signed to a third-year pharmacy student working during the summer in COSTEP (Commissioned Officer Student Training and Extern Program of the Public Health Service). She spent 1 to 2 hours a day for 3 weeks learning the system and encoding compounds. By the time she finished, she was processing more than 50 compounds an hour. Structures were obtained for about 90 percent of the compounds; "reject" messages were received for the remainder, since they were too complex for the current program and had to be manually encoded.

Currently, the WLN-composing program is being expanded to cover more complex molecular structures; it is written in Fortran IV and is being developed on a time-sharing computer, the PDP-10. While at present this method of encoding might not be more economical than manual encoding, by which one can also handle about 50 compounds an hour, there is the assurance that once such a computer program is debugged, only correct notation will be produced.

DEENA A. KONIVER
Division of Computer Research and Technology, National Institutes of Health, Bethesda, Maryland 20014

WILLIAM J. WISWESSER
Vegetation Control Division, Edgewood Arsenal Chemical Laboratory, Fort Detrick, Frederick, Maryland 21701

EARL USDIN
Psychopharmacology Research Branch, National Institute of Mental Health, Rockville, Maryland 20852

References and Notes

1. E. J. Corey and W. T. Wipke, *Science* **166**, 178 (1969).
2. W. J. Wiswesser, *J. Chem. Doc.* **8**, 146 (1968); A. Gelberg, *Encyclopedia of Library and Information Science* (Dekker, New York, 1970), vol. 4, p. 510.
3. E. G. Smith, *The Wiswesser Line-Formula Chemical Notation* (McGraw-Hill, New York, 1968).
4. J. E. Davis and L. E. Straka, "Automatic coding via a cathode-ray tube," paper presented at the 158th national meeting of the American Chemical Society, New York, September 1969; L. H. Campey, E. Hyde, A. R. Jackson, *Chem. Brit.* **6**, 427 (1970).
5. E. Usdin and D. H. Efron, *Psychotropic Drugs and Related Compounds* (Government Printing Office, Washington, D.C., ed. 2, in press).
6. M. F. Lynch, *J. Chem. Doc.* **8**, 130 (1968).
7. J. M. Mullen, *ibid.* **7**, 88 (1967).
8. C. M. Bowman, F. A. Landee, N. W. Lee, M. H. Reslock, *ibid.* **8**, 133 (1968).
9. C. D. Farrell, A. R. Chauvenet, D. A. Koniver, *ibid.* **11**, 52 (1971); S. R. Heller and D. A. Koniver, *ibid.* **12**, 55 (1972).
10. R. J. Feldmann, S. R. Heller, K. P. Shapiro, R. S. Heller, *ibid.* **12**, 41 (1972).
11. Chemical Abstracts Service, *Desk-top Analysis Tool for the Common Data Base* (American Chemical Society, Columbus, Ohio, 1968). This is obtainable from the National Technical Information Service, U.S. Department of Commerce, Springfield, Virginia, accession No. PB 179 900.

4 February 1972; revised 24 April 1972

Pollinators in High-Elevation Ecosystems: Relative Effectiveness of Birds and Bees

Abstract. *During the rainy season bird-flowered plants at high elevations are more effectively pollinated than closely related bee-flowered plants. With good flight conditions the effectiveness of birds and bees is essentially equal. Thus, the higher incidence of bird flowers at higher elevations is attributable in part to the competitive advantage gained through greater reproductive success.*

Observations in mountain Mexico (*1*) suggest that plants with hummingbird flowers are more numerous in terms of both species and numbers at elevations above 2300 m than in mid-elevational regions (1000 to 2300 m). This observation is in part substantiated by data in Blake (*2*), where nearly twice as many species of hummingbirds are reported in high-elevation communities as in mid-elevation communities. It is doubtful that the correlation is fortuitous.

This report is addressed to three questions: (i) Why is the frequency of bird-flowered plants greater at higher elevations? (ii) Are birds or bees more efficient pollinators? (iii) Can a conceptual model be constructed for predicting the relative abundance of bird-flowered plants in particular habitats?

