Vol. 120, No. 4 The American Naturalist October 1982

FRUIT FLAGS: TWO HYPOTHESES

EDMUND W. STILES

Department of Biological Sciences (Zoology) and Bureau of Biological Research,
Rutgers University, Piscataway, New Jersey 08854

Submitted November 30, 1981; Accepted March 17, 1982

Here I examine the presence and potential selective importance of visual signals, other than ripe fruit, which may alert and attract frugivorous birds to fruits. I call these fruit flags and define them as contrastingly colored plant parts that are temporally or spatially associated with fruits, but are not quantitative indicators of the amount of ripe fruit available.

Fruits which are disseminated by birds generally are colored in a fashion contrasting with their background when they are ripe and ready for dispersal. The contrasting colors provide signals which alert birds to their presence (Turcek 1963). These signals appear to be important in dispersal of seeds (Ridley 1930; Snow 1971; Morton 1973; Janzen 1975). The rapid changes in fruit color associated with ripening, and the subsequent rapid removal of the fruits by birds for some plant species (Ridley 1930; E. W. Stiles unpubl.), as well as the mimicry of ripe fruits by seeds of some species of tropical legumes (McKey 1975) attest to the importance of colors in fruit dispersal.

The position of the fruits on the plant and the size and arrangement of individual fruits, either singly or in clusters, influence their visibility to potential dispersal agents. Fruit position on a plant is determined in large part by the position of the flowers. Below I present two hypotheses that suggest the importance of fruit flags under conditions of spatial and temporal reduction of visual stimulus from ripe fruits. The first hypothesis examines conditions under which fruit may be difficult to locate from long distances. Fruit flags creating large images may be advantageous in some situations. The second hypothesis illustrates conditions under which it may be advantageous to distribute ripe fruit over long periods of time and treats situations in which the distribution of ripe fruits in time may select for the presence of fruit flags.

Fruit flags are in many ways analogous to pollinator flags, which are extrafloral elements of plants attracting potential pollinators to flowers. Pollinator flags are usually closely associated with the flower and are temporally coincident with flowering. Flags are persistent and provide visual stimuli that, as with fruit flags, are quantitatively unrelated to the food resources for the pollinator. One of the best studied examples is the large neotropical genus *Heliconia*, the bracts of which

Am. Nat. 1982. Vol. 120, pp. 500–509.
© 1982 by The University of Chicago. 0003-0147/82/2004-0005$02.00. All rights reserved.

serve as flags for visiting hummingbirds (Stiles 1975). The term flag-flowers has also been used to describe certain floral morphologies (Proctor and Yeo 1973). Strictly speaking, flowers of all types, unlike fruit, signal the potential presence rather than the assured presence of a food supply. The visual signal from flowers usually remains constant but the amount of the reward varies with the visitation rate by species collecting the reward. Flower flags need not be closely associated with the flower and some species (e.g., *Dalburgia*, Gesneriaceae) maintain flags on the leaves in the form of red spots, hairs, or other contrasting markings.

Hypothesis I: Foliar Fruit Flags

Early leaf-color change, resulting in loss of energy from photosynthesis, may increase seed dispersal from some plants by creating a large contrasting signal for migrating birds. These birds may be attracted to potential fruit sources.

Many flowers have evolved with visual pollinators and are placed prominently on the plant. This results in a prominent placement of fruits which are then evident to dispersal agents. Flowers and fruits are often displayed so that they are not hidden by foliage and they are often either large or in clusters, increasing the visual stimulus to both pollinators and frugivores (Proctor and Yeo 1973; Ridley 1930; Stephenson 1979). Not all fruits, however, are prominently placed or easily located by frugivores.

In the eastern deciduous forest of North America, bird-disseminated fruits of various plants ripen as early as June or as late as October, depending upon the species of plant and the latitude (U.S. Dep. of Agriculture, Forest Service 1974; Stiles 1980). For most species, ripening of fruit occurs well before freezing temperatures in the fall and any physiological limit to photosynthesis. The interval between fruit ripening and the physiological limit on photosynthesis in leaves of deciduous woody species may be as short as several weeks (e.g., *Viburnum*, *Crataegus*, *Sorbus*, *Aronia*, *Ilex*) or as long as several months (e.g., *Amelanchier*, *Rubus*, *Vaccinium*, *Morus*, *Gaylussacia*).

