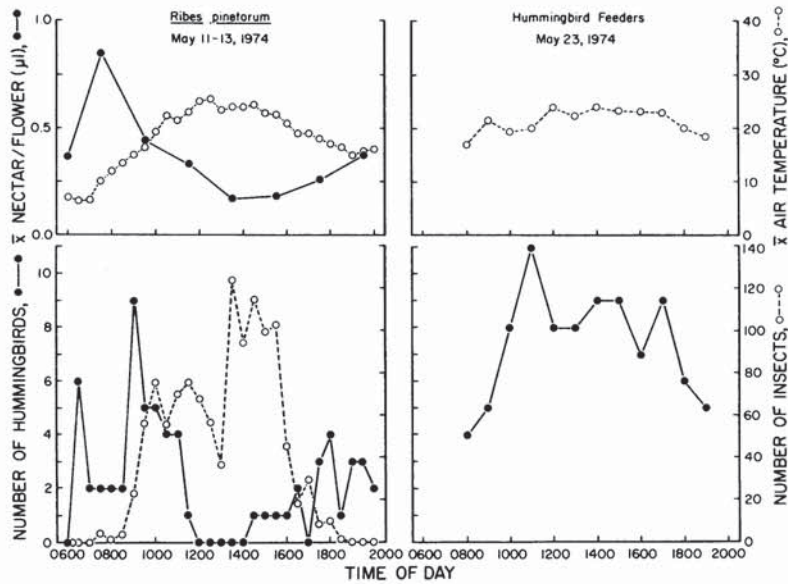


FIG. 2.—Daily pattern of nectar availability, ambient temperature, and animal visits for *Ribes pinetorum*, and hummingbird visits to feeders in the same area. Plotted values represent means for more than 100 flowers and total number of animal visits for the days indicated. Standard errors in nectar availability are 0.26  $\mu$ l when nectar levels are high and <1  $\mu$ l when they are low. Note that when a continuous supply of food is provided, there is no midday depression in the foraging activity of hummingbirds, as observed at flowers of *Ribes pinetorum*.

mingbird numbers. This analysis showed that number of hummingbirds recorded in a census was positively correlated with quantity of available nectar, but was not related to any of the other variables tested (Table 3). On the other hand, the pattern of insect visitation was not dependent on nectar availability, but was closely related to environmental temperature (Figs. 1 and 2). Insects were almost totally inactive during early morning and late afternoon when nectar levels were high but temperatures were less than about 18°C, and they foraged most intensely at midday when temperatures

TABLE 3.—Factors affecting visitation by hummingbirds and insects to *R. pinetorum* on 11-12 and 13 May 1974 as indicated by linear multiple regression analysis.

Dependent variable: number of insects <sup>a</sup>			
Independent Variable	Correlation Coefficient ( $r_{xy}$ )	T Value	Significance
Ambient Temperature (°C)	0.80	8.21	<0.0001
Available nectar ( $\mu$ l)	-0.41	-0.32	N.S.
Number of hummingbirds	-0.33	-0.82	N.S.
Coefficient of multiple correlation = 0.80			
Dependent variable: number of hummingbirds			
Independent Variable	Correlation Coefficient ( $r_{xy}$ )	T Value	Significance
Available nectar ( $\mu$ l)	0.37	1.96	<0.05
Number of insects	-0.33	-0.82	N.S.
Ambient Temperature (°C)	-0.32	-0.32	N.S.
Coefficient of multiple correlation = 0.42			

<sup>a</sup>In order to express numbers of pollinators on a per flower basis, numbers of both insects and hummingbirds on 13 May were multiplied by 2 (see Table 2).

were highest but standing crops of nectar were low. Again, this pattern was confirmed by multiple regression analysis, which showed that number of insects recorded in a census was positively correlated with ambient temperature, but independent of nectar availability and number of hummingbirds foraging (Table 3).

