Pacific Science (1985), vol. 39, no. 4

Role of Alien and Native Birds in the Dissemination of Firetree (*Myrica faya* Ait.—Myricaceae) and Associated Plants in Hawaii[1]

ANNE M. LAROSA,[2] CLIFFORD W. SMITH,[3] AND DONALD E. GARDNER[3]

ABSTRACT: The food habits of several forest birds and their potential role in the dispersal of firetree (*Myrica faya*) were studied in two areas of Hawaii Volcanoes National Park. Observations were made during peak firetree fruiting (October–November 1983) in areas where ʻohiʻa (*Metrosideros polymorpha*) and firetree are codominant. Both native and introduced birds foraged in firetree and ʻohiʻa, but introduced birds were more common in firetree. Of the six bird species observed, ʻomaʻo (*Phaeornis obscurus*) and house finches (*Carpodacus mexicanus*) were the principal dispersal agents in the areas studied, while the common ʻamakihi (*Hemignathus virens*) was secondarily important. Japanese white-eyes (*Zosterops japonicus*), though feeding on the fruit, rarely ingested the seed. ʻApapane (*Himatione sanguinea*) and Northern American cardinals (*Cardinalis cardinalis*) were not observed eating firetree fruit. Germination rates and successes of several native and alien species are generally unaffected by passage through the digestive tracts of captive Japanese white-eyes and common mynas (*Acridotheres tristis*).

FIRETREE (*Myrica faya* Ait.) is a fleshy-fruited, semideciduous tree reaching heights of 10 m. It is a native of the Azores, Canary Islands, and Madeira (Neal 1965) and is one of several aggressive, introduced woody plants designated for biological control in Hawaii. Since its introduction to Hawaii in the late 1800s, it has become established on all major islands except Molokai. About 34,080 ha are infested statewide (Whiteaker and Gardner, in press). Dense, monotypic stands of firetree are common and prevent reproduction of native species, as demonstrated by the absence of undergrowth in the firetree infestation sites at Hamakua, Hawaii.

Smathers and Gardner (1979) suggested that the pattern of invasion of firetree around Kilauea Iki Crater in Hawaii Volcanoes National Park (HVNP) was correlated with the distribution of the Japanese white-eye (*Zosterops japonicus* Temminck & Schlegel). Fleshy-fruited trees commonly depend upon frugivores for their dissemination and reproductive success, especially in the tropics (Krefting and Roe 1949; Howe 1977; Clark and Clark 1981; Howe and Vandekerkhove 1981; Stapanian 1982). The investigation reported in this study was an attempt to verify the role of Japanese white-eyes and other birds in the dispersal of firetree in Hawaii. The birds' preference for firetree fruit versus ʻohiʻa (*Metrosideros polymorpha* Gaud.) nectar, and the relative frequency of foraging for insects in both trees, was assessed.

In addition, the effect of ingestion of the seeds by birds on seed germination was also assessed for firetree and associated fleshy-fruited plant species. Merely observing an animal swallowing fruit does not describe dispersal; the germinability and deposition of seeds following passage through the gut are also essential elements (Janzen 1983). Frequently a large percentage of vertebrate-dispersed seed is destroyed in the digestive process (Janzen 1983). On the other hand,

[1] Funds were made available for this study by National Park Service account 8854-2500-182. Manuscript accepted April 1985.

[2] Department of Botany, University of Hawaii at Manoa, 3190 Maile Way, Honolulu, HI 96822. Current address: Resource Management Division, Everglades National Park, P.O. Box 279, Homestead, FL 33030.

[3] Department of Botany, University of Hawaii at Manoa, 3190 Maile Way, Honolulu, HI 96822.

TABLE 1

TIME OF OBSERVATION OF BIRD FORAGING DURING FIXED PERIODS OF THE DAY AT KILAUEA CRATER RIM AND PUHIMAU, HAWAII VOLCANOES NATIONAL PARK

	TIME OF OBSERVATION AND NUMBER OF VISITS							
	6–9 AM		9–12 AM		12–3 PM		3–6 PM	
	HR	NO.	HR	NO.	HR	NO.	HR	NO.
Crater Rim	10.5	5	6	3	3.5	2	7.75	4
Puhimau	1.5	1	4.5	2	5.0	3	7.25	5

many plants depend on birds for seed dispersal. The final destination of seeds is determined by the birds' foraging behavior (dispersive or sedentary, for instance) and seed retention time.

