We can only speculate as to whether nest-building, like copulation and territorial behavior, has a permanent substratum. The case already mentioned where females I and III showed a cumulative interest in small sections of their mate's territory in which the nest-sites were finally chosen, suggests the possibility. In 1934 the breeding area of male I included the lawns and shrubbery between the Life Sciences Building and California Hall, as well as the narrow lawns on the south sides of both buildings. During fall and winter each female was seen occasionally in almost every part of this area, but female I was found more often in the northeastern part, by the flag-pole in front of California Hall, while female III was seen more frequently in the southeast part, by the lawn south and southwest of California Hall. The broad lawn in front of the Life Sciences Building which comprised the west half of the territory was only rarely visited by either female. A certain amount of restriction within the male's area was apparent, then, even in winter. This became more marked from early February on, when I noticed that female I stayed almost entirely within an area surrounding the flag-pole about 30 yards square, near the center of which stood the small thuja where she had built a nest the year before. Female III, on the other hand, stayed in an adjacent part, the southern corner of the lawn south of California Hall. At the edge of this lawn was a clump of raphiolepis bushes and a small tree in which female III frequently perched. In mid-March, when female I started to build her nest, she chose the thuja as the nest-site. Female III started to build in late March, and put her nest in the clump of raphiolepis bushes.

I do not mean to imply that as early as February 1, the birds had begun to take interest in possible nesting places conceived as such. I simply want to point out that from the beginning there was substantial segregation of the two females to subdivisions, that with the advance of the season each female restricted her activities more and more, and that later when she started to build her nest, she chose a tree or bush within this section.

I have described a few outstanding elements of breeding behavior. There are undoubtedly many others, shading back no one can say how far, emerging or intensifying no one can say how gradually or in response to how distant threshold conditions. A great deal has been discovered or rediscovered and emphasized in the last twenty years in the field of behavior, yet in minute and coherent observation we are merely beginning. Adequate observation, unfortunately, demands an almost prohibitive amount of time, not only in numbers of hours but in numbers of seasons and years, with small assurance of significant results.

Museum of Vertebrate Zoology, Berkeley, California, April 4, 1936.

STEPS IN THE DEVELOPMENT OF THE BIRD-FLOWER

By A. L. PICKENS

Again red leads, with purple as a lagging second, in this the second list of bird-visited flowers (see Condor, vol. 33, 1931, pp. 23-28). Pink, orange, blue, yellow, white, green and maroon follow in descending order of avian choice as indicated by this and preceding investigations. Figworts, mints, peas, lilies, and composites are in order the five favorite families of flowers as so far indicated.

While assembling the new list of avian flowers, over seven hundred associations between flowers and insects have been recorded. Maroon or brownish flowers show the highest proportion of associations with insects of primitive or unspecialized mouth-

parts; then come white, green, yellow, pink, blue, orange, purple and red in order of association with insects of increasing complexity or specialization of mouth-parts. This in general reverses the order of avian choice of color, and is very significant, since red has not always been regarded as the highest advance in floral color, although it is the complement of the ancestral green. The natural relation of red, purple, blue, green, yellow, orange, and the maroon or brown they combine to form is thus shown graphically by the initials of each:

R
O P
M
Y B
G

J. M. Breazeale in "Color Schemes of Cacti" (University of Arizona, 1930, p. 5) says of the law of color, "The law did not originate with the artist, but with Nature, and it became a law on account of its origin." Apparently, then, flowers in evolving should show some relation, in the color evolution, to this color-wheel. Green, it would seem, should first evolve into yellow, maroon and blue. Even without insect aid the wind-pollinated pines and junipers show yellow and brown in the proto-flowers, and the yellow of pollen-masses may well have been the lure to a food supply for the first pollinating insects, say beetles. Thus blue, the other color component of green, must have been handicapped, not only by its lack of contrast with the ancestral green, but by the early getaway made by the showy, though usual, color of pollen. If primitive eyes see only in shades of gray, certain whites might have brightness survival-value over the duller primitive yellows. Again, increase of red in the green would lead to maroon or brown shades. Perhaps the hemipterous bugs would be drawn to these tender shoots that produced flowers since they were punctured more readily for sap-sucking. Flies might well follow for the excess leakage, and then wasps, first to catch the congregating insects and later to partake of the oozing fluids. Thus perhaps nectar evolved. Maroon, so nearly like torn flesh in color, would appeal to flesh-flies, especially as corresponding odors were developed.