Taken together these patterns suggest that hummingbirds and insects competed for the nectar of *R. pinetorum*. Day to day changes in hummingbird and insect densities in response to numbers of flowers in bloom (Table 2) showed that overall food availability limited the number of foragers of both taxa. Daily patterns of flower visitation in relation to nectar availability (Figs. 1 and 2) provided evidence that both hummingbirds and insects harvested nectar that otherwise would be available to the other taxon. On the one hand, hummingbirds rapidly harvested nectar when temperatures were low but secretion rates were high, thereby limiting the quantity of nectar that accumulated in flowers, which in turn limited the number of insect foragers that could be supported when temperatures were high enough for them to be active. On the other hand, once insects became active in mid-morning, their foraging contributed to the decline in the standing crop of nectar, which by midday was no longer sufficient to support hummingbirds. One might argue that as the morning progressed the hummingbirds used up their own food supply and excluded themselves without any significant competition from insects. Hummingbirds undoubtedly affected nectar levels and competed among themselves in this fashion, but the extensive overlap in foraging activity between hummingbirds and insects between 0900 and 1200 h (Figs. 1 and 2) indicates that insects contributed importantly to the declining nectar levels and consequent exclusion of hummingbirds. Because we censused insects within 1 m<sup>3</sup> volumes in only four shrubs but counted all hummingbirds present on the entire study site, the actual densities of foraging insects depicted in Figures 1, 2, 4, and 5 were often several orders of magnitude greater than hummingbird densities when they were foraging simultaneously.

An alternative explanation for the cessation of hummingbird foraging on *R. pinetorum* at midday is that it reflects a normal pattern of bimodal daily activity rather than a direct response to low nectar availability. We tested this possibility by recording hummingbird visits to artificial feeders in an area immediately adjacent to our study area. These feeders provided a constant level of nectar availability throughout the day, and hummingbirds visited them at almost constant rates from early morning to late afternoon (Fig. 2). Controlled laboratory studies also have shown that hummingbirds feed frequently at almost constant rates throughout the day from feeders which provide a constant nectar source (Wolf and Hainsworth, 1977). We conclude that the cessation of hummingbird foraging at *R. pinetorum* flowers at midday was a direct response to low nectar levels resulting in part from insect foraging.

*Chilopsis linearis*.—Daily patterns of nectar secretion, nectar availability, and animal visitation for flowers of *C. linearis* (Figs. 4 and 5) showed both similarities and differences when compared to data for *R. pinetorum*. Nectar secretion of *C. linearis* was bimodal with a large peak before dawn and