For most species leaf-color change occurs substantially after fruit ripening and is usually associated with cold weather in late autumn. However, in some plant species with bird-disseminated seeds leaf-color change is coincident with fruit ripening and well before the physiological limit to photosynthesis.

Leaf-color change is associated with activation of chlorophyllases in the leaves which break down chlorophylls and transport "valuable" chemicals, such as nitrogen and magnesium, out of the leaves prior to abscission. The flavonoids and membrane-bound carotenoids are unmasked by this process yielding the reds, yellows, and browns of autumn leaf color. Breakdown of the chlorophylls results in the cessation of most if not all photosynthesis.

This hypothesis compares the fitness loss incurred by reducing or eliminating photosynthesis prior to some time limit created by physical factors, relative to the fitness gain from the increased probability of disseminating seeds by presenting a contrasting optical signal to alert potential dispersal agents (fig. 1). To compare the potential importance of these factors, I use fitness units. The relative scales of the fitness units are unknown and the relationship is presented as an unquantified

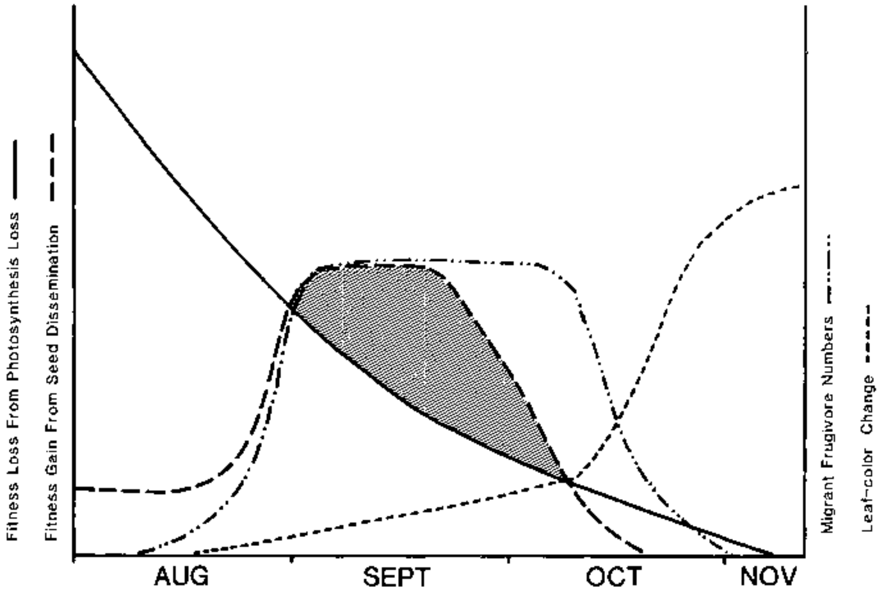

FIG. 1.—Foliar fruit flags have positive fitness value when the gain from increased seed dissemination exceeds the photosynthesis loss from leaf-color change (hatched area). This occurs only in early fall during fall bird migration, but before most plants change leaf color.

hypothesis which awaits future testing. This hypothesis assumes there is a time limit on the positive accrual of energy by maintaining leaves and it is therefore concerned with deciduous plants. Photosynthesis loss from chlorophyll destruction prior to this physiological limit is a decreasing curvilinear function of time in the autumn because of decreasing temperature and day length. The loss from early leaf-color change may be countered by a gain in fitness from increased seed dispersal by birds if two criteria are met.