The recorded seven hundred associations between Nearctic insects and flowers indicate today that maroon, white, greenish and yellow flowers are primitive in the appeal to insects, drawing strongly on beetles, bugs, flies and wasps and their allies. Once symbiosis was established, mutual specialization followed. Whites developed as we may suppose into pinks, maroons into purples; bees developed, small primitive short-tongued, and though lured by the primitive colors they also favored pinks and purples. Larger, long-tongued bees developed, and though favoring several colors, they raised purple and blue flowers to high favor.

Pink appeals about equally to primitive and specialized pollinators; but orange, purple, and red make in ascending order an appeal to more specialized pollinators. The rise in importance of butterflies as red increases is strikingly shown in these observations. Third in choice with blues and pinks, second with purple and orange, with the reds they stand first as insect visitors. Day-loving butterflies favor long wave lengths; cranny-loving bees short ones, and thus the red and blue in the purple flowers meet two forces that tend to lead in opposite directions. Blue is thus a more advanced color than purple, but we recall the tendency of the eye to see red and green as a pair and yellow and blue as another pair. Apparently primitive yellow-perceiving insects, also able to perceive the blue which they failed to develop, are setting upon these blues and leading them to primitive shapes to appeal to primitive short tongues. The larger bees have helped develop most admirable pollination mechanisms among the purples,

and yet rival the flies in favoring flowers of a rather primitive greenish. *Polygonum* is not only greenish; it actually seems to be hidden beneath the foliage. Perhaps some greenish, and some of the purple, flowers among dark almost blackish foliage are perceived by means of eyes that make use of the ultra-violet rays. Certainly some bee-flowers like *Dalea, Lobelia, Polygonum,* and *Nabalus* affect those settings and shades we find used in fluorescent exhibits. But bright reds and greens of plants by ultra-violet appear inconspicuous or even blackish, while yellows, blues and whites show to advantage.

In Otto Porsch's "Grellrot als Vogelblumenfarben" (Biologia Generalis, vol. 7, 1931, pp. 647 ff) we get some interesting suggestions. While certain bees perhaps see ultra-violet they fail to see the long waves of red, and the reds that birds favor are probably black or gray to the bees. While Europe is rich in red berries such as might lure berry-eating birds, it lacks flower-visiting birds and is markedly poor in bright red flowers. To further emphasize the dependence of our reds on the avian influence I might add that in teaching on the Atlantic slope, on the Pacific, and in the upper Mississippi Valley, I have found one can rather safely predict a speedy return of migrant hummingbirds when he finds a tubular red flower blooming in the wild. Had the Cherokees known how gulf sage, Cherokee bean, coral honeysuckle, and Virginia fire-pink succeed one the other before the spring advance of the Ruby-throat, they might have woven about it some of the lore attached to the Cardinal, alleged daughter of that Sun to whom red was sacred, even had they never seen the little midget stretch in the sun on a modern sidewalk or other bare area. But surprising as it seems at first, red not only lures hummingbirds, but tends to protect from certain insect eyes like those of bees, Porsch suggesting it may even appear black or gray to such. I have been interested in testing the showiness of certain greenish and red flower forms by ultra-violet light. The results at times are surprising. Coral honeysuckle (*Lonicera sempervirens*), cross-vine (*Bignonia capreolata*), Solomon's seal (*Polygonatum commutatum*), jack-in-the-pulpit (*Arisaema triphyllum*) and green dragon-root (*A. Dracontium*) were placed in ultra-violet light on a slaty-black background. The first was almost invisible; the second despite its yellow spots was almost as obscure. The green dragon was a very green example but appeared plainer than either. The leaf of the jack was almost black, but the spathe showed fairly well, while the normally inconspicuous flowers of *Polygonatum* were now conspicuous above all the others. The fact that real green and red tend to make an obscure pair, and violet and yellow a conspicuous pair by ultra-violet light recalls similar phenomena observed in the study of color-blindness. (See W. H. Howell's "Text-book of Physiology," 1933.)

