



The Wilson Journal of Ornithology

Published by the Wilson Ornithological Society

VOL. 119, NO. 3

September 2007

PAGES 325–522

The Wilson Journal of Ornithology 119(3):325–333, 2007

BIOGEOGRAPHY OF 'ELEPAIO: EVIDENCE FROM INTER-ISLAND SONG PLAYBACKS

ERIC A. VANDERWERF¹

ABSTRACT.—I used inter-island song playbacks and information on geology, ecology, and behavior to investigate biogeography and species limits in the 'Elepaio (*Chasiempis sandwichensis*), a monarch flycatcher (Monarchidae) endemic to the Hawaiian Islands. 'Elepaio occur on Kaua'i, O'ahu, and Hawai'i, but are absent on the four islands of the Maui Nui group in the center of the Hawaiian Archipelago. It is unlikely that 'Elepaio became extinct on Maui Nui or were excluded by the presence of competing species. 'Elepaio are absent in the fossil record on all four islands of Maui Nui, but occur in the fossil record on all three islands they currently inhabit. They have adapted to a variety of forested habitats and are more resistant to alien diseases than other bird species that have persisted on Maui Nui. 'Elepaio on each island responded most strongly to songs from their own island. Response to foreign songs was asymmetrical. Hawai'i 'Elepaio responded to songs from Kaua'i, suggesting that 'Elepaio on Kaua'i and Hawai'i share a more recent common ancestry. The sequence of colonization events that led to the current distribution was most likely: (1) Kaua'i to O'ahu and (2) Kaua'i to Hawai'i. Geologic and genetic evidence indicate the 'Elepaio lineage arrived in the Hawaiian Islands ~1.5–1.9 million years ago. 'Elepaio probably were blown from Kaua'i to Hawai'i during storms, skipping several of the stepping-stones in the Hawaiian chain. The low level of foreign song recognition indicates song could inhibit interbreeding and might serve as an isolating mechanism. *Received 13 February 2006. Accepted 8 November 2006.*

The 'Elepaio (*Chasiempis sandwichensis*) is a monarch flycatcher (Monarchidae) endemic to the Hawaiian Islands. 'Elepaio occur on the islands of Kaua'i, O'ahu, and Hawai'i, but are absent on the four islands of the Maui Nui group (Maui, Moloka'i, Lana'i, and Kaho'olawe) in the center of the Hawaiian Archipelago (Pratt et al. 1987, VanderWerf 1998). 'Elepaio have been classified into three or more taxa based primarily on plumage dif-

ferences, each found on a single island. Each island taxon was originally described as a separate species: *C. sandwichensis* Gmelin 1789 on Hawai'i; *C. ibidis* Stejneger 1887 (formerly *C. gayi* Wilson 1891) on O'ahu; and *C. sclateri* Ridgway 1882 on Kaua'i (Pratt 1980, Olson 1989, VanderWerf 1998). These taxa were later reclassified as subspecies by Bryan and Greenway (1944) without any explanation or justification, and this taxonomy has been followed since. Some authorities continue to treat them as species (Olson and James 1982, Conant et al. 1998), and the American Ornithologists' Union is considering a taxonomic

¹ Pacific Rim Conservation, 320 Kupaua Place, Honolulu, HI 96821, USA; e-mail: erwerf@hawaii.rr.com

revision of 'Elepaio in which the forms on different islands would again be separated as species (AOU 2000). Two additional subspecies, *C. s. ridgwayi* and *C. s. bryani*, are recognized on Hawai'i by some authorities, based on variation in plumage color on the head, back, and breast (Henshaw 1902, Pratt 1979, Pratt 1980).

The Hawaiian Islands are volcanic in origin and were formed sequentially as the Pacific plate of the earth's crust moved northwest over a "hot spot" where magma from the mantle reaches the surface (Walker 1990, Carson and Clague 1995). The most common biogeographic pattern in the Hawaiian Islands is that of a stepping stone or conveyor belt where organisms sequentially colonized each new island from west to east (Freed et al. 1987, Wagner and Funk 1995, Fleischer et al. 1998, Fleischer and MacIntosh 2001). The absence of 'Elepaio on Maui, Moloka'i, Lana'i, and Kaho'olawe is peculiar given the ordered geologic history of the Hawaiian Islands. There are two possible explanations for this absence: (1) 'Elepaio have become extinct on these islands or (2) 'Elepaio never occurred on these islands, or at least failed to become established on them. These four islands formed a single island called Maui Nui (literally "big Maui") during prehistoric periods of lower sea level (Carson and Clague 1995, Price and Elliott-Fisk 2004), and the absence of 'Elepaio on all four islands could be related.