First, the loss in photosynthesis must not be too great. Fruits ripening in mid to late summer (June, July, and August) would not be expected to have an associated leaf-color change at the time of fruiting. In fact, of the 44 species I examined for fruiting time, none of those that ripen fruits in June, July, or early August (*Amelanchier, Vaccinium, Gaylussacia, Morus, Fragaria, Rubus, Ribes, Prunus*) have extensive leaf-color change, although some (e.g., *Rubus, Fragaria*) often display some red leaves at this time. Total time for photosynthesis by these deciduous plants is limited to the period from late April to late October, a period of about 6 mo. Even taking into account the seasonal changes in carbon fixation, withdrawing chlorophyll as early as July would reduce photosynthetic gain by about one-half. Second, the increase in attraction of birds to the plant must be large enough to counter the loss in photosynthesis (fig. 1). For species of plants that display fruit in prominent positions or in large groups (e.g., *Sorbus, Crataegus, Viburnum, Phytolacca*), the visual stimulus advertising the availability of ripe fruit is great enough to make any additional attraction created by leaf-color change small. The change in the number of seeds disseminated by birds would be greatest for those species that do not have a whole-plant growth form that is easily identifiable from a distance and for which fruits are hyperdispersed on the plant. In addition plants bearing fruits with high lipid content should suffer greater fitness loss from low rates of seed dispersal than species with low lipid content because rapid rotting renders their fruits unacceptable for birds (Janzen 1977; Stiles 1980). Therefore these species would benefit from foliar fruit flags.

The importance of the change in leaf color as a signal is dependent in part on the degree of conspicuousness created by the change. Hailman (1977) discussed the principles of conspicuousness which include contrast in hue, image size, repetition of coloration in space, and signal variety. These principles are instructive in understanding the importance of fruit flags. Although many factors, including brightness and spectral distribution of light, are involved in determining which hue creates the greatest visual contrast against a given background, the green foliage contrasts markedly with the red and yellow flavonoids and carotenoids unmasked by the destruction of chlorophyll. The color change of the leaves of the entire plant creates a large image size which is repeated in space by other individuals of the same species. Cook et al. (1971) found that small doveweed plants (*Eremocarpus setigerus*) escaped seed predation by doves because they were "less detectable to predators" (p. 280) than large, clustered plants. For foliar fruit-flagging species, birds learn to associate the presence of fruit with the contrasting color, increasing visits to other individuals. These signals lose value, however, as other plants unmask their carotenoids and the signal is no longer a unique indication of that species (fig. 1). Because of limitations created by photosynthesis loss early in the summer and lack of contrast later in the fall, the importance of foliar fruit flags is restricted to the early fall. This time period, however, is important because it corresponds with the peak of fall migration of frugivorous birds in the eastern deciduous forest.

In the eastern deciduous forest, many bird-disseminated fruits ripen coincident with the beginning of fall bird migration (Stiles 1980; Thompson and Willson 1979). Migration brings large numbers of facultatively frugivorous birds. Many species, especially in the families Turdidae, Mimidae, and Bombycillidae, feed primarily on fruit during this period, depositing subcutaneous fat between migratory flights. Following nocturnal migrations these birds are unfamiliar with the environments in which they find themselves. Any signal for these naive birds would increase the probability of their locating fruits and disseminating the seeds. The fitness value of fruit flags visible from long distances increases during the period of fall bird migration (fig. 1).

A nonrandom assortment of plants change leaf color in New Jersey during the first week in September. This is fully 3 wk prior to leaf-color change in the first woody species that is not bird disseminated (*Acer rubrum* L.) and over 1 mo before the majority of woody plants withdraw chlorophyll from their leaves. Change in leaf color is difficult to quantify because the change is gradual both within and among individuals. Some individuals and some leaves of the species described here do not change leaf color in early September, but the majority do and their appearance is striking. The species that change color at this time include poison ivy (*Toxicodendron radicans* L.) in the Anacardiaceae and Virginia creeper (*Parthenocissis quinquefolia* L. Planch.) in the Vitaceae. These are vines that have no easily identifiable growth form when climbing various species of trees.

Their color change in early September creates contrasts enabling a human observer to identify the species presence from great distances (personal observation). Poison ivy unmasks yellow, orange, or red pigments while Virginia creeper unmasks red pigments. These species stand in stark contrast against green foliage from early September until mid-October when cold weather induces color change in most other species.

Spicebush (*Lindera benzoin* L. Blume) and sassafras (*Sassafras albidum* L. Roxb.) in the Lauraceae and black gum (*Nyssa sylvatica* Marsh.) in the Cornaceae also change leaf color early in September. These species all have fruits borne singly or in small groups which do not yield a signal that is visible from a great distance. Black gum is restricted edaphically to wetter areas. The leaf-color change to bright red allows identification from great distances. Spicebush, an understory shrub, holds its leaves parallel to the ground during the summer months. When the chlorophyll is withdrawn from the leaves, turning them yellow, they often droop, thereby increasing the visual signal from all angles but vertical.