Here is an interesting field for ornithophily. And are not crimson pea (*Lathyrus splendens*), scarlet loco (*Astragalus coccinea*), western azalea (*Rhododendron occidentale*), pink honeysuckle (*Lonicera hispidula*), bell phacelia (*Phacelia whitlavia*), fire-cracker (*Brodiaea coccinea*) and thistle sage (*Salvia carduacea*) being neglected? I believe these are surely visited by hummingbirds, or even specialized for them. The old genus *Mimulus*, with blue, pink, scarlet, salmon and golden forms, must afford a striking study in the evolution of the ornithophilic from the insect flower. This is a rare combination of color when we recall that the rule of DeCandolle limited many families to red-orange-yellow and to red-purple-blue combinations, even allowing now an additional blue-violet and yellow grouping joined by an intermediate maroon or brown as in the iris and violet genera. We must beware of rule-of-thumb methods. Hummingbirds, like bees, in the absence of favorites visit poverty-flowers and flowers of less-favored colors. Our finds as to insects are offered as suggestions only. Thousands of such observations might shed some light on the evolution of floral color, a story the colorless and almost absent fossil flowers leave intriguingly neglected.

In the list here presented, "Test" indicates mere trial visit; "Insects" a visit to a flower for insects by birds. Others appear to be for nectar.

Polygonaceae. Silver Lace Vine. White; rose; green. *Polygonum auberti.* Test.
Amaranthaceae. Cock's-comb. Red. *Celosia cristata.*
Cactaceae. Drink Cactus. Yellow. *Echinocactus cylindraceus.*
Euphorbiaceae. Summer Poinsettia. Red. *Euphorbia heterophylla.*
Lauraceae. Avocado. Greenish. *Persea americana.*
Avocado. Greenish. *Persea drymifolia.*
Ranunculaceae. Dwarf Larkspur. Blue. *Delphinium tricorne.*
Papaveraceae. Flanders Poppy. Red. *Papaver Rhoeas.* Test.
Plume Poppy. Pinkish. *Bocconia cordata.*
Bleeding Heart. Pink. *Dicentra spectabilis.*
Cruciferae. Siberian Wall-flower. Orange. *Cheiranthus allioni.*
Squaw Cabbage. Purple. *Streptanthus inflatus.*
Crassulaceae. *Crassula* spp. Red.
Echeveria spp. Red; orange.
Dudleya lanceolata. Orange; red.
American Orpine. Pale Pink. *Sedum telephoides.*
Rosaceae. Almond. Pink. *Prunus amygdalus.*
Peach. Pink. *Persica vulgaris.*
Leguminosae. Goat's Rue. In red stage. *Cracca hispidula.* Test.
Everlasting Pea. Pink; white. *Lathyrus latifolia.*
Pea-vine Clover. Red-purple. *Trifolium pratense.*
Pink Clover. Pink. *Trifolium repens.*
Texas Mountain Laurel. Purple. *Sophora secundiflora.*
Wild Sweet Pea. Lilac. *Bradburya virginiana.*
Butterfly Pea. Lilac. *Clitoria mariana.*
Bush Clover. Violet-purple. *Lespedeza virginica.*
Pole Bean. White and yellow. *Phaseolus vulgaris* var.
Western Locust. Pale rose. *Robinia Neo-Mexicana* (?).
Common Locust. White. *Robinia pseudacacia.*
Punicaceae. Pomegranate. Scarlet. *Punica granatum.*
Onagraceae. Wild Primrose. Yellow. *Oenothera biennis.*
Primrose Honeysuckle. White to red. *Gaura Drummondi.*
Malvaceae. Texas Fuchsia. Vermilion. *Malvaviscus Drummondi.*
Tree Mallow. Purple-rose. *Malva sylvestris.*
Sapindaceae. Red Texas Buckeye. Red. *Aesculus discolor* (?).
Pink Texas Buckeye. Pink. *Ungnadia speciosa* (?).
Balsaminaceae. Pale Jewel-weed. Yellow. *Impatiens pallida.*
Convolvulaceae. Palmate Cypress-vine. Red. *Quamoclit quamoclit* × *hederifolia* (?).
Texas Morning-glory. Lavender. *Ipomea trifida.*
Ivy-leaf Morning-glory. Blue. *Ipomea hederaceae.*
Polemoniaceae. Standing or "Tree" Cypress. Red. *Gilia coronopifolia.*
Blue Gilia. Blue. *Gilia capitata.*
Boraginaceae. Geiger Tree. Scarlet, or orange. *Cordia sebestena* (?).
Anchusa sp. Blue; purple.
Chinese Forget-me-not. Blue. *Cynoglossum amabilis.*
Solanaceae. Red Tobacco. Red. *Nicotiana forgetiana.*
Snow-berried Cestrum. Yellow. *Cestrum* sp.
Horse Nettle. White. *Solanum carolinense.* Test.
Scrophulariaceae. Scarlet Bugler. Red. *Pentstemon centranthifolius.*
Paint Brush. Red. *Castilleia oblongifolius.*
Turtle-head. Pink and White. *Chelone glabra.*
Veronica. Lilac; blue. *Veronica longifolia.*
Spiked Veronica. Blue. *Veronica spicata.*
Torenia Fournieri. Blue and violet.
Slipper-flower. Yellow and brown. *Calceolaria crenatiflora.*
Fern-leaved False Foxglove. Yellow. *Dasystoma pedicularia.*
Great Tree Trumpet; Empress Tree. White. *Paulownia Fortunei.* Test perhaps.
Acanthaceae. "Justicia." Red. *Jacobinia carnea.*
Beloperone. Red, white, and purple. *Beloperone guttata.*