MATERIALS AND METHODS

Field sampling was conducted from 21 October to 28 November 1983 at two sites on the island of Hawaii: Kilauea Crater Rim and Puhimau Crater. Kilauea, the wetter of the two sites (approximately 2700 mm annual rainfall at 1130 m elevation), is a closed *Metrosideros–Cibotium* forest. Puhimau, an open *Metrosideros* forest, is more arid (approximately 2200 mm annual rainfall at 1100 m elevation). Both sites were selected for the presence of locally codominant stands of ‘ohi‘a and firetree. The ratio of mature ‘ohi‘a to firetree was 3.3 : 1 at Kilauea and 1.2 : 1 at Puhimau. Observations of bird foraging behavior were limited to these species.

All observations of bird foraging behavior were made with 8 × 24 power binoculars in selected areas where fruiting firetree and blooming ‘ohi‘a occurred together. Random walks were made through an area and all visitations and foraging bouts were recorded, or an observation post was chosen and records were made of all visits and foraging in trees visible in the immediate area. Tree species, bird species, total visitation time, number of attempts at gleaning and probing flowers, and the number of firetree fruit fed upon were recorded. When several birds entered the area simultaneously, one bird was arbitrarily selected for observation. Observation periods lasted from 1 to 3 hr in each of the following time periods: 6–9 AM, 9 AM–12 noon, noon–3 PM, and 3–6 PM. The total observation time was 56 hr. Birds were known to forage more actively in early morning and late afternoon, so we made most of our observations at those times (Table 1). All visits to flowers were considered nectar-feeding bouts because determination of the exact feeding activity was not possible.

Additionally, the effect of ingestion by birds on germination of seeds (see Table 3 for list of species) was evaluated. Ripe fruit were collected and separated into two groups: one was fed to captive Japanese white-eyes or common mynas (*Acridotheres tristis* L.); the other was separated from the pulp and allowed to air-dry for controls in the germination studies.

During the testing period, captive birds were maintained in 2 × 2 ft cages and fed a diet of papayas, bananas, and a cereal–sugar–vitamin mixture. Fruits of the test plant species were introduced with the diet, and relative preferences of the birds for the fruit of each species were noted during feeding trials. Food preferences were defined as follows: high—birds readily ate the fruit of test species and favored them over their regular diet; medium—birds ate moderate amounts of test fruit but showed a preference for their regular diet; low—birds ate few of the test fruit and showed a decided preference for their regular diet; none—birds refused test fruit.

Seeds were collected from scats and allowed to air-dry. All seeds were then planted in sterile vermiclite and placed in a greenhouse where they were misted once daily. Germination was determined by emergence of the hypocotyl above the vermiculite. Germination success and rate (GT_{50}—time for 50% germination of controls) were assessed. Germination rates were categorized after Ng (1973) as follows: rapid—all viable seeds germinate within the first 12 weeks; delayed—all viable seeds germinate after 12 weeks; intermediate—germination period spans the 12-week period. The very small seeds of *Vaccinium calycinum* Sm., *V. reticulatum* Sm., *Rubus ellipticus* Sm., and *R. rosaefolius* Sm. were germinated (time to emergence of the radicle) on moist filter paper in petri dishes.

Germination tests were replicated six times unless insufficient seeds were passed by either bird species. Data were analyzed with Duncan's Multiple Range test.

RESULTS AND DISCUSSION

Foraging Preference of Birds

Of the six bird species observed foraging, only the Japanese white-eye and the 'apapane (*Himatione sanguinea* Gmelin) were regular visitors to either firetree or 'ohi'a. Both native and alien birds made visits to firetree, but native birds made more frequent visits to 'ohi'a where they spent the majority of their time (Table 2). The 'oma'o (*Phaeornis obscurus* Gmelin), a native frugivore, spent about the same amounts of time in 'ohi'a and firetree.

Japanese white-eyes, the most common bird species in both areas, spent only slightly more time in firetree than in 'ohi'a (Table 2). Northern cardinals (*Cardinalis cardinalis* L.), uncommon in the study areas, spent most of their time foraging on the ground or in 'ohi'a trees. In contrast, seed-eating house finches (*Carpodacus mexicanus* Say) spent 30% more time in native 'ohi'a trees than in firetrees. Consistent with observations in other studies (such as Howe and Vandekerkhove 1981), most birds ate nothing during visits; therefore, visitation frequency alone is not indicative of the relative importance of various dispersal agents. Only a small percentage of visitors to a given tree may be important dispersers.

