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EXPLOITATION OF NECTAR RESOURCES BY HUMMINGBIRDS, BEES (*BOMBUS*), AND *DIGLOSSA BARITULA* AND ITS ROLE IN THE EVOLUTION OF *PENSTEMON KUNTHII*

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The negative effect of illegitimate nectar foraging (i.e., obtaining nectar in a fashion other than that "intended" by the morphology of the blossom) on successful pollination is reflected in various generalizations concerning pollination syndromes. For example, hummingbird flowers have long narrow tubular flowers which to a greater or lesser degree discourage hymenopterous visitors. It is assumed, perhaps a priori, that illegitimate foraging will result in fewer legitimate visits and hence a lowered number of successful pollinations. Below, we present our observations and discuss the possibility that illegitimate visitation may have a positive rather than negative effect on the evolution of a bird flower. Specifically, our study is concerned with the possible effect the flower-piercer (*Diglossa baritula*) and bumblebees (*Bombus pulcher* and *B. trinomatus*) have had on the evolution of the hummingbird pollinated *Penstemon kunthii*.

Under certain circumstances both insects and birds forage for nectar in such a manner that pollination is not effected. Often this involves various physical mis-fittings between flower and visitor such that, even

though foraging is legitimate, pollination does not occur. Thus small bees and hummingbirds, for example, may visit flowers structurally adapted for pollination by large bees and obtain nectar, yet fail to contact the flowers' anthers or stigmas. Illegitimate foraging rarely if ever results in pollination. Bumblebees (*Bombus*) were early observed to perforate the nectar spurs of *Aquilegia* (Sprenzel 1793) and such observations have frequently been made since that time (Macior 1966, etc.). Hummingbirds also secure nectar in a similar fashion (Skutch 1954).

In some cases the perforators are followed by "gleaners," e.g., corolla perforations made by *Bombus* in *Aquilegia* are later utilized by *Apis* and *Lasloglossum* for securing nectar (Macior 1966). However, in such situations little attempt has been made to determine what effects, if any, the opportunity for additional nectar exploitation has had on populations of the secondary user, or on the floral evolution of the exploited plant species. In 1968, during the course of investigations of hummingbird ecology on Cerro San Felipe in the Sierra Madre de Oaxaca northeast of the city of Oaxaca, México, we observed a bird-bee interaction involving the Cinnamon-bellied or Slaty Flower-piercer (*Diglossa baritula*) and two species of bumblebees, *Bombus pulcher* and *Bombus trinomatus*. In this case the perforator was *Diglossa* and the "gleaners" were bumblebees. Our observations are recorded here in an attempt to shed light on some of these bird-bee population interactions, especially the possible effect usage by *Diglossa* may have had on the evolution of *P. kunthii*.

OBSERVATIONS

Starting in mid-June and continuing into October, *P. kunthii* flowers profusely in mountain meadows of the Sierra Madre de Oaxaca and is a primary nectar

TABLE 1. Diameter of thorax of *B. trinominatus* and *B. pulcher* compared to diameter of *P. kunthii* at entrance to floral tube.

	n	$\bar{x} \pm \text{SD}$ diam. (mm)
Queens	3	8.0 \pm 0.6
Workers	32	5.3 \pm 0.4
<i>P. kunthii</i>	50	5.9 \pm 0.2

source during this period for Blue-throated (*Lampornis clemenciae*), Rivoli (*Eugenes fulgens*), and White-eared (*Hylocharis leucotis*) Hummingbirds. The blue-throated and Rivoli are highly territorial, dominating, defending and largely controlling all significant stands of *P. kunthii* (Lyon, unpubl. notes). Though aggression between hummingbirds and *Diglossa* is apparent, the degree of mutual aggressiveness is considerably less than among hummingbirds and largely confined to threat displays of blue-throateds and Rivolis towards *Diglossa*. Similar hummingbird-*Diglossa* interactions have been reported by Wolf (1969) in Costa Rica. Thus, while hummingbird activities within *P. kunthii* stands are characterized by almost constant aggressiveness and continual territorial chases, individual *Diglossa* pairs have ready access to *P. kunthii* blossoms and are limited in their ranging only by their own strongly developed intraspecific territoriality.