Two areas were selected for study because they included sites which, on the basis of daily cloud formation, were classed as having good, medium, or poor flight conditions for bees. This judgment was made prior to the collection of data. In Chiapas, the study area, about 14 km southeast of San Cristóbal de las Casas, included a ridge top (altitude about 2750 m), a ridge side (2350 to 2600 m), and the adjacent valley (about 2250 m). These sites were classified as poor, medium, and good, respectively (Table 1). From 30 August to 3 September 1971 the ridge top was subject to daily rains and cloudiness from before dawn to as late as 1100 hours, which limited flight times to 0 to 3½ hours a day. These conditions spread to the sides of the ridge and the valley floor later in the day. In the state of Mexico data were collected at Tlamacas (below Popocatépetl), on the road to Tlamacas, and southwest of Toluca. At Tlamacas good flight conditions for bees extended into the late afternoon, as Tlamacas remained above the clouds most of the day. Here, poor flight conditions occurred earlier at lower elevations.

In both Chiapas and Mexico the fecundity [percentage of pollination times percentage of seed set (*3*)] of bee-flowered plants is lower in areas with poor flight conditions, whereas the fecundity or pollination, or both, of bird-flowered plants is relatively high (Table 1). The same trend is noted with respect to pollination and seed set in various mints (Labiatae) collected in Oaxaca, Chiapas, Mexico, and Durango (Table 2).

Table 1. Pollination, seed set, and fecundity in bee and bird flowers from about 12 km southeast of San Crisóbal de las Casas, Chiapas, and from Tlamacas and southwest of Toluca, Mexico. Localities were selected for good (G), medium (M), and poor (P) flight conditions for bees.

Species	Flower type	Flowers (*N*)	Pollination (%)	Seed set (%)	Fecundity (%)	Flight condition
		Chiapas				
Salvia cacaliaefolia	Bee	53	77	60	45	P
Salvia lavanduloides	Bee	205	93	66	61	M
Lepechinia schiedeana	Bee	54	96	86	83	G
Stachys coccinea	Bird	130	89	98	87	M
Salvia chiapensis	Bird	200	88	81	71	M
		Tlamacas, altitude 3940 to 4000 m				
Lupinus montanus	Bee	2106	94	92	87	G
Penstemon gentianoides	Bee	514	91			G
Stachys eriantha	Bee	150	95	90	86	G
		Road to Tlamacas, altitude 3330 m				
Lupinus montanus	Bee	1553	88	81	71	M
Penstemon gentianoides	Bee	408	95			M
		Ruta 130, southwest of Toluca, altitude 3030 m				
Lupinus cf. *persistens*	Bee	561	66	78	52	P
Penstemon kunthii	Bird	515	93			P
Salvia cardinalis	Bird	120	98	72	71	P

Table 2. Pollination, seed set, and fecundity in labiates from Chiapas, Oaxaca, Mexico, and Durango. Included are species of *Lepechinia*, *Salvia*, *Satureja*, and *Stachys*.

Flower type	Elevation	Populations (N)	Flowers (N)	Pollination (%)	Seed set (%)	Fecundity (%)
Bee	High	5	508	83	58	48
	Middle	4	424	93	91	85
Bird	High	8	766	92	87	80
	Middle	1	114	91	76	69

Pollination and particularly seed set are low (the latter significantly so) in high-elevation bee flowers compared to mid-elevation bee flowers and high-elevation bird flowers.

A comparison of the fecundity of high-elevation bird flowers and mid-elevation bee flowers suggests that bees and birds are essentially equal as pollinators, under good conditions. Although bee-flowered Labiatae have a slightly greater fecundity than the bird-flowered species (Table 2), the reverse is true in *Penstemon*. Three populations of *P. kunthii* G. Don (one each from Durango, Mexico, and Oaxaca) had pollination percentages of 88, 93, and 97, respectively, and three populations of *P. barbatus* Nutt. from Durango had pollination percentages of 91, 91, and 95. The average pollination percentage for these bird flowers was 92.9, compared to 92.6 for two populations of the bee-pollinated *P. gentianoides* (HBK) Poiret (Table 1). Further, the seed-set percentages in one population each of *P. kunthii* and *P. gentianoides* were essentially the same, 59.0 ± 9.7 and 57.8 ± 13.7, respectively.

