Movement Patterns of a Native and Non-native Frugivore in Hawaii and Implications for Seed Dispersal

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ABSTRACT

Avian frugivores historically played important roles as seed dispersers across the Hawaiian Islands, but presently, the 'Ōma'o (*Myadestes obscurus*) is the only extant native frugivore in the wild on the Island of Hawaii. During recent decades, the introduced generalist Japanese White-eye (*Zosterops japonicus*) has become the most common bird in Hawaii. The movements of avian frugivores largely dictate how far seeds get dispersed and into what kinds of microhabitats. This study compares the movement patterns and diet of the 'Ōma'o to the Japanese White-eye to understand how a native differs from a non-native frugivore in the type and distances of seeds dispersed. Radiotelemetry was conducted on nine 'Ōma'o and nine Japanese White-eyes in a system of natural forest fragments (*kīpuka*) created by lava flows. Japanese White-eyes disperse seeds approximately twice as far as 'Ōma'o; during the time of gut passage, 'Ōma'o move a mean distance of 98.1 m, and Japanese White-eyes move 170.1–194.8 m. However, the 'Ōma'o disperses the seeds of at least seven different native fruit species compared with two dispersed by Japanese White-eyes. Japanese White-eyes were found to disperse seeds smaller than 1.5 mm, whereas the 'Ōma'o dispersed seeds up to 6 mm in diameter. Despite their ecological differences, both birds distribute certain seeds within and among *kīpuka* and likely facilitate primary succession of fruiting plants in the young lava matrix. However, this study suggests that if the 'Ōma'o were extirpated, a smaller-bodied generalist cannot entirely substitute for the ecological role played by the native frugivore.

Key words: fragmented forest; *Myadestes obscurus*; radiotelemetry; *Zosterops japonicas*.

THE ROLE OF BIRDS IN PROVIDING SEED DISPERSAL SERVICES HAS LONG BEEN RECOGNIZED (Howe & Smallwood 1982, Janzen 1983). Frugivores have been shown to maintain plant communities in temperate ecosystems (Garcia *et al.* 2009) and are particularly important in tropical systems (Sekercioglu 2006, Pejchar *et al.* 2008), where often more than 75 percent of trees have evolved fleshy fruits adapted for dispersal by birds or mammals (Howe 1977). In addition, introduced birds are increasingly established in ecosystems worldwide (Blackburn *et al.* 2009). Native and non-native frugivores have the capacity to differentially impact forest dynamics depending on the seeds they disperse (Simberloff & Von Holle 1999, Foster & Robinson 2007, Chimera & Drake 2010). This is especially important in the Hawaiian Islands, where native frugivores, except for the 'Ōma'o (*Myadestes obscurus*; Wakelee & Fancy 1999), are either actually extinct, or, in the case of the 'Alalā (*Corvus hawaiiensis*) and the Puaiohi (*Myadestes palmeri*), functionally extinct, while more species of birds have been introduced than anywhere else in the world (Long 1981, Moulton & Pimm 1983). Despite being relatively common where it occurs, the 'Ōma'o now occupies only 25–30 percent of its former range on the Island of Hawaii (Wakelee & Fancy 1999) and is listed as vulnerable to extinction (Birdlife International 2012). Meanwhile, the Japanese White-eye has become the most abundant bird across the main Hawaiian Islands and thus is likely to

be one of the primary consumers of fruit in Hawaii (Garrison 2003, Foster & Robinson 2007). The White-eye is a diet generalist (Mountainspring & Scott 1985) with a gape size limitation of about 8 mm (Corlett 1998) compared with the gape size of about 17 mm in the 'Ōma'o (derived from the size of the largest fruits it swallowed in Culliney *et al.* 2012).

Frugivore movements also greatly influence seed dispersal patterns (Holbrook 2010). Frugivores can drastically increase the seed shadow (Sekercioglu 2006, Spiegel & Nathan 2007), and the microhabitats where seeds are deposited have important implications for germination success (Howe 1977, Janzen 1983). 'Ōma'o tracked at Hakalau Forest National Wildlife Refuge on Hawaii Island had a small home range of 3–4 hectares (Wakelee 1996), indicating potentially short distances of seed dispersal.). The likely only previous radiotelemetry study found that the range of Japanese White-eyes in Japan varies in inversely proportional to food density (Abe *et al.* 2011), and banding studies suggest that they make large movements (Guest 1973; P. Hart, unpubl. data). Nevertheless, there remains a gap in knowledge about their daily movement patterns and in fragmented landscapes.