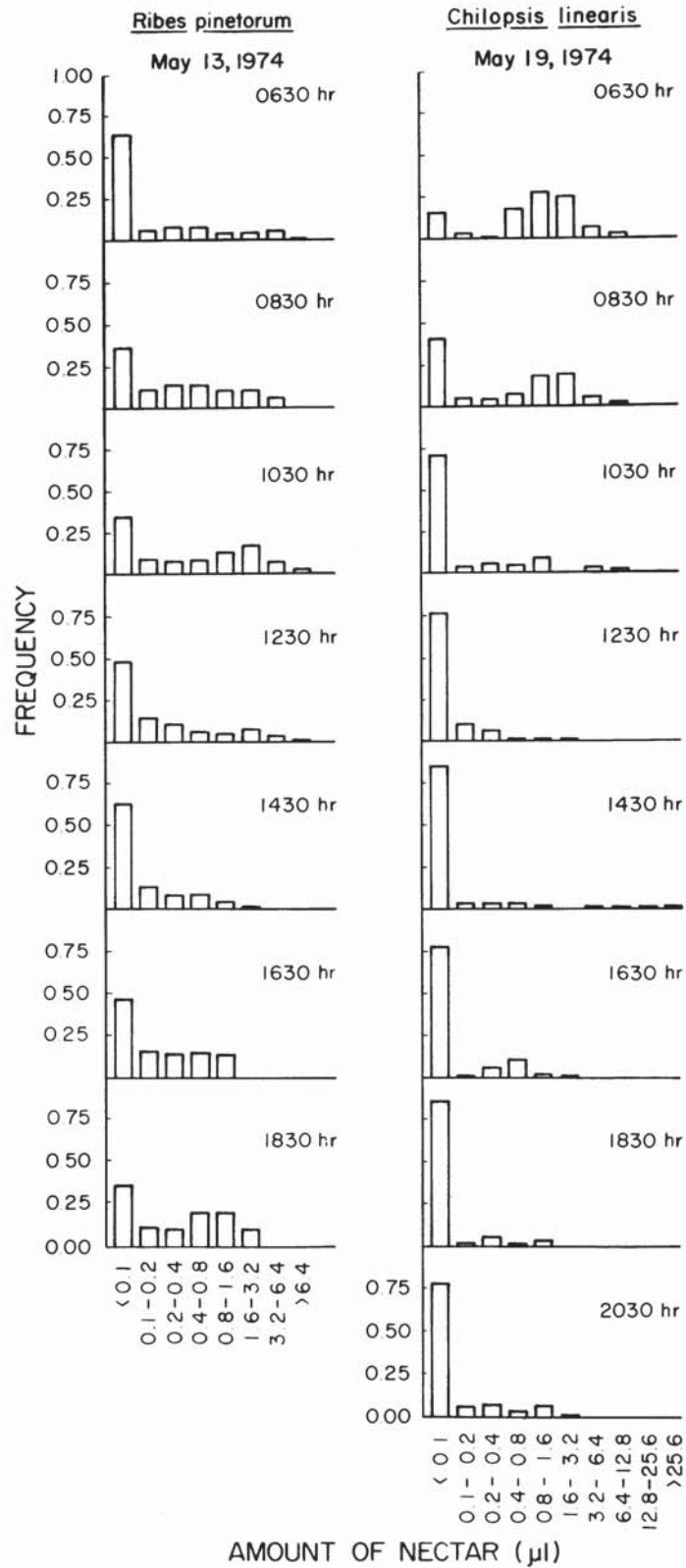


FIG. 3.—Changes in the frequency distribution of available nectar among flowers of *R. pinetorum* and *C. linearis* over a daily cycle. This pattern reflects the interaction of nectar secretion and animal foraging.