Some species which present fruits in visible clumps, including several species of sumacs (*Rhus typhina* L., *Rhus glabra* L., *Rhus copallinum* L.) and dogwoods (*Cornus florida* L., *Cornus racemosa* Lam.), also change leaf color early in the fall. These flags also augment the long-distance signal.

A larger than expected proportion of the fruits that have foliar fruit flags belong to a small group of eastern deciduous forest fruits that have pericarps with high lipid content. These include *Lindera* (41.6%), *Sassafras* (53.8%), *Cornus florida* (25.2%), *Cornus racemosa* (33.5%), *Parthenocissis* (14.5%), and *Nyssa* (14.4%) (D. White and E. Stiles, unpubl.). Of 45 northeastern U.S. species for which lipid analysis has been done only 10 have lipids proportions greater than 14% (Halls 1977; Stiles 1980). Although high lipid fruits appear to have been under strong selection for fruit flagging, selection favoring flagging does not necessarily depend upon nutrient investment in the fruit.

The loss of 1 mo of photosynthesis is a high price to pay for increased visibility to birds that may act as dispersal agents. Two examples provide additional support for the hypothesis that the early leaf-color change has evolved through its effects on increased fruit dispersal.

First, sassafras is the earliest fruiting species of the high lipid, fruit flagging species; fruit starts to ripen during the third week in August. The loss in photosynthesis by withdrawing all chlorophyll at the onset of fruiting would be larger than for other species. In the absence of dispersers, sassafras will rot quickly compared with low lipid fruit (e.g., *Aronia melanocarpa* (Michx.) Elliott, 1% lipid; fig. 2). Sassafras is unusual among the fruit flagging species in that it withdraws chlorophyll from only some leaves creating obvious orange flags in late August. This increases the ease of long-distance identification of the trees while some photosynthesis continues. Also the red pedicels persist after fruit removal, acting as additional flags.

Second, staghorn sumac (*Rhus typhina*) is a dioecious species which forms clones of plants. One would not expect nonfruiting male clones to have foliar fruit flags because they have no fruit. On October 3, 1981 in three transects (1) from Stroudsburg, Pennsylvania to Palmerton, Pennsylvania along Pennsylvania route 209, (2) from Palmerton to Easton, Pennsylvania along Pennsylvania routes 248

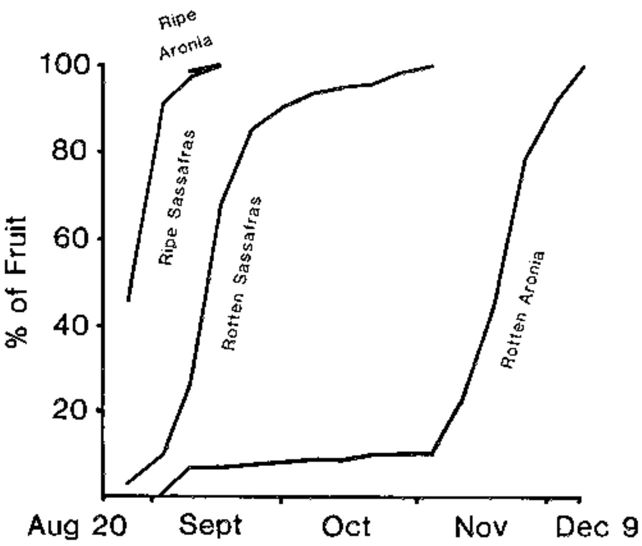

FIG. 2.—*Sassafras* (high lipid) and *Aronia* (low lipid) ripen at the same time, but they rot at very different rates.

and 512 and along U.S. route 22, and (3) from Easton, Pennsylvania to Oldbridge, New Jersey along route 178, fruiting and nonfruiting "clones" of staghorn sumac were scored as red or green depending on the primary appearance of the leaves (table 1). The differences in most cases were obvious but in intermediate cases clones were scored as green. In all three transects the fruiting individuals had significantly higher numbers of red clones ($P < .001$ for all). This strongly supports the foliar fruit flag hypothesis although the physiological mechanism needs elucidation.

