

Use of the Exotic Tree *Myrica faya* by Native and Exotic Birds in Hawai'i Volcanoes National Park¹

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ABSTRACT: The exotic nitrogen-fixing tree *Myrica faya* is invading Hawai'i Volcanoes National Park (HAVO). Observations of avian use of *M. faya* demonstrated that although four species of native birds visited the trees, they rarely fed on the fruits. Seven species of exotic birds were seen visiting *M. faya*, and five of these were observed ingesting the fruit. The most frequent visitor and consumer was the Japanese White-eye (*Zosterops japonicus*). Over one-third of the captured *Z. japonicus* produced fecal samples containing *M. faya* seeds, and those seeds were as viable as those picked from *M. faya* trees and beneath their canopies.

THE SYMBIOTIC nitrogen-fixing tree *Myrica faya* Ait. (Myricaceae) was introduced to Hawai'i from the Canary Islands or Azores late in the nineteenth century. Colonization of *M. faya* is favored by human disturbance, as is true of most exotic species in Hawai'i and elsewhere (Allan 1936, Egler 1942, Orians 1986, Crawley 1987). However, *M. faya* also colonizes and dominates otherwise undisturbed primary successional sites and seasonal submontane forests in Hawai'i Volcanoes National Park (HAVO) (Whiteaker and Gardner 1985). Within HAVO, *M. faya* is invading strongly nitrogen-deficient sites that previously lacked a symbiotic nitrogen-fixing plant. Colonization by *M. faya* significantly increases ecosystem-level inputs and biological availability of nitrogen (Vitousek et al. 1987, Vitousek and Walker 1989); it therefore represents a more serious threat to native biota and natural successional patterns than invasions that do not alter ecosystem-level properties.

In HAVO, *M. faya* establishes primarily in open-canopied areas in microsites under the

canopy of other trees and shrubs (Smathers and Gardner 1979). This pattern of establishment reflects *M. faya* seed rain; from 2.5 to 4.8 seeds per month have been captured in seed traps (1 m²) under the native tree *Metrosideros polymorpha*, while none was captured in the open (Vitousek and Walker 1989). This pattern of seed rain is characteristic of plants in which seeds are dispersed by perching birds (Glyphis et al. 1981, McDonnell and Stiles 1983, McDonnell 1986).

The fruit of *M. faya* is a fleshy drupe (Gardner 1985) believed to be bird-dispersed in its native habitat. Smathers and Gardner (1979) speculated that the exotic Japanese White-eye (*Zosterops japonicus*) is the major agent of dispersal in HAVO because of its abundance and its broad diet, which includes fruit, foliage insects, and *M. polymorpha* nectar. However, LaRosa et al. (1985) combined experiments on caged birds with 86 hr of observation on avian use of *M. faya* and concluded that although *Z. japonicus* is a frequent visitor to *M. faya*, it rarely consumes the fruit. They suggested that the exotic House Finch (*Carpodacus mexicanus*) and the native 'Ōma'ō (*Myadestes obscurus*) are more important agents of *M. faya* dispersal in HAVO.

We observed avian visits to *M. faya*, seed consumption, and presence and germination potential of seeds in the feces of captured birds across a range of sites colonized by *M. faya*.

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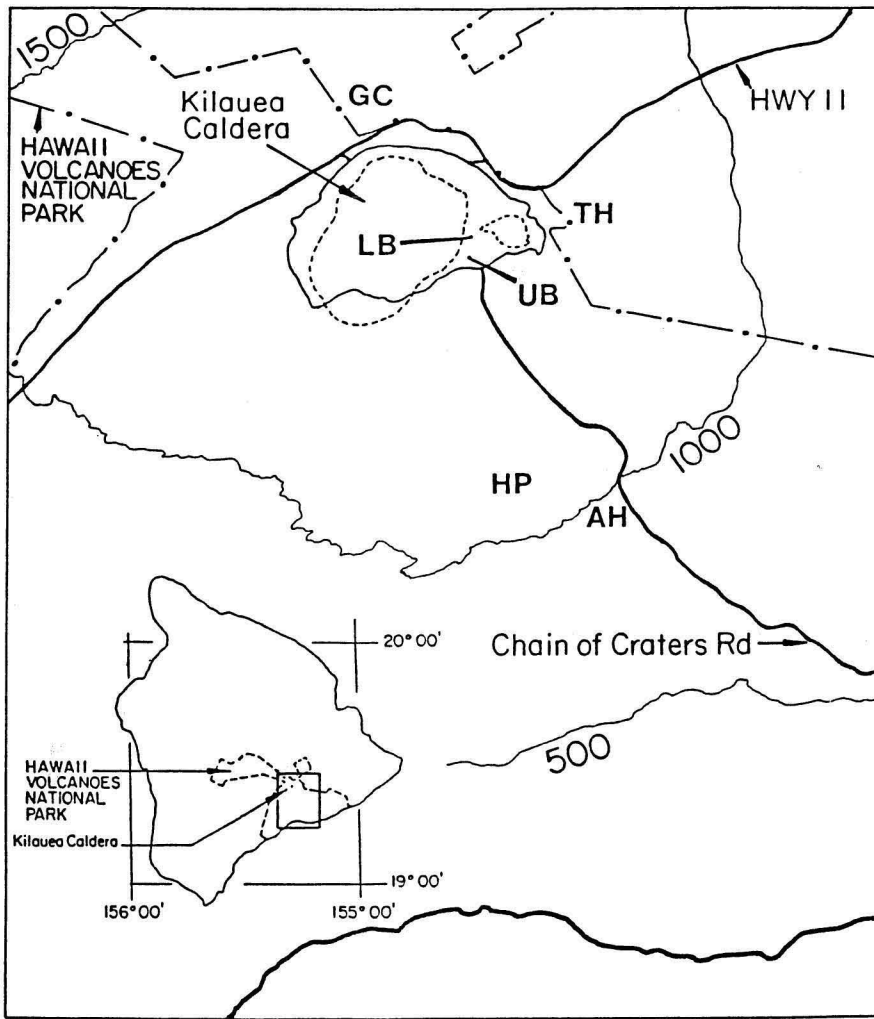