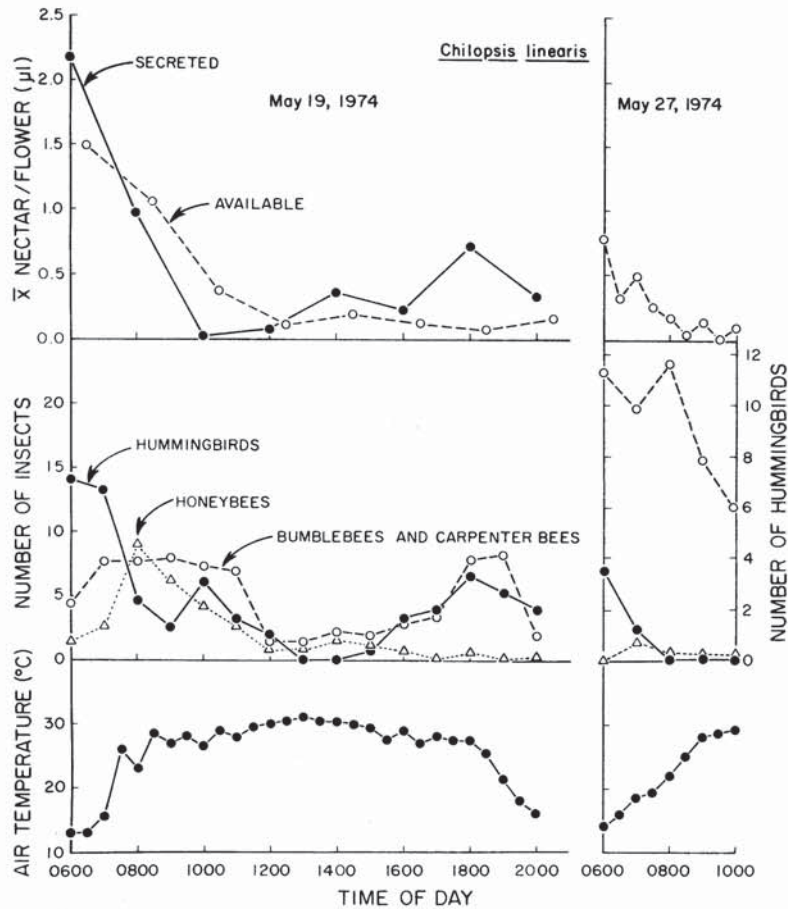


FIG. 4.—Patterns of nectar secretion and availability, animal visits, and ambient temperature for *C. linearis* on 19 May and part of 27 May 1974. Plotted values for nectar quantities represent means of samples of 50 to 200 flowers, and for animal visits represent three point running averages of census numbers. The first value for nectar secretion represents the amount produced overnight (since 2000 h) and subsequent values represent amounts produced in the previous 2-h period. Standard errors in nectar production and availability are always  $<0.24 \mu\text{l}$ .

another in late afternoon (Fig. 4). Standing crops of nectar closely followed the pattern of secretion with little time lag, so that available nectar declined rapidly during the morning and remained low for the rest of the day (Figs. 3, 4, and 5). Foraging activity by both hummingbirds and insects also was bimodal, closely following the pattern of nectar secretion and availability (Figs. 4 and 5). From these data we infer that limited nectar was available and that nectar feeders depleted the supply almost as rapidly as it was produced.

Patterns of nectar availability and animal foraging within and between days suggest that there was intense competition for nectar (Figs. 4 and 5). Although moderately low temperatures may have inhibited honeybee foraging in early morning, hummingbirds, bumblebees, and carpenter bees seemingly were unaffected and began foraging almost as soon as it became light (some bumblebees even spent the night in flowers). Hummingbirds ceased foraging earlier in the morning than insects, suggesting that they were competitively excluded when nectar standing crop was lowered to a level that

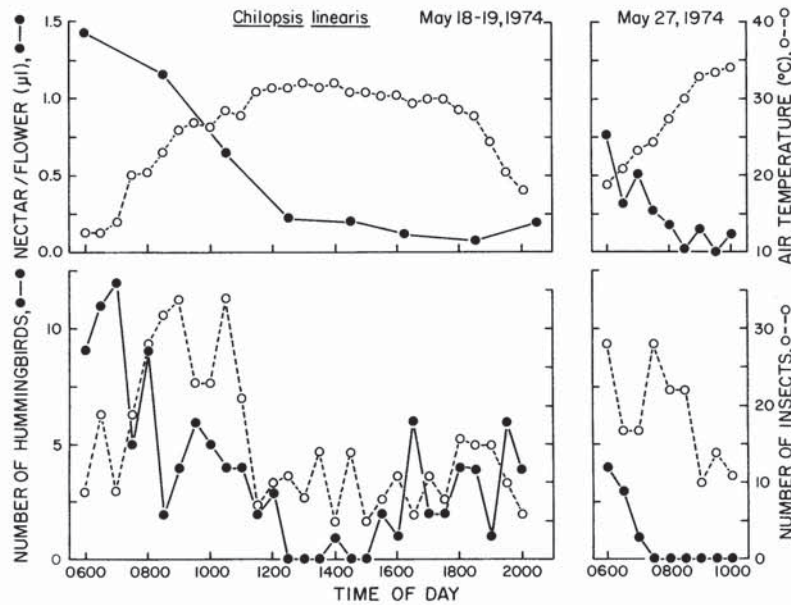


FIG. 5.—Daily patterns of nectar availability, ambient temperature, and animal visits for *Chilopsis linearis*. Plotted values for nectar quantities represent means of samples of more than 100 flowers, and total number of animal visits for the days indicated. Standard errors in nectar availability are always  $<0.24 \mu\text{l}$ . Note the large number of insects (bumblebee) visits early in the morning, the rapid decline in available nectar, and nectarivore foraging, and low frequency of hummingbird visits on 27 May, 8 days after the first measurements.

was uneconomical for them to exploit but still profitable for the insects (Figs. 4 and 5). Additional evidence for such competitive exclusion comes from comparison of patterns on 18 and 19 May with those on 27 May (Fig. 5). On the former days *C. linearis* was just coming into bloom and was being visited by many fewer insects (especially bumblebees) than on the latter date. In contrast to the earlier days, on 27 May by 0900 h nectar was almost completely depleted and insect foraging had already begun to decline; few hummingbirds were censused and none was seen foraging after 0700 h. Thus we conclude that in the absence of early morning and late afternoon temperatures sufficiently low to prevent most insect activity, bees were able to harvest nectar of *C. linearis* at rates which maintained low standing crops throughout most of the day and almost completely excluded hummingbirds.