In the Hawaiian system of forest islands naturally fragmented by lava (these island fragments are known as *kīpuka*), researchers have found that fleshy-fruited species did not appear until the early successional, wind-dispersed *Metrosideros polymorpha* grew to be perch-height (Drake & Mueller-Dombois 1993) and postulate that frugivores contribute to succession. Another study found similar fruiting plants from the smallest to the largest frag-

ment and hypothesize that the ʻŌmaʻo is partially responsible for dispersing seeds across fragments (Flaspohler *et al.* 2010). This study attempts to fill the gaps in frugivore movement and seed dispersal among fragments. First, the native and non-native birds were tracked using radiotelemetry to determine seed dispersal distances and use of the *kīpuka* and matrix areas. Secondly, diet analysis was used to determine how the ʻŌmaʻo and Japanese White-eye differ in the fruits that they consume and the seeds that they disperse. The aim of this study is to address, from these two angles, whether seed dispersal services are improved or impaired by the introduced White-eye.

METHODS

STUDY SITE.—The lava-fragmented system on the Island of Hawaii is an excellent model system to investigate questions relating to dispersal ecology. The region was once a contiguous forest on substrate that is 3000–5000 years old, but Mauna Loa volcanic eruptions in 1855 and 1880 sent flows of molten lava downslope. These new lava flows are considered 'matrix' in this study, while those islands of remnant forest missed by the flows are known as 'kīpuka.' The 16 *kīpuka* chosen for this study vary in size from 0.1–10 ha (mean 1.67 ± 2.45 ha) and in proximity to intact forest tracts. The study area is around 19°40′ N, 155°21′ W (Fig. S1). Study sites range from 1480–1740 m in elevation and receive 2000–3000 mm of rainfall per year (Giambelluca *et al.* 2013). Temperatures range from approximately 10–20 °C (State of Hawaii 1970, NOAA, National Oceanic & Atmospheric Administration 2012). The canopy in the *kīpuka* forests is dominated by the native tree, *Metrosideros polymorpha* (Myrtaceae), with very sparsely distributed *Acacia koa* (Fabaceae) at higher elevations. Fruiting plants in the mid-canopy consisted of *Cheirodendron trigynum* (Araliaceae), pilo (*Coprosma* sp., Rubiaceae), *Ilex anomala* (Aquifoliaceae), *Myrsine lessertiana* (Myrsinaceae), and *Myoporum sandwicense* (Myoporaceae). *Rubus hawaiensis* (Rosaceae) and *Leptecophylla tameiameiae* (Ericaceae) grew in the forest understory, and *Vaccinium reticulatum* (Ericaceae) grew the matrix. *Rubus hawaiensis*, *Ilex anomala*, and *Cheirodendron trigynum* peaked in fruit production during April–August, while *Coprosma* sp., *Myrsine lessertiana*, *Myoporum sandwicense*, and *Leptecophylla tameiameiae* peaked during October–February (Kovach 2012). Native birds at the site are ʻApapane (*Himatione sanguinea*), Hawaii ʻAmakihi (*Hemignathus virens*), ʻŌmaʻo, ʻIʻiwi (*Vestiaria coccinea*), ʻElepaio (*Chasiempis sandwichensis*), and ʻIo (*Buteo solitarius*). The most common non-native species is the Japanese White-eye, and less common species are Red-billed Leiothrix (*Leiothrix lutea*), House Finch (*Carpodacus mexicanus*), Kalij Pheasant (*Lophura leucomelanos*), and Yellow-fronted Canary (*Serinus mozambicus*). The Red-billed Leiothrix is more frugivorous than the Japanese White-eye (Ralph & Noon 1986, Male *et al.* 1998) but were fairly uncommon in the region where we conducted our study (Flaspohler *et al.* 2010, Kovach 2012). Although excluded from this study, ground-dwelling Kalij Pheasant (Lewin & Lewin 1984) and Hawaii ʻAmakihi (Lindsey *et al.* 1998) are also potential seed dispersers in the study area.

TELEMETRY TRACKING.—Birds were captured using 5–7 m high nylon mist nets placed both inside *kīpuka* and the surrounding matrix. Birds were held in opaque cotton bags for five to fifteen min in preparation for transmitter attachment. ʻŌmaʻo and Japanese White-eye were outfitted with radio transmitters and tracked. Six ʻŌmaʻo were captured and tracked during the breeding season (February–April; Wakelee & Fancy 1999) and three during the non-breeding season (July–September). Japanese White-eyes can breed year-round; though, the peak season is March to June (van Riper 2000). All nine individuals were captured and tracked during February and June. The sex of the both species was not determined due to lack of dimorphism, and all the birds tracked were adults. Tracking occurred in 2–3 h segments from sunrise to sunset, in all weather conditions except for heavy rain, which was rare. Two observers used the R410 receiver from Advanced Telemetry Systems (ATS), a three-element Yagi antenna, and the Trimble® GeoXH most of the time, occasionally using recreational-grade GPS units. Fixes were taken every 5–10 min when the bird was in range. Observers attempted to get as close to the bird as possible (indicated by an increase in signal strength) before taking a bearing to reduce distance-dependent biangulation error. Occasionally, the tracked bird was sighted, and in those cases, the bird's exact location was recorded as a point.

