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POLLINATOR PREFERENCES FOR YELLOW, ORANGE, AND RED FLOWERS OF *MIMULUS VERBENACEUS* AND *M. CARDINALIS*

Robert K. Vickery, Jr.[1]

ABSTRACT.—Red, orange, and yellow morphs of *Mimulus verbenaceus* and *M. cardinalis* were field tested for pollinator preferences. The species are closely similar except that *M. verbenaceus* flowers have partially reflexed corolla lobes, whereas *M. cardinalis* flowers have fully reflexed corolla lobes. On the basis of over 6000 bumblebee and hummingbird visits, highly significant ($p < .001$) patterns emerged. Yellow, which is the mutant color morph in both species and is determined by a single pair of genes, was strongly preferred by bumblebees and strongly eskewed by hummingbirds in both species. Orange and, to a lesser extent, red were strongly preferred by hummingbirds but eskewed by bumblebees in both species. Thus, strong, but partial, reproductive isolation was observed between the yellow mutants and the orange- to red-flowered populations from which they were derived. Color—yellow versus orange and red—appeared more important than shape—partially reflexed versus fully reflexed corolla lobes—in determining the preferences of the guild of pollinators in this particular test environment for *Mimulus verbenaceus* and *M. cardinalis*.

Key words: Mimulus, *speciation, flower colors, pollinator preferences, bumblebees, hummingbirds.*

How much of a change in flower color and/or shape is enough to lead to a change in pollinators and hence to reproductive isolation and potentially to speciation? The flower color and shape morphs of *Mimulus verbenaceus* Greene and *M. cardinalis* Douglas provide an excellent system for addressing this intriguing question.

MATERIALS

Mimulus verbenaceus and *M. cardinalis* are typically bright red flowered and hummingbird pollinated. However, yellow-flowered morphs occur in *M. verbenaceus*, e.g., in a population at Vassey's Paradise, Grand Canyon, Arizona, and in *M. cardinalis* populations, e.g., on Cedros Island, Baja California, Mexico, and in the Siskyou Mountains, Oregon. My experimental hybridizations show that yellow is due to a single pair of recessive genes that limit the floral anthocyanins to small dots in the corolla throat. Intermediate, orange-flowered forms are known in *M. verbenaceus*, specifically the population at Yecora, Sonora, Mexico. And, an intermediate, orange-flowered form of *M. cardinalis* was obtained by repeated cycles of selection. In both cases orange is due to a single pair of quantitative genes that reduce the amount of anthocyanin pigments in the corolla lobes. Thus, parallel series of red, orange, and yellow color forms are available for both *M. verbenaceus* and *M. cardinalis* (Table 1).

Mimulus verbenaceus and *M. cardinalis* are similar, closely related species in section *Erythranthe* (Grant 1924); however, their flowers differ in shape. Those of *M. verbenaceus* have only the upper pair of corolla lobes sharply reflexed, giving the flowers a partially tubular aspect. The side pair of lobes and the labellum curve gently forward forming a bee landing platform. Flowers of *M. cardinalis* have both the upper and side corolla lobes sharply reflexed, giving the flowers a fully tubular shape. The labellum is thrust forward and is folded on itself forming a ridge instead of a landing platform. Shapes of the flowers of both species would seem to invite hummingbirds. Flowers of *M. verbenaceus* but not those of *M. cardinalis* would appear adapted for bees as well. However, flowers of all three color morphs of both species showed no reflectance patterns in the ultraviolet, that is, no putative bee nectar guides. Thus, flower shapes of *M. verbenaceus* and *M. cardinalis* are similar in some respects but differ in others of potential significance to pollinators.

[1]Department of Biology, University of Utah, Salt Lake City, Utah 84112.

PLAN

The effect of flower color and flower shape on pollinator preferences will be addressed stepwise. First, pollinator preferences for color—red, orange, and yellow—will be ascertained for *M. verbenaceus* plants only, holding flower shape constant. Second, red-, orange-, and yellow-flowered *M. cardinalis* plants will be added to the experiment. Are pollinator preferences for red, orange, and yellow flowers of *M. cardinalis* the same as for those of the *M. verbenaceus* series? Note that the pigments are identical (Vickery 1978). Or, does the difference in corolla shape between the two species lead to a difference in pollinator preferences?