In *The Tropical Rain Forest*, Richards (1964, p. 193) states, concerning senescing leaves, that "Generally, the leaves become yellowish or flecked with yellow,

TABLE 1

LEAF-COLOR CHANGE IN "CLONES" OF STAGHORN SUMAC (*Rhus typhina*) ON THREE TRANSECTS IN PENNSYLVANIA AND NEW JERSEY ON OCTOBER 3, 1981

	CLONES OF *Rhus typhina*				
	FRUITING		NONFRUITING		
	Green	Red	Green	Red	χ^2
Transect 1	13	103	78	47	$P < .001$
Transect 2	10	63	101	27	$P < .001$
Transect 3	35	75	87	30	$P < .001$
Total	58	241	266	104	P .001

NOTE.—For 2×2 contingency: transect 1, $\chi^2 = 67.1$, df = 1, $P < .001$; transect 2, $\chi^2 = 79.9$, df = 1, $P < .001$; transect 3, $\chi^2 = 41.3$, df = 1, $P < .001$; total, $\chi^2 = 182.8$, df = 1, $P < .001$.

sometimes turning vivid red.'' Foliar fruit flagging in a more general sense may not be restricted to the temperate zone. ''In Central America, trees with dry season fruiting phenologies either lose the leaves, exposing the fruit attractant, or they utilize the trade winds that blow persistently during the dry season to produce true flags. *Didymopanax morototoni*, *Miconia argentea*, and many *Cecropia*, for example have leaf undersides that contrast markedly with the green upper surface. It is easy for an observer to see these trees a long way away as the under leaf surfaces flash rusty (in the first two species) or white (in *Cecropia*). These also rely heavily upon migrating birds for seed dispersal'' (E. S. Morton, personal communication).

Hypothesis II: Preripening Fruit Flags

Some fruiting species have either a contrasting unripe fruit color or a spatially associated plant part that is contrastingly colored. This may increase the probability that resident birds will trapline for ripe fruit and may reduce fruit loss to rotting.

Most fruits are cryptic before they ripen. During the ripening process fruits change from cryptic coloration (often green) to conspicuous coloration which increases the ease with which they can be located by dispersers (Ridley 1930). The ripening process also involves a large variety of chemical changes which increase the value of the fruit for the frugivore (Hulme 1971; Goldstein and Swain 1963; Foster 1977). This is accomplished by reductions in toxic compounds or increases in available nutrients. The preripening crypsis and unpalatability reduce the probability of destruction of immature seeds both by birds, which may eat the fruits and destroy the seeds, as well as by insects or microbes which can render the fruit and seeds unacceptable for subsequent dispersal (Janzen 1977).

For some fruiting species this pattern of unripe, cryptic, green fruits changing to colorful ripe fruits is broken by an intermediate stage of colorful unripe fruits. During the period of initial growth of these fruits they are cryptic. When fruits attain full size their color changes, but full ripening with associated increased palatability does not occur. Ripening is accompanied by a further color change and increased palatability. These preripening advertisements are not always restricted to the fruit proper but may involve contrasting petioles or pods or calyxes.

Preripening advertisements are usually found in environments in which fruit dispersers are residents. Colorful, contrasting unripe fruits or plant parts associated with the fruits are found commonly in forest understory in the tropics as well as for a large number of canopy species. They are also found in temperate fruits that ripen during the summer months when resident bird species are holding territories.

In the neotropics dual color changes in fruits are common in the Melastomaceae, Rubiaceae, Solanaceae, Musaceae, Palmae, and others. For example Corner (1966, p. 171) describes a triple color change, ''In *Ptychosperma* the fruits turn yellow for a week, then deep red during the next week, but they are not eaten by birds until three or four weeks later they have become dull crimson.'' In Papua New Guinea in an intensive study of bird-fruit interactions Thane Pratt (unpubl. data) found 177 species of trees on a 1600 m elevation forest plot on Mt. Missim, near Wau. For these, 46.9% produced fruits that were disseminated primarily by birds. Of these 83 bird-disseminated species he evaluated fruit colors for 71 species, finding 30 of them (42%) that underwent dual color change (table 2).