Transmitters from ATS weighing 1.9 g were used for the ʻŌmaʻo, which have a mass of 50 g. Transmitters were attached using a figure-eight harness (Rappole & Tipton 1991) following methods in Wakelee (1996). The transmitter and harness weigh less than 4 percent of the bird's total body mass, and ʻŌmaʻo did not appear hindered by the system (Fancy *et al.* 1993, Wakelee 1996). However, we recognize potential negative effects of transmitters, such as increased energy expenditure and decreased likelihood of nesting (Barron *et al.* 2010). We used eight 0.5 g transmitters for the Japanese White-eye from ATS and one 0.5 g transmitter from Lotek. A figure-eight harness was made from rubber bands, and later, elastic sewing thread (H. Streby, pers. comm.) with loops 16 mm from the center of the harness to the end of the loop. Some Japanese White-eye individuals were stressed while we attached the transmitter, and one bird pecked it off. White-eyes were given half an hour after release to get used to the transmitter before tracking commenced. The antennas on the ATS transmitters kinked after a few days, causing range to decrease from 1–3 km to as little as 50–100 m. One Japanese White-eye was tracked using a transmitter from Lotek (Table S1). For this individual, the non-kinking antenna gave sufficient range to capture all of the bird's movements. As there is some error associated with locations obtained via radiotelemetry (Springer 1979, Haskell & Ballard 2007), telemetry error was estimated in the *kīpuka* landscape at varying distances from the transmitter.

DIET ANALYSIS.—When ʻŌmaʻo or Japanese White-eye defecated in the handling bags, their fecal matter was collected, frozen and then suspended in 70 percent or 100 percent ethanol for analysis under a dissecting microscope. In 2011 and 2012, seventy-two ʻŌmaʻo fecal samples were collected from February to May, and thirty-four Japanese White-eye fecal samples were collected from

February to July. The proportion, by volume relative to the other items in the fecal sample, of insect, fruit, and other matter was approximated to five percent. While the proportions serve as a comparison between the species, they may not accurately reflect diet quantification (Wakelee 1996) as some food types (*e.g.*, soft insect parts) may be more thoroughly digested than others (*e.g.*, fruit skin and fibers). Fruits from all common fruiting species in the *kīpuka* were collected to create a seed library to aid in the identification of seeds found in the fecal samples.

DATA ANALYSIS.—Bird locations, biangulations, were calculated using the software Location Of A Signal (LOAS; Ecological Software Solutions LLC). Nine errant location points more than 5 km from the study area were removed after cross-referencing the raw data. Geospatial Modeling Environment (GME; Spatial Ecology LLC) was used to calculate the distances between points. No gut passage trials have been performed with *Myadestes obscurus*, but studies with the Central American species *Myadestes melanops* found a median retention time of 16–22 min for a laxative fruit (Murray *et al.* 1994) and 25 min in a food without laxative effect (Murray 1988). The thrush *Turdus merula* passed seeds between 6–50 min (Sorensen 1984). Given the best available gut passage times of thrushes of comparable mass, we estimated a range of 24–36 min for the 'Ōma'o. Distances traveled during overlapping tracking intervals (*e.g.*, 0800–0830 h and 0810–0840 h on the same day) were considered independent samples because movement and location are inherently dependent on the bird's previous location (Holbrook 2010). Furthermore, there was no significant difference between using overlapping intervals and non-overlapping intervals ($t = 0.102$, $P = 0.9188$). Medeiros (2004) conducted the only gut passage trials with the Japanese White-eye and found that they passed three species of fruits in 60–210 min. However, all other studies on congeneric species of similar size and food habits found gut retention times of 6–33 min (Stanley & Lill 2002, Brown & Downs 2003, Logan & Xu 2006). Based on a body mass of 10 g and a generalist diet, gut passage time is estimated to be 30–80 min (Herrera 1984, Levey & Karasov 1989). Because of this large variation in gut passage times, two different gut passage time intervals were selected for the Japanese White-eye with a bias toward peer-reviewed studies: 30 ± 6, 60 ± 10 min.