*Body Size, Foraging Energetics and Temperature Regulation.*—Our data consistently indicate that ability to utilize the nectar of these flowers is mediated largely by foraging energetics and thermoregulatory capacity which in turn are related primarily to body size. We can assume that metabolic expenditure for foraging in these nectar-feeders is positively correlated with body size, because hummingbirds, bees, and probably syrphid flies maintain similarly high body temperatures while in flight and their metabolic rates appear to conform to the same allometric relationship (Heinrich, 1975a and included references). Thus, for example, a hovering hummingbird (body weight, 3 g) expends approximately 30 times as much energy as a flying bumblebee, and the actual disparity in foraging costs may be even greater because bumblebees alight on flowers whereas hummingbirds hover



continuously while foraging (Heinrich, 1975a, b; Lasiewski, 1973). Although hummingbirds may visit approximately four times as many flowers per unit time as bumblebees (Heinrich, 1975a; present study), in order for foraging to be economical (i.e., for the rate of energy intake to exceed the rate of expenditure) hummingbirds still require standing crops of nectar per flower at least five times higher than the minimum which can be exploited profitably by bumblebees. The same argument applies to comparisons between hummingbirds and other kinds of insects and between insects of different taxa.

The consequence of these foraging economics is that as levels of available nectar per flower decline, different kinds of nectarivores should be excluded in decreasing order of body size. Our data show this pattern both within and between the two classes (birds and insects) of nectar feeders. Thus as nectar standing crops of *R. pinetorum* declined toward midday, animals ceased or reduced foraging activity in the following order: Rivoli's Hummingbirds (body weight, 7 g), Broad-tailed Hummingbirds (3.5 g), bumblebees (0.4 g), hawkmoths and honeybees (0.2 and 0.1 g, respectively), syrphid flies (not weighed, but obviously smaller than honeybees). A similar pattern was observed at flowers of *C. linearis* except that bumblebees were able to forage on lower standing crops than honeybees (which are not native to the study area, but were introduced from Europe), apparently because in this flower species the last few drops of nectar are held in deep grooves (Whitham, 1977) where they are inaccessible to short-tongued honeybees (proboscis length, 3.5 mm) but not to long-tongued bumblebees (7.5 mm). When food supply is limited in this way, competition will occur whenever the foraging of two organisms overlaps in time and space so that food harvested by one is not available to the other. In this case, when nectar is equally available to all kinds of nectar-feeders, species with small body size and low foraging costs can increase in density, reduce standing crops, and exclude larger competitors. This is what happens at flowers of *C. linearis*, where bumblebees virtually exclude hummingbirds.

Similar exclusion of hummingbirds does not occur at flowers of *R. pinetorum* because low morning and evening temperatures provide the hummingbirds with a temporary refuge from insect competition at a time when nectar availability is high. The insects visiting these flowers apparently are heterothermic, and the capacity to thermoregulate and be active at low environmental temperatures is positively correlated with body size (Heinrich, 1975a and included references). Thus our data showed that bumblebees were consistently active at temperatures above 15°C, honeybees and hawkmoths only above 18°, and syrphid flies only above 22°. As a result of these patterns of temperature dependence, hummingbirds, whose activity was independent of temperature, had exclusive use of the high standing crops that accumulated as nectar was secreted in early morning and late afternoon. As temperatures increased toward midday, successively smaller insects foraged, reduced the standing crop, and excluded larger competitors.