Bombus pulcher and *B. trinominatus* were the two most abundant bumblebees in the meadows and appeared to depend largely on three species of *Penstemon* (*P. perfoliatus*, *P. gentianoides*, and *P. kunthii*) for their nectar needs, utilizing each species with about equal frequency. *P. perfoliatus* and *P. gentianoides* are adapted to bee pollination. The flowers are light and dark violet, respectively, with a rather short, large-diametered corolla. Though the bees utilized the ornithophilous *P. kunthii*, *Diglossa* was never observed to utilize either *P. perfoliatus* or *P. gentianoides*, possibly because *P. kunthii* proved more attractive, due to its apparent greater nectar production. Thus, while *Diglossa* appeared almost entirely dependent on *P. kunthii*, bumblebees exploited all three penstemons; *P. kunthii* blossoms, however, were usually exploited only if first perforated by *Diglossa*.

The functioning of the mandibular mechanism of *Diglossa* during the process of corolla perforation and feeding has been described by Skutch (1954). The strongly hooked and lightly serrated upper mandible grasps the upper side of the base of the blossom securely while the lower, pointed, slightly recurved lower mandible punctures the blossom on the side facing the feeding bird. Thus, two perforations actually result: one large, located on the dorsum of the blossom and extending on to the opposite side, the apparent result of pressure exerted by the upper mandible, and the "intended" puncture itself. The large dorsal puncture becomes an active feeding site for both species of *Bombus*.

Apparently perforation of *P. kunthii* blossoms by the bees is difficult and therefore rare. During a nine-week period of observation we observed only two bees, one of each species and both queens, that, failing to locate *Diglossa* punctures, actually perforated a flower. The entire operation, including puncture and feeding, required well over 20 sec. Smaller *Bombus* workers were never observed attempting puncture of *P. kunthii* blossoms.

Queens of both species were too large to enter the floral tube of *P. kunthii* (table 1), although they made

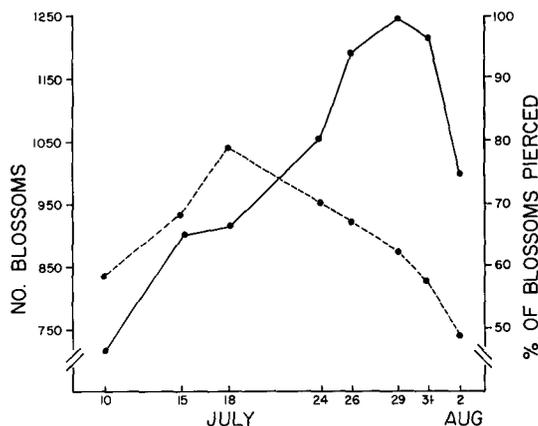


FIGURE 1. Rate of exploitation of *Penstemon kunthii* blossoms by *Diglossa baritula*, June–August 1968 in Cerro San Felipe, México. (Solid line = number of blossoms; broken line = % of blossoms pierced).

rare attempts to do so. Queens may have contacted the exerted anthers and pistil with their head during the more persistent and forceful entrance attempts, but the number of pollinations resulting from these attempts was probably very low.

On the other hand, workers of both species were able to enter the floral tube for various distances with varying degrees of success. It is likely that a few of the smaller workers were able to enter far enough to feed (table 1), but whether they were successful is unknown. The internal structural arrangement of anthers, pistil, and staminoide, however, in combination with the protected position of the nectary, would make it difficult for a bee to secure nectar even if it was sufficiently far into the tube to reach the nectary. In support of this interpretation we observed that of those workers which successfully entered the floral tube in a legitimate attempt to obtain nectar, a large proportion of them, upon retreating from the tube, proceeded to search on the same blossom for *Diglossa* punctures, indicating that these had not been able to secure nectar from their position within the corolla. Workers able to enter the floral tube partially or wholly, however, appeared able to bring about pollination; contact between bees and stamens and pistil sometimes occurred in the process of entering and leaving the blossom.

Both queens and workers usually alighted at the corolla opening, crawled up over the top or along the side of the blossom, searching for *Diglossa* perforations; not finding any, they then flew to another blossom, usually on the same plant. Only rarely did a bee fly directly to the base of the corolla and search for a puncture, and seldom did one attempt to enter the floral tube. During one 5-hr observation period only 67 (3.4 per cent) attempted entry to the floral tube, while 1943 feedings occurred from *Diglossa* punctures. Of the 67 entering, 33 (1.7 per cent) were judged to have remained within the tube long enough to have actually obtained nectar.