Labiatae. Hemp-nettle. Red. *Gaeleopsis ladanum.*
Columbian Salvia. Scarlet. *Salvia gesneraefolia.*
Tree Salvia. Red. *Salvia arborea.*
Gulf-coast Wild Sage. Red. *Salvia coccinea.*
Wild Sage. Blue. *Salvia azurea.*
Wild Sage. Blue. *Salvia farinacea.*
Showy Dragon-head. Purple. *Dracocephalum speciosum.*
Bee Balm. Purple. *Monarda fistulosa.*
Desert Sage. Purple and blue. *Ramona incana.*
Verbenaceae. Verbena. Pink. *Verbena* sp. or hybrid.
Loganiaceae. Maryland Pink-root. Red. *Spigelia marilandica.*
Apocynaceae. Madagascar Periwinkle. Rose. *Vinca rosea.*
Myrtle Vine Periwinkle. Blue. *Vinca major.*
Asclepiadaceae. Purple Milkweed. Magenta. *Asclepias purpurascens.*
Rubiaceae. *Manettia glabra.* Red.
Snowy Portlandia. White. *Portlandia platantha* (?).
Caprifoliaceae. Bush Honeysuckle. Yellow. *Diervillea lonicera.*
Lobeliaceae. Cardinal flower. Red. *Lobelia hybrida.*
Campanulaceae. Bell Flower. Blue or white. *Campanula persicifolia.*
Dipsacaceae. Mourning Bride. Purple, rose. *Scabiosa atropurpurea.*
Ambrosiaceae. Giant Ragweed. Green. *Ambrosia trifida.* For insects.
Compositae. New England Aster. Violet-purple. *Aster novae-angliae.*
Globe Thistle. Blue. *Echinops ritro.*
Golden Coreopsis. Orange. *Coreopsis tinctoria.*
Veldt Marigold. Orange. *Venidium decurrens.* Test.
Straw-flower. Orange. *Helichrysum bracteatum.* Test.
Small-head Sunflower. Yellow. *Helianthus microcephalus.* Insects.
Artichoke. Yellow. *Helianthus tuberosus.*
Leaf-cup. Yellow. *Polymnia uvedalia.*
Clammy Weed. Whitish. *Polinsia graveolus.*
Boneset. White. *Eupatorium perfoliatum.*
Araceae. Calla Lily. White. *Zantedeschia aethiopica.* Test.
Liliaceae. New Zealand Flax. Maroon. *Phormium tenax.*
Showy Lily. Rosy white. *Lilium speciosum rubrum.*
Red-hot Poker. Orangeaceous. *Kniphofia uvaria.*
Showy Lily. Orange. *Lilium henryi.*
Canada Lily. Yellow. *Lilium canadense.*
Madonna Lily. White. *Lilium candidum.*
African Lily, albino. White. *Agapanthus umbellatus.*
Star-of-Bethlehem. White. *Ornithogalum umbellatum.*
California Hyacinth. Purple. *Brodiaea capitata,* etc.
Aloes spp. Probably some new forms here in red, orange, and yellow.
Amaryllidaceae. Orange Mescal. Deep Yellow. *Agave parryi* (?).
Iridaceae. *Watsonia coccinea.* Red.
Blackberry lily. Orange. *Belamcanda chinensis.*
German Iris. Purple. *Iris germanica.*
Leafy Blue Flag. Blue. *Iris foliosa.*
Commelinaceae. Day-flower. Blue. *Commelina communis.*

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