Distances for each species were lumped across individuals to compare the 'Ōma'o with the Japanese White-eye as species based on methods used in the study described by Holbrook (2010). However, we recognize that one potential issue with this method is that movement distances are dependent on the individual. One-sided, two-sample *t*-tests were used (H_a of Japanese White-eye movements being larger) to assess difference between species in distance traveled during gut passage time. The distances moved by the six 'Ōma'o tracked during the breeding season were compared with the three tracked during the non-breeding season using a two-sample *t*-test. This comparison was not made for Japanese White-eyes because all were tracked during their breeding period. The distance from the mean center point was calculated as a metric of the birds' range of movement

(Fancy *et al.* 1993, Wakelee 1996) using ArcMap 10 (ArcInfo, ESRI®) and GME. Two-sample *t*-tests were used to assess difference between species (H_a of Japanese White-eye movements being larger). As a third metric of range, the home range sizes of the two bird species were calculated, and one-sided Wilcox tests were used to compare the 'Ōma'o to the White-eye (H_a of Japanese White-eye home range being larger). The minimum convex polygon (MCP) was calculated in ArcMap 10. GME was used to calculate the 50 percent and 95 percent kernel home range (KHR) sizes for the 'Ōma'o and White-eye, and the least-squares cross-validation bandwidth estimator method and a cell size of 20 was used (Gitzen & Millspaugh 2003, Katajisto & Moilanen 2006). Data from one Japanese White-eye were eliminated in home range analysis because it only contained 11 data points (Table S1). One-way ANOVA and subsequent Tukey's tests were carried out using Minitab® 16. Normality tests, *t*-tests, Wilcox tests, and graphs were carried out using R (v. 2.13.2).

RESULTS

MOVEMENT.—'Ōma'o traveled, on average, 98.1 ± 6.2 m over a 30-min period. A total of 518 location points were obtained from the nine 'Ōma'o that were tracked for 12–60 d (mean = 36.0) over approximately 160 h (Fig. 1; Table S1). As there was no difference in distance traveled between breeding and non-breeding season ($t = 1.51$, df = 203.93, $P = 0.93$), data were lumped in analysis. Seventy percent of 'Ōma'o location points were in *kīpuka* and forests, but all the individuals tracked made trips to the surrounding matrix, with two of nine birds spending more than 50 percent of the time in the matrix. Japanese White-eyes traveled 170.1 ± 6.8 m over a 30-min period, and 194.8 ± 7.4 m over a 60-min period (Table 1). A total of 680 location points were obtained from the nine Japanese White-eyes that were tracked over approximately 225 h (Fig. 2; Table S1). Individuals were tracked for 1–23 d (average 11.9 d; Table S1). Sixty percent of White-eye location points were in *kīpuka* and forests, seven of nine birds spent more than 50 percent of the time in the matrix with one individual being found only in the matrix for the duration of tracking (20 d). Distances during the 30- and 60-min period for the Japanese White-eye were significantly different from one other ($t = 2.96$, df = 1306.57, $P = 0.003$), and thus, the 'Ōma'o mean was compared with the Japanese White-eye mean from each gut passage period.