FIGURE 1. Locations of the study sites in Hawai'i Volcanoes National Park.

Our goals were to determine the relative importance of frugivory by native versus exotic birds in the six sites, and to determine their relative effectiveness in dispersing seeds of *M. faya* in two of those sites.

MATERIALS AND METHODS

Study Sites

Six sites were selected in and near the summit area and upper east rift of Kilauea Volcano

(19°20' N, 155°15' W) in HAVO (Figure 1). Two of these (UB and LB) were in areas with an intermittent overstory of *M. polymorpha* that had survived 1–2 m of cinderfall from a 1959 eruption of Kilauea Iki Crater (Smathers and Mueller-Dombois 1974). The LB site has a large population of *M. faya* (now ca. 1100 individuals per ha), but *M. faya* colonization is much less advanced in the UB site (ca. 100 individuals per ha). Two sites (HP and AH) were set up in seasonal submontane forest south of the upper east rift of Kilauea (Mueller-Dombois et al. 1981), which is characterized

by a sparse overstory of *M. polymorpha* with an understory of *M. faya* and exotic grasses. Another site (TH) was selected in closed-canopy montane rainforest that dates from an explosive eruption of Kīlauea in 1790. A sparse *M. faya* population (40 individuals per ha) persists in the understory of this site; they can reach the canopy following treefall or stand-level canopy dieback (Mueller-Dombois 1987). Finally, the sixth site (GC) was established in a residential subdivision near HAVO; *M. faya* is now the dominant tree in vacant house lots that were bulldozed and then abandoned.

Methods

Observations of bird use of *M. faya* were conducted from July to December 1987, a period spanning *M. faya*'s peak fruiting season (Whiteaker and Gardner 1987). Each observation lasted for $\frac{1}{2}$ hr and included one to four *M. faya* trees. The location, sex, fruiting phenology, and growth form of each tree were recorded. Observers chose a concealed location (6 to 20 m away) from which to observe; every tree watched during a $\frac{1}{2}$ -hr observation period was counted as $\frac{1}{2}$ tree-hour. Observations were conducted in all weather conditions and throughout the day.

We recorded the species of each bird visiting a tree, the duration it stayed, and its activities while in the tree. From September to December, we also recorded the number of fruits observed to be removed from the tree. However, because birds were often hidden by foliage within the tree, this number is an underestimate of all seeds taken.

Between 10 October and 24 November, mist-nets were maintained in the UB and LB sites to obtain fecal samples from birds. The mist-nets were 6 to 12 m long and 2.5 m high; the mesh size was 38 mm. Nets were situated either against a row of *M. faya* and *M. polymorpha* trees or within a corridor between trees. Mist-netting was carried out for a total of 212.5 net-hours in UB and 146.4 net-hours in LB. Captured birds were held in a muslin bag for 30 min to obtain a fecal sample. Seeds found in the fecal samples were planted in a

greenhouse along with control groups of *M. faya* seeds collected from trees.