Vocalizations can provide important information in studies of avian biogeography and systematics (Payne 1986, Isler et al. 1998). Song is involved in species recognition in many birds (Catchpole and Slater 1995), can change rapidly through cultural evolution (Payne 1986), and may have an important role in speciation (Martens 1996). The importance of geographic variation in song can vary but, in some cases, it provides a clue to underlying patterns of cryptic morphological variation and reproductive isolation (Groth 1993, Balakrishnan and Sorenson 2006). Playbacks of recorded songs can be a useful method of demonstrating whether song may act as an isolating mechanism (Grant and Grant 2002, Balakrishnan and Sorenson 2006). The objectives of this study were to investigate biogeography and species limits in 'Elepaio using

inter-island song playbacks, and to assess the possibility that 'Elepaio have become extinct on Maui Nui using information on geology, ecology, and behavior.

METHODS

The primary song of 'Elepaio, given almost exclusively by males, is used in territory defense and mate attraction (VanderWerf 1998). Female 'Elepaio often respond to this song with a distinctive two-note call. The primary song differs somewhat among islands, having the fewest phrases and least frequency modulation on Kaua'i and the most on Hawai'i (Fig. 1; VanderWerf 1998). There is some song variation within islands, but the extent of variation within islands is much less than among islands (Fig. 1; E. A. VanderWerf, unpubl. data). The Hawaiian name 'Elepaio is derived phonetically from this song.

I conducted three song playback experiments with 'Elepaio: one on O'ahu in Kuli'ou'ou and Pia valleys on 29 February 1996, one on Kaua'i along the Mōhihi-Wai'alae Trail in the Alaka'i Wilderness Preserve on 5 April 1996, and one on Hawai'i at Hakalau Forest National Wildlife Refuge on 21 April 1996. 'Elepaio remain paired and defend territories year-round, but territorial aggression peaks just prior to and during nest construction, declines rapidly once incubation begins, and remains low during the nonbreeding season (VanderWerf 1998, VanderWerf and Freed 2003). Playback experiments were timed to coincide with the usual peak in nest construction on each island to ensure the strongest possible response (VanderWerf 1998).

I used a Marantz PMD222 cassette recorder and a Telinga microphone and parabolic reflector to record primary songs and calls of adult males at each site. I made 1-min loop cassettes from these recordings that consisted of songs and calls from three different adult males at each site to reduce pseudoreplication (Catchpole 1989, Kroodsma 1989). Male 'Elepaio often intersperse calls between series of songs, and calls were included with songs on the cassettes in an attempt to make the recordings sound more realistic. Sound spectrograms of male 'Elepaio songs were prepared using Raven 1.2 (Cornell Laboratory of Ornithology 2004).

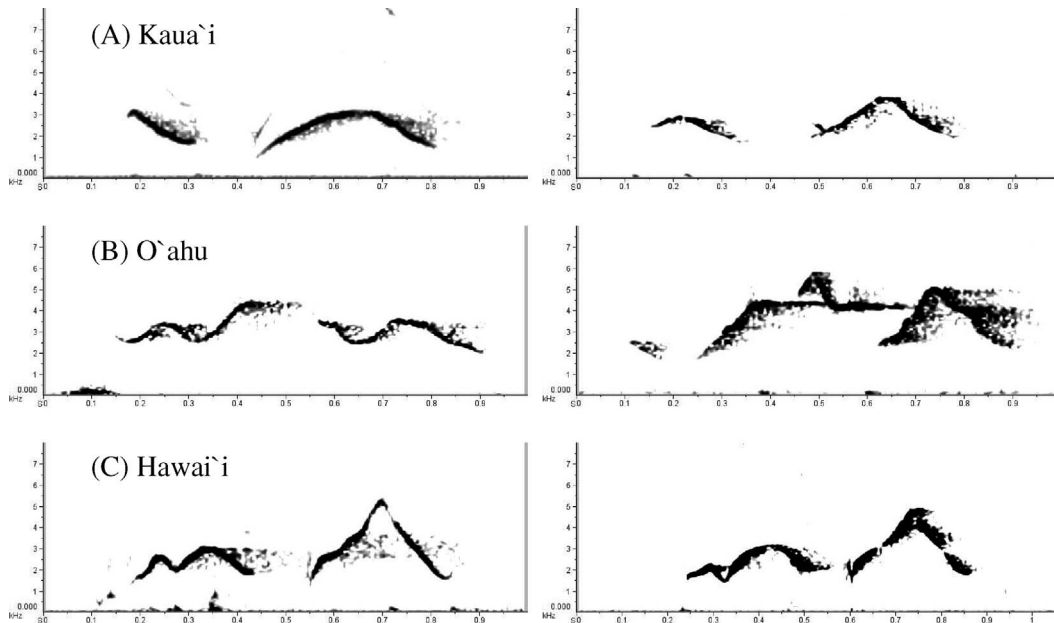


FIG. 1. Sound spectrograms of songs from male 'Elepaio on (A) Kaua'i, (B) O'ahu, and (C) Hawai'i. Single songs from two different males on each island.

Nine male 'Elepaio were used as experimental subjects at each site. It would have been useful to examine the response by female 'Elepaio to assess the extent of intersexual selection, but during playback tests females generally followed the male and their response was not independent. None of the recordings used in the playbacks was from any of the subjects or their neighbors. Recordings from each island were played to each subject for 3 min, with a 3-min rest period between playbacks, so the total duration of a trial with each subject was 15 min (island one, rest; island two, rest; island three). The order in which recordings were played was systematically varied among subjects so that recordings from a given location were played first, second, and third an equal number of times (three). The playback length was deliberately short to reduce potential habituation (a decline in response strength in later trials).