Over a 30-min period, Japanese White-eyes moved significantly farther than 'Ōma'o ($t = 7.95$, df = 613.26, $P < 0.001$; Table 1; Fig. 3). Over a 60-min period for the White-eye and 30-min period for the 'Ōma'o, White-eyes also moved significantly farther than 'Ōma'o ($t = 10.67$, df = 625.99, $P < 0.001$; Table 1; Fig. 3). Japanese White-eyes had significantly higher distances from the center of activity than 'Ōma'o ($t = 5.94$, df = 1159.32, $P < 0.001$; Table 2). Minimum convex polygon (MCP) home range sizes did not differ significantly between the two species ($W = 41$, $P = 0.50$; Table 2). There were also no significant differences for 50 percent KHR size ($W = 43$, $P = 0.27$) and 95 percent KHR size ($W = 37$, $P = 0.48$; Table 2). Mean error from biangula-
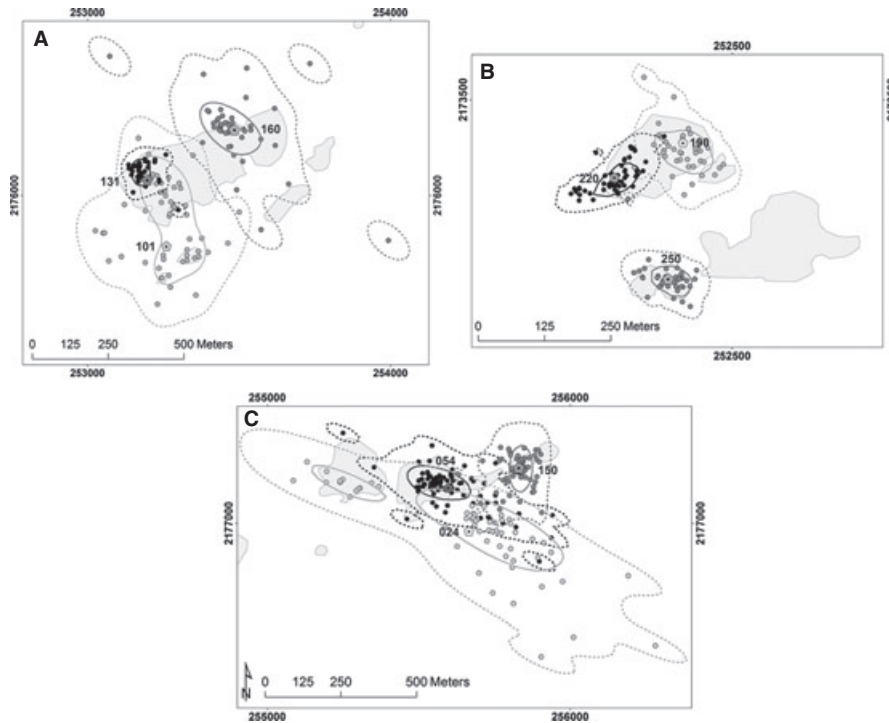
FIGURE 1. A detailed view of the nine 'Ōma'o tracked. The pentagon shapes represent the mean center location for each bird, and dots represent each location obtained. Birds are labeled according to the last digits of the transmitter frequency (see Table S1 for individual details). Solid lines represent the 50 percent KHR boundaries, and dashed lines represent the 95 percent KHR boundaries for each bird: (A) three 'Ōma'o tracked from March–April 2011; (B) three 'Ōma'o tracked from March–April 2011; and (C) three 'Ōma'o tracked from July–September 2011.

TABLE 1. *Distances traveled in gut passage time (GPT) for 'Ōma'o and Japanese White-eyes (JAWE).*

	OMAO 30 min	JAWE 30 min	JAWE 60 min
Distance traveled in GPT (m)			
Sample size	249	634	707
Mean (SE)	98.1 (6.2)	170.1 (6.8)	194.8 (7.4)
Median (IQR)	55.9 (28.1–114.7)	125.9 (54.3–240.7)	147.0 (68.7–303.0)

tion in the *kīpuka* system was calculated to be 12.76 ± 4.24 m. Recreational GPS units used for part of this study had an average error of 9.23–12.91 m under a forest canopy.

DIET ANALYSIS.—Seventy-two fecal samples were collected from 'Ōma'o, and 34 were collected from Japanese White-eyes. Of the 1148 seeds in all the fecal samples, 1146 were identified to the genus or species, and two were not identifiable. The seeds of *Vaccinium reticulatum* and *V. calycinum* are indistinguishable under the microscope, as are three species of pilo (*Coprosma* sp.) that occur in the region (Wagner *et al.* 1999, Table 3). However, pilo seeds could be distinguished from kūkaenēnē (*Coprosma ernodeoides*). Four seeds were identified only to the *Coprosma* genus because they were not similar enough to pilo or kūkaenēnē. Seeds ranging from 0.5–6 mm in size were found in 'Ōma'o fecal samples,

whereas Japanese White-eyes only dispersed the two smallest seeds in the study area, which were 0.5 and 1.5 mm in size (Table 3). 'Ōma'o dispersed seeds of at least seven different native species, whereas the Japanese White-eye was found to disperse *Vaccinium* and *Rubus hawaiensis* seeds. Eighty-five percent of 'Ōma'o fecal samples contained seeds compared with twenty-one percent of Japanese White-eye fecal samples. The frequency of fecal samples that contained seeds was significantly higher in 'Ōma'o than Japanese White-eyes ($\chi^2 = 40.2$, df = 1, $P < 0.0001$). Fruit pulp, skin, and seeds comprised 99.7 percent of 'Ōma'o diet; insect matter comprised 0.3 percent of its diet. Fruit pulp, skin, and seeds comprised 29.8 percent of Japanese White-eye diet; insect matter comprised 69.9 percent of its diet. 'Ōma'o consumed significantly more fruit than Japanese White-eyes ($W = 0.5$, $P < 0.001$), and Japanese White-eyes consumed significantly more insect than 'Ōma'o ($W = 614.5$, $P < 0.001$).