The data in Table 2 also suggest that pollination is not necessarily a good measure of fecundity. This is shown by a comparison of three bee-flowered populations, one each from sites with poor, medium, and good flight conditions. A population of *Salvia* from Durango had 94 percent pollination and 43 percent seed set. Flowers from this population set 0, 1, 2, 3, and 4 seeds in the proportions 6, 44, 35, 13, and 3, respectively. The proportions for *S. lavanduloides* Kunth (93 percent pollination and 66 percent seed set) and *Stachys eriantha* Benth. (95 percent pollination and 90 percent seed set) were 7, 18, 24, 27, and 23 and 5, 2, 7, 20, and 66, respectively. Since the percentage of pollination is essentially constant in the three cases, the difference in seed set must be due to differences in the numbers of visits made to the flowers. Thus, in localities subject to prolonged daily cloudiness and rain the bees may complete a few foraging trips before poor flight conditions prevail, but the number of trips is not sufficient to assure maximum seed set. The poor flight conditions force the bees to forage elsewhere or to remain in their nests. In contrast, hummingbirds work throughout the day regardless of clouds or rain. As a consequence, bird flowers are visited often enough to assure good seed set.

A further question can be asked. Do bird-flowered plants have to pay for their higher fecundity? Data from *Salvia* and *Stachys* (Labiatae) suggest that higher fecundity is purchased by an increased energy expenditure in terms of increased pollen production. *Salvia chiapensis* Fernald and *S. cardinalis* Kunth (bird flowers) produce about 12,200 and 17,000 pollen grains per ovule, respectively, whereas two bee-flowered species have ratios of pollen to ovules (*P/O*) of 5800/1. Similarly, *Stachys coccinea* Jacq. has a *P/O* of 14,500/1 and *St. eriantha* a *P/O* of 3500/1. In both genera the bird flowers that were studied produce significantly more pollen than the bee flowers. However, *Satureja mexicana* (Benth.) Briq., a typical bird flower, produces much less pollen (*P/O* is 1685/1) than do the bee flowers in *Salvia* and *Stachys*. That bird-flowered plants need not produce significantly more pollen than bee-flowered plants is also shown by a comparison of *Penstemon kunthii* and *P. gentianoides*, which have similar *P/O* ratios.

Several conclusions may be drawn from the observations. First, there is little or no difference in effectiveness between bees and birds as pollinators, provided that flight conditions are favorable. Second, birds are more effective pollinators at high elevations during the rainy season because they remain active during cloudy and rainy weather, whereas bees are relatively poor pollinators under such conditions. I suggest that the greater number of bird-flowered plants at high elevations is due, in part, to their greater reproductive success during the rainy season. Third, in some groups, such as *Salvia*, bird-flowered plants may achieve their higher fecundity at the cost of greater pollen production.

Further, as a model for making predictions for other plant groups and perhaps other geographic localities, I suggest that the relative number of bird-flowered plants will be greater in habitats and at seasons with limited bee activity. Conversely, the relative number of bee-flowered plants will be greater in habitats and at seasons favorable to bee activity.

A comparison of two closely related taxa in Iridaceae indicates that the model has predictive power. In *Tigridia* subgenus *Tigridia* (bee-flowered), seven of eight species flower at the beginning of the rainy season, a period of sporadic rains, and six of eight species grow at mid-elevations. Only a single species grows at high elevations and flowers during the middle of the rainy season (*4*). In contrast, all four species of *Rigidella* (bird-flowered) grow at high elevations. The flowering seasons of two species extend well into the rainy season, and a third species flowers only during the rainy season. Thus, as predicted, the bee-flowered *Tigridia* occur at mid-elevations or flower early in the rainy season, or both, and avoid poor flight conditions, whereas the bird-flowered *Rigidella* occur at high elevations and flower during the rainy season.

ROBERT W. CRUDEN

Botany Department, University of Iowa, Iowa City 52240

References and Notes

1. Herbert G. Baker first called my attention to this phenomenon, which he had observed in the mountains of Durango in January 1966. Subsequently, we made similar observations in Durango in June 1967, and I have observed the same phenomenon elsewhere in Mexico (1968 to 1971). Our unpublished data show that a minimum of 12 to 14 bird-flowered species are in bloom at any particular time at higher elevations. Rarely are more than three or four bird-flowered species observed over a similar transect at mid-elevations.
2. E. R. Blake, *Birds of Mexico* (Univ. of Chicago Press, Chicago, 1959).
3. Seed set is the percent of ovules that develop into seeds.
4. Excluded from this discussion is *Tigridia pavonia*, which also flowers at high elevations during the rainy season, but is self-pollinating.
5. Fieldwork supported in part by a grant from the Associates in Tropical Biogeography, University of California, Berkeley, to Herbert G. Baker and R.W.C. I thank Herbert G. Baker, Hugh Dingle, David L. Lyon, and William Platt for reading the manuscript. Robert Stabenow aided with the fieldwork.

16 March 1972; revised 21 April 1972