The foraging behavior of most species studied was predictable, based on their generalized dietary patterns (Table 2). The wide-ranging native 'apapane spends most of its time and effort searching for nectar and insects in 'ohi'a and was seen less frequently visiting firetree (Table 2), even during the peak fruiting period. Some time was spent foraging in firetree, but 'apapane were never seen feeding on fruit, and insects were taken infrequently. This observation may not be surprising since the introduced firetree probably does not yet have an extensive insect fauna (a complete complement of insects), as indicated by the relative time Japanese white-eye spent foraging for insects in firetree compared with 'ohi'a.

Data on the remaining species of birds are limited, but the same general foraging pattern was found for the other native omnivore, the common 'amakihi (*Hemighathus virens* Gmelin). However, two 'amakihi were seen feeding on firetree berries in the Ainahou area of HVNP during reconnaissance, suggesting that firetree may be at least an occasional component in the diet of this species. Their sedentary behavior (Mountainspring and Scott 1985) suggests that, if important, they may only disperse seeds locally.

'Oma'o were infrequent visitors to firetree when compared with more common species (Japanese white-eyes and 'apapane), but the high number of fruit eaten per visit (Table 2) and their opportunistic foraging behavior indicate that these birds could be important dispersal agents of firetree. Similarly, the introduced house finch, a granivore-insectivore, is less common in these areas but feeds on firetree fruit (Table 2) and may be of secondary importance in its dispersal. The omnivorous myna, relatively common in the vicinity of nearby Volcano Village, was not observed in the study areas but is possibly an important disperser in areas where its distribution overlaps that of firetree.

Germination Trials Following Ingestion of Seeds by Japanese White-eyes and Common Mynas

Firetree seeds passed through Japanese white-eye and myna guts unaffected. The results of foraging behavior in firetree first might suggest that Japanese white-eye is potentially the most effective dispersal agent of

TABLE 2

Foraging Behavior of Six Bird Species at Puhimau Crater and Kilauea Crater Rim, Hawaii Volcanoes National Park

			Foraging Visits*				Foraging Activity†				
			ʻOhiʻa		Firetree		ʻOhiʻa		Firetree		
Species	Status		No.	Total time	No.	Total time	Glean insects	Probe flowers	Glean insects	Berries eaten	× Berries per visit
ʻApapane	native	no.	160	78.4	29	27.8	86	68	9	0	0
(*Himatione sanguinea*)		%	84.66	73.82	15.34	26.18	52.76	41.72	5.52	0	0
ʻOmaʻo	native	no.	5	6.4	3	4.6	0	0	0	7	0
(*Phaeornis obscuris*)		%	62.50	58.18	37.50	41.82	0	0	0	100	
ʻAmakihi	native	no.	10	5.2	1	0.3	9	0	0	0‡	0
(*Hemignathus virens*)		%	90.91	94.55	9.09	0.05	100	0	0	0	
Japanese white-eye	alien	no.	111	63.8	140	66.9	73	37	24	37	0.2
(*Zosterops japonicus*)		%	44.22	48.81	55.78	51.19	40.96	22.29	14.46	22.29	
House finch	alien	no.	18	22.0	12	14.4	0	3	0	8	0.7
(*Carpodacus mexicanus*)		%	60.00	60.44	40.00	39.56	0	27.27	0	72.73	
Northern cardinal	alien	no.	1	0.1	2	0.8	0	0	0	0	0
(*Cardinalis cardinalis*)		%	33.33	11.11	66.67	88.89	0	0	0	0	

* Time in minutes.

† Number of attempts.

‡ ʻAmakihi were observed foraging on firetree berries during reconnaissance studies at Ainahou, Hawaii Volcanoes National Park, but were not seen foraging on berries during the study period at either of the two study sites.

firetree in the Puhimau and Crater Rim areas of HVNP (Table 2). The birds are the most frequent visitors to firetree. However, studies on food preferences in captivity (Table 3) indicate that Japanese white-eyes do not normally ingest the seeds. Furthermore, it is noteworthy that in captivity Japanese white-eyes showed little interest when offered firetree fruit itself. This, in contrast to their behavior in the wild, suggests a need for caution when extrapolating the behavior of captive birds from laboratory to field situations. Captive mynas showed a slightly higher preference for firetree fruit, but field data are not available.