Fruit flags for resident birds in the tropics are also found in the form of bract or pod color changes prior to fruit ripening in the Leguminosae, Zingiberaceae, Olacaceae, Lauraceae, and probably many others. In taxonomic works authors rarely record fruit or associated parts' color changes prior to ripening.

In the temperate zone, and specifically in the eastern deciduous forest, fruits that ripen in the summer when resident birds are present often show dual color change, whereas plant species that exploit primarily migrant birds as dispersal agents do not. Summer ripening species of the genera *Rubus*, *Gaylussacia*, *Vaccinium*, *Amelanchier*, *Morus*, and *Prunus* all show green to red or pink color change while still not ripe followed by a change to dark color upon ripening. None of the species of 30 woody plant genera ripening during late August, September, or October in New Jersey has dual color change.

The species that show dual color change during the ripening process ripen only a few fruit at a time. Early in the fruiting season a foraging bird encounters only colorful, unripe fruits. Subsequent to this a few fruits ripen in any one day leaving many unripe flags. This may encourage traplining by frugivores, much in the same fashion as found in pollinating hummingbirds (Stiles 1975) and euglossine bees (Janzen 1970).

The colored unripe fruit or associated plant parts create a larger and persistent stimulus that attracts frugivores to the plant. The regular checking of fruits by resident frugivores would result in rapid removal of ripe fruits. This reduces the time during which ripe fruits are available for nondispersing frugivores such as insects and microbes (Janzen 1977). Fruits become much more vulnerable to attack at this time because many of the toxins are altered or eliminated during the ripening process (Hulme 1971). Also by offering only a few fruits each day, the plant may gain a wider dispersal of its seeds because the frugivore would not remain at the plant for long periods and would neither disgorge nor defecate seeds near the parent plant.

SUMMARY

Signals that identify the presence and availability of fruits ready for dispersal probably increase the rates of seed dissemination for bird-dispersed seeds. The two hypotheses presented here illustrate how fruit flags may increase conspicuousness of fruiting species thereby increasing visitation by frugivorous birds.

In temperate deciduous forests, foliar fruit flagging species lose energy from photosynthesis by changing leaf color early, but create a large contrasting signal. The contrasting leaves may attract migrant frugivores that are unfamiliar with resource locations at any given stopover point along their migratory route. Contrasting long-distance fruit flags may also be important for some tropical plant species.

Preripening fruit flags do not create a long-distance signal but rather alert resident frugivores to the presence of fruit that will soon ripen. This increases the probability that resident frugivores will remove the fruit and disseminate the seeds

TABLE 2

BIRD-DISSEMINATED TREE SPECIES SHOWING DUAL COLOR CHANGE AT 1600 m ELEVATION MT. MISSIM, PAPUA NEW GUINEA (Thane Pratt, unpublished)

	Preripening Color	Ripe Color
Podocarpaceae		
Prumnopitys amara (Bl.) Laubenf.	red	dark red
Winteraceae		
Bubbia sp.	red	purple
Himantandraceae		
Galbulimima belgraveana (F. Muell.) Sprague	red	purple
Myristicaceae		
Myristica womersleyi Sincl.	red	red w̄ yellow cap
Myristica subaluata Miq.	red	red w̄ yellow cap
Myristica longipes Warb.	red	red w̄ yellow cap
Monimiaceae		
Levieria sp.	yellow	orange w̄ black marks
Lauraceae		
Cinnamomum sp.	?	purple
Cryptocarya sp. "RLRF"	red-purple	purple
Litsea sp. "WAU"	red	red-purple
Litsea sp. "SLF"	red	red-purple
Litsea sp. "#3"	red-purple	purple
Litsea sp. "#5"	red	red-purple
Ulmaceae		
Trema orientalis (L.) Bl.	red-purple	purple
Rosaceae		
Prunus gazelle-peninsulae (Kan. & Hat.) Kalkm.	red	red-purple
Prunus sp. "#2"	red	red-purple
Meliaceae		
Vavaea amicorum Benth.	?	maroon
Euphorbiaceae		
Bischofia javanica Bl.	red	red-purple
Drypetes aff. lasiogynoides Pax. & Hoffm.	orange	red
Antidesma molucannum Airy Shaw	white	?
Sapotaceae		
Planchonella sp. "#3"	?	purple
Myrtaceae		
Syzygyum sp. "PKP"	?	purple
Syzygyum sp. "WTH"	white	?
Syzygyum sp. "DTP"	white	red
Decaspermum sp.	?	purple
Rhamnaceae		
Emmenosperma alphitonoides F. Muell.	orange	?
Myrsinaceae		
Myrsinaceae sp.	red-purple	purple
Aquifoliaceae		
Ilex c.f. brassii Merr. & Perry	red	purple
Urticaceae		
Dendrocnide c.f. ternatensis (Miq.) Chew	white	lavender
Pipturus argenteus (Forst. f.) Wedd.	white	lavender