DISCUSSION

Seed dispersal in the *kīpuka* region is improved by the Japanese White-eye, particularly to matrix and neighboring *kīpuka*, but it cannot fully compensate for the 'Ōma'o if the native thrush were to be extirpated. Based on these results, Japanese White-eyes are likely to disperse seeds approximately twice as far (170.1–194.8 m) during gut passage period as 'Ōma'o (98.1 m) but disperse fewer, smaller seeds and fewer species of seeds. Distance travelled during gut pas-
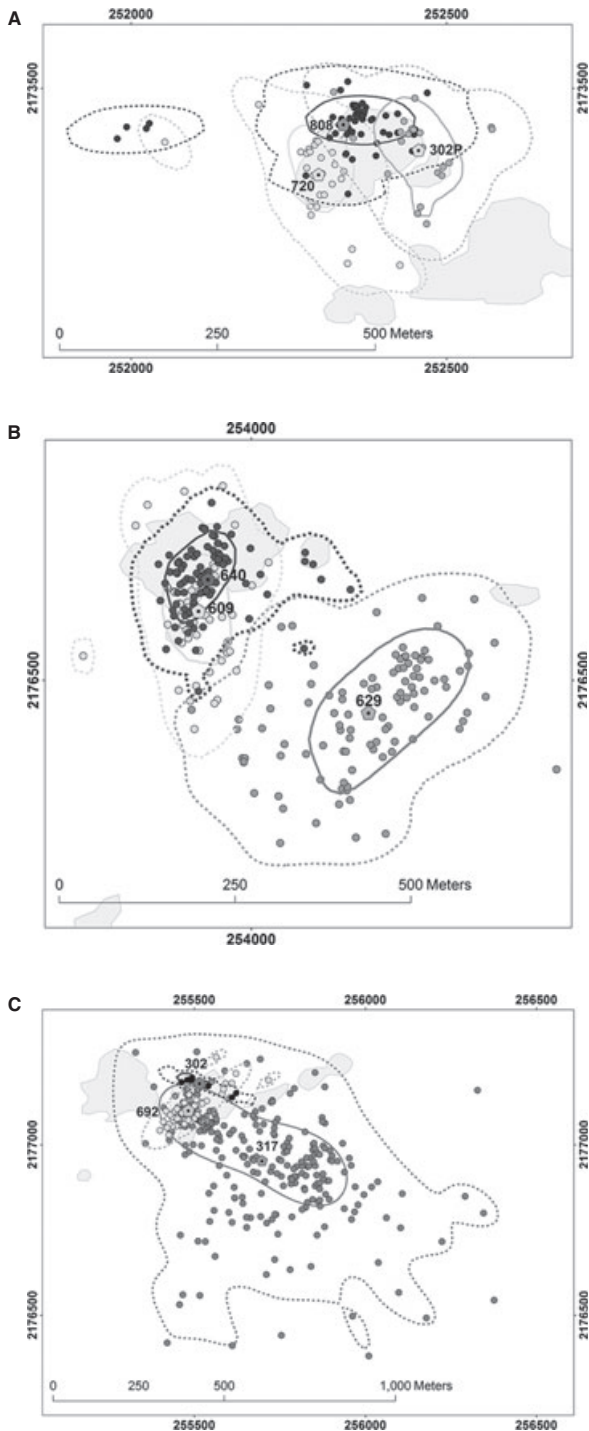
FIGURE 3. Graph showing the distances traveled during the bird's gut passage time. For ʻŌmaʻo, the distance moved in a 30-min period (N = 249) is graphed. For Japanese White-eyes, distance traveled is over a 30-min period (N = 634) and 60-min period (N = 691). Mean and SE are displayed above each bar.

TABLE 2. *Distance from the center of activity and home range metrics for ʻŌmaʻo and Japanese White-eyes (JAWE).*

	OMAO	JAWE
Distance from center of activity (m)		
Sample size	518	680
Mean (SE)	90.4 (4.7)	127.6 (4.3)
Median (IQR)	55.4 (27.3–106.0)	96.3 (44.3–182.5)
MCP (ha)		
Sample size	9	8
Mean (SE)	11.5 (4.1)	14.5 (9.2)
Median (IQR)	4.5 (1.7–16.7)	4.8 (4.1–7.3)
50 percent KHR (ha)		
Sample size	9	8
Mean (SE)	2.3 (0.9)	2.4 (1.1)
Median (IQR)	0.9 (0.5–2.3)	1.1 (1.0–2.0)
95 percent KHR (ha)		
Sample size	9	8
Mean (SE)	13.2 (4.7)	13.9 (6.9)
Median (IQR)	6.9 (2.4–21.8)	6.8 (5.9–8.9)

MCP = minimum convex polygon, KHR = kernel home range.