GENERAL DISCUSSION.—Animals of several taxonomic groups actually or potentially compete for floral nectar. Nectar is an energetically rich, easily digestible food which is potentially attractive to many kinds of animals. Two primary factors, physical access and foraging economics, influence the



kinds of animals that can utilize the nectar of particular flowers, determine whether competition is likely to occur, and affect its outcome. Interference competition by aggressive defense of floral resources which is adaptive when the benefits of exclusive use outweigh the costs of defense, is common among hummingbirds (e.g. Gill, 1978; Kodric-Brown and Brown, 1978; and included references) and has been reported between hummingbirds and some large insects (e.g., Grant and Grant, 1968; Lyon, 1973; Primack and Howe, 1975). However, because of the large differences in body size and foraging energetics between hummingbirds and most insects, we would not expect interference to be a common mechanism of interaction between the two taxa. Exploitative competition by depletion of nectar availability probably occurs much more frequently than interference between distantly related kinds of nectarivores, but it is less well documented, probably because it depends primarily on the economics of foraging and hence is not so obvious as overt aggression. Schaffer et al. (1979) described patterns of exploitative competition and competitive exclusion among three species of bees of different body size that are somewhat similar in mechanisms and outcome to the interactions among hummingbirds and insects reported here.

Competition between such distantly related nectar-feeders as hummingbirds and insects may play a major role in the ecology and evolution of many plant-pollinator associations. If different kinds of animals visit the flowers and compete for the nectar of the same plant species, then natural selection resulting from differential pollination will tend to lead to evolution of floral characteristics, which, on the one hand, promote visitation by the best or most efficient pollinator and, on the other hand, discourage visitation by ineffective pollinators which deplete the nectar and make the flowers less attractive to good pollinators. Thus the odorless, red, tubular flowers of specialized hummingbird-pollinated plants have been interpreted as adaptations to prevent competing insects from exploiting their rich nectar rewards (Faegri and van der Pijl, 1971; Heinrich and Raven, 1972; Heinrich, 1975a). Our observations suggest that more subtle adaptations, such as the timing of nectar secretion, can also reduce competition from less desirable nectar-feeding insects and promote hummingbird pollination. Thus *Ribes pinetorum* has attained a high degree of hummingbird specificity without morphological specializations to exclude insects, because it secretes its nectar at times of day when temperatures are low and insects are inactive. It is tempting to speculate that the bimodal pattern of daily nectar secretion in *R. pinetorum* reflects the absence of morphological adaptations to exclude insects. More specialized temperate hummingbird-pollinated flowers, which possess tubular corollas that are effective in preventing most insects from taking their nectar, tend to show a single broad peak of nectar secretion lasting throughout the daytime (Brown and Kodric-Brown, 1979; see also Hainsworth and Wolf, 1972). Temporal patterns of nectar secretion similar to those observed in *R. pinetorum* which favor birds at the expense of insects may represent an important early stage in the evolution of specialized ornithophilous flowers. It may not be coincidental that high densities and diversities of both nectarivorous birds and bird-pollinated flowers often occur at intermediate and high elevations in tropical and subtropical lati-



tudes where morning and evening temperatures may be sufficiently low to inhibit the activity of many insects.

Within the last few years several ecologists have presented evidence that distantly related organisms often compete for food and other limited resources and have suggested that such interactions play major roles in the structure and function of natural communities (e.g., Brown and Davidson, 1977; Reichman, 1979 and included papers and references). Many of the important competitive interactions among distantly related animals in terrestrial ecosystems appear to occur between vertebrates and insects: for example, seed-eating rodents and ants (Brown and Davidson, 1977; Brown et al., 1979), leaf-eating ungulates and grasshoppers (Sinclair, 1975), and nectar-feeding birds and insects (Carpenter, 1979; Kodric-Brown and Brown, 1979; present study). Large differences between vertebrates and insects in body size, energy requirements, thermoregulatory capacity, and life history characteristics may enable these distantly related taxa simultaneously to compete strongly and to subdivide resources so as to coexist stably. It may not be coincidental, therefore, that we have observed particularly intense competition and competitive exclusion between some of the smallest vertebrates (hummingbirds) and large insects (e.g., bumblebees). This supports the suggestion made elsewhere (Brown et al., 1978) that the lower limits of body size in nectar-feeding birds and upper limit in nectar-feeding insects might be determined in part by competition for food between the two classes.

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