RESULTS AND DISCUSSION

Visitation Rates

Avian activity in *M. faya* was observed for a total of 986.5 tree-hours (504.5 total hours) in the six sites. A total of 1965 visits by 11 species of birds (4 native, 7 exotic) was recorded. The largest number of visits per hour occurred in the morning, while the lowest visitation rate was at midday. No variation in visits as a function of weather was observed. There was significant variation in visits per tree-hour depending on sex of the *M. faya* observed; pistillate and bisexual trees were preferred over staminate trees by a factor of ca. 2 : 1 ($P < .001$, χ^2). Of the total visits to *M. faya*, 80% were by *Z. japonicus*, which was the most important visitor in each site (Table 1). The two other exotic species seen frequently were *C. mexicanus* (House Finch) and *Cardinalis cardinalis* (Northern Cardinal). Both were observed most often at the GC site, the most disturbed of the study areas. The most frequent native bird was *Himatione sanguinea* ('Apapane). Though restricted principally to the UB, LB, and TH sites, *H. sanguinea* had an overall visitation rate second only to that of *Z. japonicus*. In the TH site, the native *M. obscurus* ('Ōma'o) was also seen frequently.

Seed Ingestion

Consumption of *M. faya* seeds was limited almost entirely to exotic birds. One native species (*M. obscurus*) was observed ingesting two seeds throughout the 6-month study, and none of the other natives now present in the sites (with the possible exception of *Hemignathus virens*) would be expected to consume fruit. *Z. japonicus* was the most frequent consumer of *M. faya* seeds and was seen ingesting fruit at all sites (Table 2). *Z. japonicus* was also observed carrying the intact fruit in its bill, and on one occasion an individual was seen bringing fruit to a nest.

TABLE 1
AVIAN VISITS TO *M. faya* (IN NUMBER OF VISITS PER TREE-HOUR OF OBSERVATION)

	UB	LB	HP	AH	TH	GC
Total number of tree-hours	126	276	173	133.5	76	202
Exotic birds						
<i>Zosterops japonicus</i>	1.79	1.89	1.45	2.16	0.66	1.66
<i>Carpodacus mexicanus</i>	0	0.01	0.01	0.01	0	0.28
<i>Cardinalis cardinalis</i>	0.03	0.02	0	0.01	0	0.15
<i>Lophura leucomelana</i>	0.05	0.05	0	0	0	0
<i>Acridotheres tristis</i>	0	0	0	0	0	0.03
<i>Garrulax canorus</i>	0.01	0.01	0	0	0	0
<i>Lonchura punctulata</i>	0	0	0	0	0	0.02
Exotic bird total	1.88	1.98	1.46	2.18	0.66	2.14
Native birds						
<i>Himatione sanguinea</i>	0.14	0.21	0	0.02	0.17	0
<i>Chasiempus sandwichensis</i>	0	0.02	0	0	0	0
<i>Hemignathus virens</i>	0.02	0	0.02	0.04	0	0
<i>Myadestes obscurus</i>	0.01	0	0.01	0	0.12	0
Native bird total	0.17	0.23	0.03	0.06	0.39	0
Combined total	2.05	2.21	1.49	2.24	1.05	2.14

TABLE 2
AVIAN CONSUMPTION OF *M. faya* (IN NUMBER OF FRUITS INGESTED PER TREE-HOUR OF OBSERVATION)

	UB	LB	HP	AH	TH	GC
Total number of tree-hours	126	276	173	133.5	76	202
Exotic birds						
<i>Zosterops japonicus</i>	0.16	0.09	0.05	0.05	0.21	0.09
<i>Carpodacus mexicanus</i>	0	0	0	0	0	2.7
<i>Cardinalis cardinalis</i>	0	0	0	0	0	0.10
<i>Acridotheres tristis</i>	0	0	0	0	0	0.01
Native birds						
<i>Myadestes obscurus</i>	0.01	0	0	0	0.03	0

Feeding by exotics other than *Z. japonicus* was noted during regular observations only at the GC site, where *C. mexicanus* was observed to consume large numbers of fruit on two occasions. Though we could not determine whether the finches were crushing the seeds or swallowing them intact, ingestion by *C. mexicanus* could be substantial. In 202 hr of observation at this human-disturbed site, 546 seeds were taken by *C. mexicanus*, while only 42 were ingested by *Z. japonicus*. *C. cardinalis* and *Acridotheres tristis* (Common Myna) were also observed ingesting a few *M. faya* fruits at this site. Outside our regular observation periods, Kalij Pheasants (*Lophura leucomelana*)

were observed ingesting seeds from *M. faya* in both the UB and LB sites.

Mist-netting Results

Fifty-six birds of five species, only one of which was native, were captured with mist-nets in the UB and LB sites (Table 3). Eighty-four percent of the birds caught were *Z. japonicus*; this species accounted for 86% of the visitation in these sites. Only *Z. japonicus* passed *M. faya* seeds or fruit. Of the 47 *Z. japonicus* netted, 17 (36%) passed one to six *M. faya* seeds, and an additional 5 (11%) yielded *M. faya* fruit pulp only.