sage time and distance from center of activity both show the Japanese White-eye to be more volant than the ʻŌmaʻo within a similar sized home range. Both species spend much of the time in a core home range, but also go to neighboring *kīpuka* and to the matrix, thereby disseminating seeds across fragments. Most ʻŌmaʻo tracked did go to neighboring *kīpuka*, but three of nine never left their *kīpuka* during the months tracked. Anecdotally, White-eyes have a greater tendency to spend time in the matrix than ʻŌmaʻo. Movement rates of the first eight White-eyes are almost certainly underestimates as the birds that moved farther often could not be tracked. Another potential shortcoming is ʻŌmaʻo, and Japanese White-eyes

FIGURE 2. A detailed view of the nine Japanese White-eyes tracked. The pentagon shapes represent the mean center location for each bird and are labeled according to the last digits of the transmitter frequency (see Table S1 for individual details). Solid lines represent the 50 percent KHR boundaries, and dashed lines represent the 95 percent KHR boundaries for each bird: (A) three White-eyes tracked from February–March 2012; (B) three White-eyes tracked in March 2012; and (C) White-eyes 302 and 692 were tracked in February 2012, and 317 was tracked from May–June 2012. The latter is the only transmitter that experienced no range limitations.
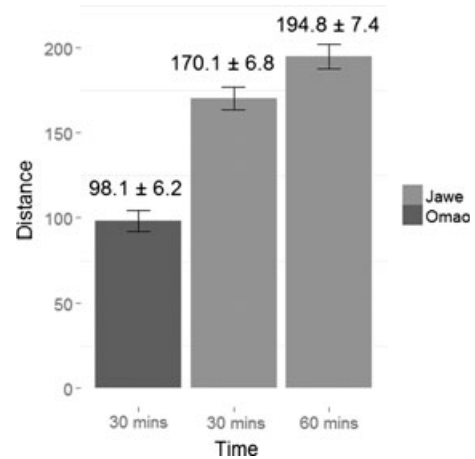
TABLE 3. *Total counts of seeds of the different species found in fecal samples of 'Ōma'o and Japanese White-eyes (JAWE).*

Species	Hawaiian name	Family	Fruit size (mm)	Seed size (mm)	OMAO (N = 72)	JAWE (N = 34)
Vaccinium reticulatum and *V. calycinum*	'Ohelo	Ericaceae	12[1]	0.5[1]	877	153
Rubus hawaiensis	'Akala	Rosaceae	35	1.5	3	7
Cheirodendron trigynum	'Ōlapa	Araliaceae	7.5[1]	5[1]	23	0
Coprosma ernodeoides	Kūkaenēnē	Rubiaceae	11	6	55	0
Coprosma ochracea, C. rhynchocarpa, and *C. pubens*	Pilo	Rubiaceae	10[1]	4	20	0
Other *Coprosma* spp.	NA	Rubiaceae	NA	5	4	0
Ilex anomala	Kāwa'u	Aquifoliaceae	9[1]	3[1]	2	0
Leptecophylla tameiameiae	Pūkiawe	Ericaceae	5[1]	3[1]	2	0
Unknown	NA	NA	NA	NA	2	0

[1]From Wagner *et al.* 1999. Other data are author's measurements.

Rubus hawaiensis numbers represent the number of druplets ingested.

NA = not applicable.

were not always tracked in the same *kīpuka*; resource availability increases with *kīpuka* size (Flaspohler *et al.* 2010, Kovach 2012), and so movement differences may partially track these differences (Abe *et al.* 2011). Nevertheless, the study of frugivore movement across a fragmented landscape is a critical area of research in an increasingly human-affected world (Fischer & Lidenmayer 2007, McConkey *et al.* 2012). The findings in this study, based on distance traveled over gut passage time and distance from mean center, are consistent with other studies that find the Japanese White-eye to be a wide-ranging bird (Guest 1973, van Riper 2000, Weir & Corlett 2007, Kawakami *et al.* 2009, Corlett 2011). However, the home ranges found in this study are an order of magnitude larger than small volcanic islands of Japan (Abe *et al.* 2011), likely owing to numerous habitat and resource differences between the study areas.