METHODS

Seeds for each of the six populations of the study (Table 1) were collected in the wild or harvested from transplants brought into the greenhouse except those of orange *M. cardinalis*, which were obtained by selection. A large population of red *M. cardinalis* from Cedros Island was grown and the most orange-red flowered plant self-pollinated. Its progeny included several orange-flowered plants. Progeny of these plants were grown and found to breed true for orange and were used as the source of seeds for the orange *M. cardinalis* morph.

Seeds of the six populations were sown in early April 1988 in the University of Utah greenhouse, following which seedlings were transplanted into 4" plastic pots and grown to flowering. Pots were placed in plastic trays to facilitate bottom-watering, plants being randomly arranged as to flower color.

When plants began flowering, they were moved outdoors to test pollinator preferences. Instead of using Red Butte Canyon Natural Research Area as before (Vickery 1990), with its relative paucity of pollinators, I scattered the plants on a lawn adjacent to native gambel oak clumps at the mouth of Parley's Canyon of the Wasatch Mountains in an area rich in pollinators. Some 50 to 100 plants of each color morph of *M. verbenaceus* made up the artificial population of the first part of the experiment. Some 50 to 100 plants of red and of orange *M. cardinalis* plus 20 plants of yellow *M. cardinalis* (all that were available) were added to the *M. verbenaceus* plants for the second part of the experiment.

TABLE 1. Origin of populations studied.

Mimulus verbenaceus Greene
Vassey's Paradise, Grand Canyon, Arizona, USA, elev. ~650 m
  Red morph = culture number 14,088
  Yellow morph = culture number 14,089
Yecora, Sonora, Mexico, elev. ~1,550 m
  Orange = culture number 13,256

Mimulus cardinalis Douglas
Isla Cedros, Baja California, Mexico, elev. ~100 m
  Red morph = culture number 13,106
  Yellow morph = culture number 13,250
  Orange = culture number 13,249
   (obtained by selection from the red morph)

Pollinator visits to the flowers were observed and recorded for an average of 1½ hours per observation period for 15 periods for each of the two parts of the experiment (Tables 2, 3). Time of day of the observations was varied to be sure of noting all the different kinds of visitors. To count as a visit, a hummingbird had to thrust its beak into a flower. A bee had to land on the flower and crawl into the flower far enough to brush the stigma and anthers. A fly, butterfly, etc., had to walk on the reproductive structures. The numbers of flowers rather than plants of each color of each species were recorded for each observation period.

For analysis of visits, chi-square tests were run for each observation period for each part of the experiment. The null hypothesis was that hummingbirds or bumblebees (very few flies, butterflies, etc., visited the flowers and were not listed) would visit the three colors of flowers of *M. verbenaceus* in the first part of the experiment and the three colors of *M. verbenaceus* and *M. cardinalis* in the second part of the experiment in proportion to the numbers of those flowers in the experimental population (Tables 2, 3). If the overall chi-square value for a period of, for example, bee visits to *M. verbenaceus* or hummingbird visits to *M. cardinalis* indicated a significant deviation from expected values, then the frequency of visits to each color was inspected. Those high or low enough that their term in the chi-square equation was large enough by itself to produce a significant deviation at the 5% level were considered to be significant (Tables 2, 3).

TABLE 2. Pollinator preferences for red, orange, or yellow flowers of *Mimulus verbenaceus* in 1988.

	Numbers of flowers			Bumblebee visits				Hummingbird visits			
Month:day:time	Red	Orange	Yellow	Red	Orange	Yellow	*P*	Red	Orange	Yellow	*P*
7:26:1630	48	56	70	28↓[a]	523↑	198↓	<.001	0	3	0	<.100
7:29:0745	56	91	74	30	50	58	<.200	0	81↑	29	<.010
7:30:0710	46	79	114	24	67	67	<.010	55↑	66	70	<.010
8:02:1640	85	77	74	3↓	88↑	53	<.001	27	49	27	<.010
8:03:0630	92	101	133	53	99↑	81	<.001	33	79↑	36↓	<.001
8:03:1540	120	117	172	31↓	74	209↑	<.001	100↓	241↑	183	<.001
8:04:0640	86	73	178	0↓	5	52↑	<.001	83	145↑	170	<.001
8:05:0715	120	100	169	33↓	71	125	<.001	9↓	77↑	28↓	<.001
8:05:1645	126	104	174	12↓	22↓	126↑	<.001	36↓	149↑	92↓	<.001
8:05:1830	126	104	174	5↓	4↓	73↑	<.001	75	150↑	82↓	<.001
8:06:0840	126	88	151	74↓	159↑	291↑	<.001	66	100↑	26↓	<.001
8:06:1445	126	98	150	6↓	6↓	60↑	<.001	49	94↑	24↓	<.001
8:06:1810	130	117	142	50	105	257↑	<.001	31	48↑	1↓	<.001
8:07:1515	130	119	142	0↓	4↓	68↑	<.001	52	125↑	5↓	<.001
8:08:0725	118	91	124	12↓	32	131↑	<.001	32	67↑	5↓	<.001