TABLE 3
BIRDS CAPTURED BY MIST-NETTING IN THE UB AND LB SITES (COMBINED)

SPECIES	NO. CAPTURED	% WITH <i>M. faya</i> IN FECES
<i>Zosterops japonicus</i>	47	47
<i>Himatione sanguinea</i>	4	0
<i>Cardinalis cardinalis</i>	1	0
<i>Carpodacus mexicanus</i>	2	0
<i>Leiothrix lutea</i>	2	0

Sixty seeds collected from *Z. japonicus* feces were planted to ascertain germination potential, along with 72 control seeds picked from and under *M. faya* trees. After 10 months, 21 *Z. japonicus*-passed seeds and 27 of the control seeds had germinated. This difference was not significant ($P > .05$, χ^2).

CONCLUSIONS

Our results indicate that *Z. japonicus* is the primary dispersal agent for the seeds of *M. faya* in natural areas of HAVO. It is the most frequent visitor, and *Z. japonicus* collected in the field passed viable *M. faya* seeds. Other exotic birds (particularly *C. mexicanus*) may be important in more modified habitats. These results contrast with LaRosa et al.'s (1985) conclusion that "white-eyes [*Z. japonicus*] rarely ingest the seeds," but support Smathers and Gardner's (1979) suggestion of a correlation between the foraging patterns of *Z. japonicus* and the *M. faya* invasion.

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LITERATURE CITED

- ALLAN, H. H. 1936. Indigene versus alien in the New Zealand plant world. *Ecology* 17: 187-193.
- CRAWLEY, M. J. 1987. What makes a community invasible? Pages 429-453 in A. J. Gray, M. J. Crawley, and P. J. Edwards, eds. *Colonization, succession and stability*. Blackwell Scientific Publications, Oxford.
- EGLER, F. E. 1942. Indigene versus alien in the development of arid Hawaiian vegetation. *Ecology* 23: 14-23.
- GARDNER, D. E. 1985. Observations on some unusual flowering characteristics of *Myrica faya*. *Newsl. Hawaii. Bot. Soc.* 24: 14-17.
- GLYPHIS, J. P., S. J. MILTON, and W. R. SIEGFRIED. 1981. Dispersal of *Acacia cyclops* by birds. *Oecologia (Berlin)* 48: 138-141.
- LA ROSA, A. M., C. W. SMITH, and D. E. GARDNER. 1985. Role of alien and native birds in the dissemination of fire tree (*Myrica faya* Ait.-Myricaceae) and associated plants in Hawaii. *Pac. Sci.* 39: 372-378.
- MCDONNELL, M. J. 1986. Old field vegetation height and the dispersal pattern of bird-disseminated woody plants. *Bull. Torrey Bot. Club* 113: 6-11.
- MCDONNELL, M. J., and E. W. STILES. 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia (Berlin)* 56: 109-116.
- MUELLER-DOMBOIS, D. 1987. Forest dynamics in Hawaii. *Trends Ecol. Evol.* 2: 216-220.
- MUELLER-DOMBOIS, D., K. W. BRIDGES, and H. L. CARSON, eds. 1981. *Island ecosystems: Biological organization in selected Hawaiian communities*. Hutchinson Ross, Stroudsburg, Pennsylvania.

- ORIAN, G. H. 1986. Site characteristics favoring invasions. Pages 133–148 in H. A. Mooney and J. Drake, eds. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York.
- SMATHERS, G. A., and D. E. GARDNER. 1979. Stand analysis of an invading firetree (*Myrica faya* Aiton) population, Hawaii. Pac. Sci. 33:239–255.
- SMATHERS, G. A., and D. MUELLER-DOMBOIS. 1974. Invasion and recovery of vegetation after a volcanic eruption in Hawaii. Nat. Park Serv. Sci. Monogr. no. 5.
- VITOUSEK, P. M., and L. R. WALKER. 1989. Biological invasion by *Myrica faya* in Hawaii: Plant demography, nitrogen fixation, and ecosystem effects. Ecol. Mongr. 59: 247–265.
- VITOUSEK, P. M., L. R. WALKER, D. MUELLER-DOMBOIS, and P. A. MATSON. 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. Science 238:802–804.
- WHITEAKER, L. D., and D. E. GARDNER. 1985. The distribution of *Myrica faya* Ait. in the state of Hawaii. Technical Report no. 55. Cooperative National Park Resources Study Unit, University of Hawaii at Manoa, National Park Service.
- . 1987. The phenology and stand structure of *Myrica faya* Ait. in Hawaii. Technical Report no. 62. Cooperative National Park Resources Study Unit, University of Hawaii at Manoa, National Park Service.