Aside from movement patterns, the 'Ōma'o also had a different diet from the Japanese White-eye at the *kīpuka* study sites. Perkins (1903) and Wakelee (1996) suggest 'Ōma'o consume a large quantity of invertebrates; the latter found that 80 percent of the fecal samples collected contained invertebrate matter. However, this study found that only seven percent of the fecal samples contained invertebrates, and Henshaw (1902) found that less than five percent of the dissected stomachs contained invertebrates. Seasonal variation could partially explain this difference. All of the fecal samples, in this study, were collected from February to July, approximately the peak season of fruit abundance in the *kīpuka* region (Kovach 2012); 'Ōma'o in this region may eat less fruit when fruit abundance is relatively lower. It is also important to understand birds' diets and movements during the non-breeding season, because they may forage over larger areas or on different foods when not defending a breeding territory or feeding nestlings (Holbrook & Smith 2000). From field observations, a greater frequency of fecal samples containing pulp matter than seeds, and results from past studies, Japanese White-eyes may be pecking at fruit larger than its gape size with its small, piercing bill rather than taking the seeds with the fruit. Japanese White-eyes prefer small-seeded over large-seeded fruit (LaRosa *et al.* 1985, Chimera & Drake

2010) and have been shown to consume fruits less than 6 mm in diameter (Noma & Yumoto 1997). The White-eye's gape size is larger than most seeds in this study area, but by taking pecks at fruits such as *Coprosma*, which has two large seeds in the center, the White-eye is not likely to swallow and disperse its seeds. *Vaccinium* and *Rubus hawaiensis* both have fruits larger than 12 mm (Table 3) but have numerous small seeds interspersed in the fruit's flesh, facilitating dispersal by small-billed frugivores. Large-seeded plant species are more susceptible to the effects of fragmentation (Cramer *et al.* 2007), an effect that may be compounded by a lack of larger seed dispersers on the other islands of Hawaii.

As opportunistic generalists, White-eyes demonstrate high flexibility in their diet, and thus, it can play a variable ecological role as a seed disperser. By both species and quantity of seeds dispersed, the Japanese White-eye was found to be much less frugivorous in this study than on Maui (Foster & Robinson 2007). Studies elsewhere also showed the Japanese White-eye to be among the most important seed dispersers of all birds present (Corlett 1998, 2011, Au *et al.* 2006, Kawakami *et al.* 2009). One possible outcome for the *kīpuka* is that if 'Ōma'o were to be extirpated in the future, as it has been across much of its range, larger seeded plants may be particularly susceptible to dispersal failure. While Japanese White-eyes may not fully replace the 'Ōma'o as a seed disperser, seed dispersal services are augmented by the presence of this introduced species, at least in the absence of invasive fruiting species. Both species contribute to primary succession in the *kīpuka* region; 'Ōma'o disperse more seeds, and White-eyes spend more time in the matrix. Approximately one in five Japanese White-eyes at any time carry seeds in their droppings. However, they are still likely to play a big role in the ecosystem as the second most abundant bird in the *kīpuka*, with a density of 14.8 birds per hectare (Kovach 2012). While the 'Ōma'o and the Japanese White-eye are the most important frugivores in the *kīpuka*, the Hawaii 'Amakihi (Lindsey *et al.* 1998) and Kalij Pheasant (Lewin & Lewin 1984) disperse some seeds as well, and the Red-billed Leiothrix is found to disperse at least

Vaccinium and *Rubus hawaiensis* seeds from limited samples in this study. Plant recruitment to matrix areas is often dispersal-limited (McConkey *et al.* 2012), and both study species contribute to the regeneration of understory fruiting plants, as observed during this study when an 'Ōma'o perched on a *Metrosideros polymorpha* sapling colonizing the matrix excreted a dropping, fitting with findings by Drake and Mueller-Dombois (1993).

Worldwide, native frugivores are increasingly becoming replaced by smaller, non-native generalists that cannot effectively substitute for native frugivores (Meehan *et al.* 2002, Mandon-Dalger *et al.* 2004, Babweteera & Brown 2009, Chimera & Drake 2010, Staddon *et al.* 2010). Many Hawaiian plants evolved fleshy fruits historically dispersed by frugivorous birds, but with the extinction of most native frugivores, seed dispersal services, particularly by birds capable of processing larger fruits and seeds, are threatened (Culliney *et al.* 2012). It is also important to consider the impacts that anthropogenic fragmentation can have on 'Ōma'o, a species that may not be inclined to cross large gaps. The population status of the 'Ōma'o is stable, and the bird has even recolonized an area where it was formerly found (Judge *et al.* 2012); however, continued preservation of the last remaining native frugivore in Hawaii is crucial, particularly because functional extinction may occur long before a seed disperser becomes rare (McConkey & Drake 2006). As ecosystems worldwide face increasing anthropogenic pressures, avian seed dispersers are one of the most important factors that will determine the persistence and dissemination of fleshy-fruited plant species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Map of study site on the Big Island. Each of the 16 *kīpuka* is outlined and numbered.

TABLE S1. *Basic statistics on birds tracked showing the bird ID (signal frequency), times tracked, location obtained, and movement rates. Japanese White-eye (JAWE) movement rates are averaged based on a 30-min GPT.*

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