before the fruits are rendered unacceptable through microbial attack. This pattern is found in both tropical and temperate systems.

ACKNOWLEDGMENTS

I wish to thank Alice S. Tempel for critical discussion of the concepts presented here and Eugene S. Morton, Thane Pratt, Douglas White, and two anonymous reviewers for comments on the manuscript. The fall 1981 Community and Ecosystems Dynamics course at Rutgers helped with data collection on staghorn sumac clone color. Financial support came in part from a grant from the Rutgers Research Council.

LITERATURE CITED

Cook, A. D., P. R. Atsatt, and C. A. Simon. 1971. Doves and doveweed: multiple defenses against avian predation. Bioscience 21:277–281.

Corner, E. J. H. 1966. The natural history of palms. University of California Press, Berkeley.

Foster, M. S. 1977. Ecological and nutritional effects of food scarcity on a tropical frugivorous bird and its fruit source. Ecology 58:73–85.

Goldstein, J. L., and T. Swain. 1963. Changes in tannins in ripening fruits. Phytochemistry 2:371–383.

Hailman, J. P. 1977. Optical signals: animal communication and light. Indiana University Press, Bloomington.

Halls, L. K., ed. 1977. Southern fruit-producing woody plants used by wildlife. Southern Forest Experiment Station, Forest Service, USDA.

Hulme, A. C., ed. 1971. The biochemistry of fruits and their products. Vol. 2. Academic Press, New York.

Janzen, D. H. 1970. Euglossine bees as long distance pollinators of tropical plants. Science 171:203–205.

———. 1975. Ecology of plants in the tropics. Inst. Biol. Stud. Biol. no. 58. Edward Arnold, London.

———. 1977. Why fruits rot, seeds mold, and meat spoils. Am. Nat. 111:691–713.

McKey, D. 1975. The ecology of coevolved seed dispersal systems. Pages 159–191 *in* L. E. Gilbert and P. H. Raven, eds. Coevolution of animals and plants. University of Texas Press, Austin.

Morton, E. S. 1973. On the evolutionary advantages and disadvantages of fruit eating in tropical birds. Am. Nat. 107:8–22.

Proctor, M., and P. Yeo. 1973. The pollination of flowers. Collins, London.

Richards, P. W. 1964. The tropical rain forest. Cambridge University Press, London.

Ridley, H. N. 1930. The dispersal of plants throughout the world. L. Reeve, Ashford, Kent.

Snow, D. W. 1971. Evolutionary aspects of fruit-eating by birds. Ibis 113:194–202.

Stephenson, A. G. 1979. An evolutionary examination of the floral display of *Catalpa speciosa* (Bignoniaceae). Evolution 33:1200–1209.

Stiles, E. W. 1980. Patterns of fruit presentation and seed dispersal in bird-disseminated woody plants in the eastern deciduous forest. Am. Nat. 116:670–688.

Stiles, F. G. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. Ecology 56:285–301.

Thompson, J. N., and M. F. Willson. 1979. Evolution of temperate fruit/bird interactions: phenological strategies. Evolution 33:973–982.

Turcek, F. J. 1963. Color preference in fruit- and seed-eating birds. Proc. XIII Int. Ornithol. Congr. 1:285–292.

U.S. Department of Agriculture, Forest Service. 1974. Seeds of woody plants in the United States. Agric. Handbk. no. 450. Washington, D.C.