[a]↑ or ↓ = significantly high or low; see text.

TABLE 3. Pollinator preferences for red, orange, or yellow flowers of *M. verbenaceus* and *M. cardinalis* in 1988.

	Number of flowers			Bumblebee visits				Hummingbird visits			
Month:day:time	Red	Orange	Yellow	Red	Orange	Yellow	*P*	Red	Orange	Yellow	*P*
				Mimulus verbenaceus							
8:08:1600	117	92	132	17↓[a]	29	62↑	<.001	23	40↑	3↓	<.001
8:09:0750	115	73	116	16↓	36	131↑	<.001	70	70↑	18↓	<.001
8:09:1705	115	73	116	2↓	21↓	124↑	<.001	171	167↑	135↓	<.001
8:10:0815	145	90	143	84↓	129↑	190↑	<.001	13	10	3	<.001
8:10:1640	145	90	143	13↓	56	202↑	<.001	40↓	80↑	38↓	<.001
8:11:0810	175	83	177	84↓	106↑	237↑	<.001	60	50↑	0↓	<.001
8:12:0805	200	111	198	96↓	97	160	<.001	196	166↑	99↓	<.001
8:12:1700	200	111	198	5↓	9↓	120↑	<.001	168	147↑	163	<.001
8:13:0855	180	83	175	54↓	66	172↑	<.001	115	63↑	56↓	<.001
8:13:1800	180	87	175	3↓	4↓	160↑	<.001	44	31↑	2↓	<.001
8:14:0815	212	81	165	27↓	37	162↑	<.001	71	64↑	24↓	<.001
8:15:0740	184	94	183	39↓	36	167↑	<.001	54	37	38	<.010
8:15:1700	184	94	183	2↓	3	50↑	<.001	7	2	2	<.300
8:16:0830	206	112	153	14↓	8↓	174↑	<.001	21	30↑	0↓	<.001
8:17:0630	214	86	177	3↓	2↓	128↑	<.001	66	72↑	26↓	<.001
				Mimulus cardinalis							
8:08:1600	79	47	61	36↓	59	89↑	<.001	28	25	1↓	<.001
8:09:0750	69	45	32	21↓	37	34↑	<.001	61	36	0↓	<.001
8:09:1705	69	45	32	18	8	22↑	<.001	137	117↑	24↓	<.001
8:10:0815	61	39	23	49	59	26	<.010	4	6	0	<.100
8:10:1640	61	39	23	48	10↓	48↑	<.001	81	53	12↓	<.010
8:11:0810	61	55	12	27↓	62	49↑	<.001	34	20	0	<.020
8:12:0805	65	51	18	33	26	34↑	<.001	63	95↑	13	<.001
8:12:1700	65	51	18	18	8	10	<.050	130	88	21	<.100
8:13:0855	64	42	14	35	40	17	<.010	59	41	0↓	<.010
8:13:1800	89	81	14	28	15	16↑	<.001	91	92	14	<.300
8:14:0815	83	69	15	39	24	19↑	<.001	77	52	3↓	<.020
8:15:0740	53	71	15	20	33	26↑	<.001	55	58	0↓	<.001
8:15:1700	53	71	15	13	4	6↑	<.010	11	24	0	<.010
8:16:0830	79	78	21	18↓	21	34	<.001	34	74↑	0↓	<.001
8:17:0630	89	79	18	19↓	47	12	<.001	20↓	115↑	4↓	<.001

[a]↑ or ↓ = significantly high or low; see text.