Fruit of several other fleshy-fruited native and weedy alien plants were fed to the captive Japanese white-eyes and mynas (Table 3). In captivity, Japanese white-eyes readily ate the fruit of small-seeded species, while showing a lower preference for larger-seeded fruit. Mynas exhibited no discernible preference for various fruits but refused those of *Pyracantha angustifolia* (Franch.) Schneid, *Psidium guajava* L., and *Schinus terebinthifolius* Raddi. Both mynas and Japanese white-eyes also refused the fruit of three native species: *Cheirodendron trigynum* (Gaud.) Heller, *Osteomeles anthyllidifolia* Lindl., and *Styphelia tameiameia* (Cham.) F. Muell. (Table 3).

Japanese white-eyes ate all the seeds of the species tested that were apparently easy to swallow. Mynas, on the other hand, were much more selective and did not eat fruit of some species well within their capability to swallow (for example, *Schinus terebinthifolius*, *Psidium guajava*, and *Pyracantha angustifolia*). Most of the plant species tested are weedy and/or pioneer species, and uningested seed exhibited rapid or intermediate germination rates (*sensu* Ng 1973: table 3). Passage of seeds through guts of mynas and Japanese white-eyes resulted in a germination rate equal to or slightly higher than control seeds, but this did not change the rate classification (rapid, intermediate, or delayed) of any species (Table 3). Germination success was generally not affected by passage, although it was reduced slightly for several species (Table 3). Some loss of viability is not uncommon in animal-dispersed seeds (Krefting and Roe 1949).

CONCLUSIONS

The common occurrence of Japanese white-eyes in firetree and their frequent foraging visits between ‘ohi‘a and firetree would suggest that the close physical association between these two tree species in HVNP (Smathers and Gardner 1979) is a consequence of the Japanese white-eye's foraging and movement patterns. However, Japanese white-eyes rarely ingest the seeds. Therefore they cannot disperse the seed over great distances. These results do not preclude the possibility that other birds, such as ‘oma‘o and house finches, do not act in this way. In fact, there is some evidence supporting this idea (Table 2). The alternative possibility that germination and establishment of firetree are favored by the environment under ‘ohi‘a cannot be excluded, although Smathers and Gardner (1979) noted a relative shade intolerance of firetree. Other studies have indicated that germination and establishment may be augmented by birds' removal of seeds from the parent tree. Such removal may reduce the problems associated with intense seedling competition (Howe 1977; Howe and Vandekerkhove 1981) or possible self-allelopathy under the parent tree.

As with most vertebrate-dispersed seeds, firetree is also disseminated by animals other than birds. Feral pigs and rats spread these seeds in Hawaii (Stone and Taylor 1984; L. D. Whiteaker, pers. comm.). The rapid spread of firetree in Hawaii is probably the result of its high reproductive capacity and effective dispersal by both native and introduced animals.

ACKNOWLEDGMENTS

Our thanks to Dina Kageler for her assistance in the field portion of this study, as well as for helping to maintain the captive birds. We appreciate the help of Charles P. Stone, James D. Jacobi, Lani Stemmerman, and Paul C. Banko in reviewing portions of the manuscript.

TABLE 3

Effect of Seed Ingestion by Common Mynas (*Acridotheres tristis*) and Japanese White-eyes (*Zosterops japonicus*) on the Germination of Seeds of Various Fleshy-Fruited Plant Species as Calculated with Duncan's Multiple Range Test