During late June, July, August, and probably September and October as well, heavy use was made of the *P. kunthii* nectar resource by *Diglossa*. Data collected from 4 \times 6 ft randomly selected quadrats scattered throughout *P. kunthii* stands in several small meadows June–August 1968 indicated a usage of *P. kunthii* by *Diglossa* ranging from 50 per cent to over 80 per cent (fig. 1). Since little perforation of *P.*

kunthii blossoms by *Bombus* queens occurred and workers were unable to secure nectar while positioned within the floral tube, probably as much as 10–20 per cent more nectar was available to *Bombus pulcher* and *Bombus trinominatus* populations during this period due to the feeding activity of *Diglossa*.

DISCUSSION AND CONCLUSIONS

Grant and Grant (1968) have proposed an explanation for the reciprocal evolution of hummingbirds and the plants upon which they feed. According to this interpretation most hummingbird-pollinated flowers, especially temperate species, have evolved from bee flowers (Grant 1961; Grant and Grant 1965). The process involves an incipient stage during which a primitive hummingbird or progenitor already "preadapted" to feed on a particular bee flower (in the sense of securing insects within the corolla, or nectar, or both), causes at first occasional but then increasingly frequent pollinations. This stage is followed by a resultant eventual elongation (and presumably a decrease in diameter) of the floral tube and thus an increasing exclusiveness for bird pollination. The following discussion assumes that the evolutionary history of *P. kunthii* follows the model, i.e., that this Mexican highland species has evolved from a relatively unspecialized bee-pollinated form to its present condition as a hummingbird-pollinated species with a high degree of exclusiveness.

More specifically, the *Diglossa-Bombus* exploitation could aid in the selection of *P. kunthii* as a bird flower, as indicated in the following chronological schema.

1. Initial increase in nectar production is favored by hummingbird visitation concomitant with beginnings of corolla tube elongation due to increasing pollination by hummingbirds compared with bees (i.e., birds visit those plants with the greatest nectar supply).
2. Nectar production becomes sufficient to encourage exploitation by *Diglossa*.
3. Perforations attract *Bombus* spp., diminishing bee pollination and thus decreasing or removing bees as a selective force.
4. More rapid evolution of tube elongation and nectar production occurs, caused by a self-reinforcing feedback system in which greater nectar production encourages an increasing exploitation by *Diglossa*, which further discourages bee pollination relative to bird pollination, enhancing further increase in exclusiveness and nectar production.

The stage in the evolution of *P. kunthii* at which *Diglossa* exploitation began is unknown and would

depend on many factors. That hummingbirds and the ancestor of *P. kunthii* co-existed may be assumed; otherwise its adaptation to hummingbird pollination would make little sense. Thus it is possible that *P. kunthii* could have undergone much of its development under selective pressure from hummingbirds; still, it is clear that *Diglossa baritula* has co-existed with hummingbirds throughout New World montane habitats for some time and therefore an earlier and more important role in the evolution of *P. kunthii* would not be unexpected. This is not to suggest that exploitation late in the evolutionary development of *P. kunthii* would be insignificant. Even at present, given the potential counter-selection pressures on *P. kunthii* from bees, the presence of *Diglossa* perforations undoubtedly precludes a certain amount of bee pollination which would probably otherwise occur, helping to maintain the selection pressures on *P. kunthii* which favor continued floral specialization for hummingbird pollination.

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AN EARLY PLEISTOCENE EAGLE FROM NEBRASKA

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In the collections of the University of Nebraska State Museum (U.N.S.M.) are a number of fossil birds from the Early Pleistocene Broadwater and Lisco Local Faunas. Included with this collection is a new species of eagle from U.N.S.M. Coll. Loc. Gd-12. Other animals from this locality are *Megalonyx*, *Geomys*, *Procastoroides*, *Canis*, *Borophagus*, *Ischyrosmilus*, *Mammut* (*Pliomastodon*), *Plesippus*, and

Gigantocamelus fricki Barbour and Schultz (holotype). An account of the stratigraphy and fauna of the Broadwater and Lisco localities is given by Schultz and Stout (1948).

The eagle is represented by the distal end of a tarsometatarsus and most of the shaft. The proximal end of a femur and the badly crushed distal end of a tibiotarsus was found associated with the tarsometatarsus and may belong to the same bird. The tarsometatarsus is too large and massive to be satisfactorily compared with any of the North American Buteoninae, which also have the tarsometatarsus tapering more abruptly distally. It resembles the tarsometatarsus of *Aquila chrysaetos* very closely, but differs from that form in being more elongate and in having the papilla for the tibialis anticus more proximally situated. It