PLANT	BIRD	FOOD PREF.	GERMINATION %	GERMINATION RATE GT_{50} WK	"BEHAVIOR"*
Introduced					
Hedychium gardnerianum	control	—	56.67b†	4.16a	intermed.
	myna	med.	87.33a	3.83a	
	Japanese white-eye	—	—	—	
Myrica faya	control	—	35.60a	3.33a	intermed.
	myna	med.	33.00a	3.17a	
	Japanese white-eye	low	—	—	
Passiflora mollissima	control	—	90.00a	9.17a	intermed.
	myna	high	83.30a	7.83b	
	Japanese white-eye	low	—	—	
Psidium cattleianum	control	—	34.40a	5.80b	rapid
	myna	low	12.70b	7.00a	
	Japanese white-eye	med.	20.40b	5.00c	
Psidium guajava	control	—	47.70a	4.00a	rapid
	myna	0	—	—	
	Japanese white-eye	low	42.70a	3.83a	
Pyracantha angustifolia	control	—	46.30a	3.33a	rapid
	myna	0	—	—	
	Japanese white-eye	low	54.30a	3.17a	
Rubus ellipticus	control	—	83.30a	9.17a	intermed.
	myna	high	44.00c	10.50a	
	Japanese white-eye	high	63.70b	9.83a	
Rubus glaucus	control	—	32.30b	11.33b	intermed.
	myna	low	54.60a	14.17a	
	Japanese white-eye	high	37.30b	12.33ab	
Rubus penetrans	control	—	21.00a	21.33a	delayed
	myna	high	27.30a	17.50b	
	Japanese white-eye	high	19.30a	16.33b	
Rubus rosaefolius	control	—	37.70a	19.33a	intermed.
	myna	low	27.70a	14.00b	
	Japanese white-eye	med.	19.30a	14.67b	
Schinus terebinthifolius	control	—	34.30a	3.00a	rapid
	myna	0‡	—	—	
	Japanese white-eye	med.	15.50a	2.33b	
Native					
Astelia mensiesiana	control	—	33.33a	23.00a	intermed.
	myna	med.	38.17a	21.67a	
	Japanese white-eye	low	—	—	
Vaccinium calycinum	control	—	72.00a	3.66b	intermed.
	myna	low	73.66a	4.17ab	
	Japanese white-eye	low	43.00a	6.00a	
Vaccinium reticulatum	control	—	88.70a	3.17a	rapid
	myna	med.	88.30a	3.00a	
	Japanese white-eye	low	64.50a	3.50a	
Cheirondendron trigynum	myna	0	—	—	
	Japanese white-eye	0	—	—	
Osteomeles anthyllidifolia	myna	0	—	—	
	Japanese white-eye	0	—	—	
Styphelia tameiameia	myna	0	—	—	
	Japanese white-eye	0	—	—	

* "Behavior" of germination *sensu* Ng (1973).
† Means with the same letter are not significantly different.
‡ 0 = birds would not eat fruit when offered; therefore germination was not tested.

LITERATURE CITED

CLARK, D. A., and D. B. CLARK. 1981. Effects of seed dispersal by animals on the regeneration of *Bursera graveolens* (Burseraceae) on Santa Fe Islands, Galápagos. Oecologia 49:73–75.

HOWE, H. F. 1977. Bird activity and seed dispersal of a tropical wet forest tree. Ecology 58:539–550.

HOWE, H. F., and G. A. VANDEKERKHOVE. 1981. Removal of wild nutmeg (*Virola surinamensis*) crops by birds. Ecology 62:1093–1106.

JANZEN, D. H. 1983. Dispersal of seeds by vertebrate guts. Chap. 11 *in* D. J. Futuyma and M. Slatkin, eds., Coevolution. Sinauer Assoc., Sunderland, MA.

KREFTING, L. W., and E. I. ROE. 1949. The role of some birds and mammals in seed germination. Ecol. Monog. 19:269–286.

MOUNTAINSPRING, S., and J. M. SCOTT. 1985. Interspecific competition among Hawaiian forest birds. Ecol. Monog. 55:219–239.

NEAL, M. C. 1965. In gardens of Hawaii. B. P. Bishop Mus. Pub. 50. Bishop Museum Press, Honolulu.

NG, F.S.P. 1973. Germination of fresh seeds of Malaysian trees. Malay. For. 36:54–65.

SMATHERS, G. A., and D. E. GARDNER. 1979. Stand analysis of an invading firetree (*Myrica faya* Ait.) population, Hawaii. Pac. Sci. 33:239–255.

STAPANIAN, M. 1982. A model for fruiting display: Seed dispersal by birds for mulberry trees. Ecology 63:1432–1443.

STONE, C. P., and D. D. TAYLOR. 1984. Status of feral pig management and research in Hawaii Volcanoes National Park. Proc. Hawaii Volcanoes Natl. Park Nat. Sci. Conf. 5:106–117.

WHITEAKER, L. D., and D. E. GARDNER. 1985. Distribution of *Myrica faya* Ait. in the state of Hawaii. Natl. Park. Serv. CPSU/Univ. Haw. Tech. Rep. 55. 36 pp.