Recordings were broadcast through a speaker placed on the ground in the approximate geographic center of each subject's territory because aggressiveness of response often declines toward territory margins (Melemis and Falls 1982). Recordings were played from a Sony TCM cassette player connected

to the speaker by a 10 m cable. Observations were made from a position next to the cassette player.

Response by each subject to each 3-min playback was measured with three variables: vocal response, physical response, and latency (time to first vocal or physical response). Each variable was scored on a scale from 0 to 4 (Table 1). Categories of physical response were chosen so they represented progressively more aggressive behaviors. Approach distance was measured from the speaker. A "song display" was a distinctive behavior in which songs were delivered while the feathers on the throat and crown were erected, the tail was held at 90° and fanned to display the white tips, and the wings were drooped to expose the white wing bars and rump (VanderWerf 1998). A "swoop" was when a bird dove toward the speaker. Categories of latency and vocal response were chosen so the distribution of observations was as close as possible to normal.

An overall response score ranging from 0 to 12 was derived by summing the scores of the three variables. Variation in response by birds on each island was examined with a General Linear Model using overall response

TABLE 1. Variables used to measure strength of response by male 'Elepaio during song playbacks. Latency was measured as the time to first response (song or approach). A single overall measure of response strength ranging from 0 to 12 was derived for use in analyses by summing the scores from all three variables.

Latency (sec)	Number of songs	Physical approach	Score
No response	0	None	0
>60	1–5	Distant approach (>10 m)	1
20–60	6–10	Close approach (<10 m)	2
10–19	11–20	Song display	3
<10	>20	Swoop	4

score as the dependent variable and song type (Kaua'i, O'ahu, or Hawai'i), song order (first, second, or third), and individual bird as independent variables. Pair-wise tests were conducted between groups using Tukey's correction for multiple comparisons if there was significant overall variation in response.

'Elepaio are naturally curious and can be attracted by a variety of sounds, including human voices and "pishing" (VanderWerf 1998). Thus, a low level of response can be expected to any persistent loud sound in the territory. Weak responses to playbacks were interpreted with caution and greater emphasis was placed on the relative response to different treatments. I considered using songs of another monarch flycatcher, a different bird species, or another sound as a control, but elected not to do so because of the increased potential for habituation that might have resulted from an additional trial with each subject.

RESULTS

'Elepaio on each island responded most strongly to songs from their own island (Fig. 2). Responses to foreign songs were weaker and did not differ in most cases (Fig. 2). For example, 'Elepaio on Kaua'i responded more strongly to songs from Kaua'i than to songs from O'ahu or Hawai'i, and response to songs from O'ahu and Hawai'i did not differ (Fig. 2A; $F_{2,14} = 15.33$, $P < 0.001$). Similarly, 'Elepaio on O'ahu responded more strongly to songs from O'ahu than to songs from Kaua'i or Hawai'i, and response to songs from Kaua'i and Hawai'i did not differ (Fig. 2B; $F_{2,14} = 12.30$, $P = 0.002$). However, 'Elepaio on Hawai'i responded more strongly to songs from Hawai'i and Kaua'i than to songs from O'ahu (Fig. 2C; $F_{2,14} = 4.92$, $P = 0.02$).

The nature of the responses to foreign songs

also is instructive. On O'ahu, seven of nine birds did not sing in response to either foreign song and responded with only a distant (>10 m) approach. On Kaua'i, four of nine birds did not sing in response to either foreign song, and six and five birds responded with only a distant approach to songs from O'ahu and Hawai'i, respectively. On Hawai'i, all birds except one sang in response to all songs, although most birds sang more often in response to songs from Hawai'i.

There was no evidence that habituation occurred in any of the three experiments. Response strength was not affected by the order in which songs were played ($F_{2,14} = 0.42$, 0.73 , and 0.76 , $P = 0.66$, 0.51 , and 0.48 on Kaua'i, O'ahu, and Hawai'i, respectively). There was some tendency for certain birds to respond more strongly, but the overall levels of individual variation were not significant ($F_{8,14} = 1.59$, 2.16 , and 1.73 , $P = 0.22$, 0.14 , and 0.18 on Kaua'i, O'ahu, and Hawai'i, respectively).

DISCUSSION

Are 'Elepaio Reproductively Isolated Among Islands?

Mitochondrial DNA evidence indicates there is little or no gene flow among islands and the extent of differentiation in 'Elepaio among islands is consistent with species level differences (Burgess 2005). In addition to the obvious physical barrier posed by the Pacific Ocean, low levels of foreign song recognition among islands could serve as an additional premating isolation mechanism. There is no information on song learning in 'Elepaio, but it is likely they learn songs from adult tutors early in their developmental period like virtually all oscine passerines (Catchpole and

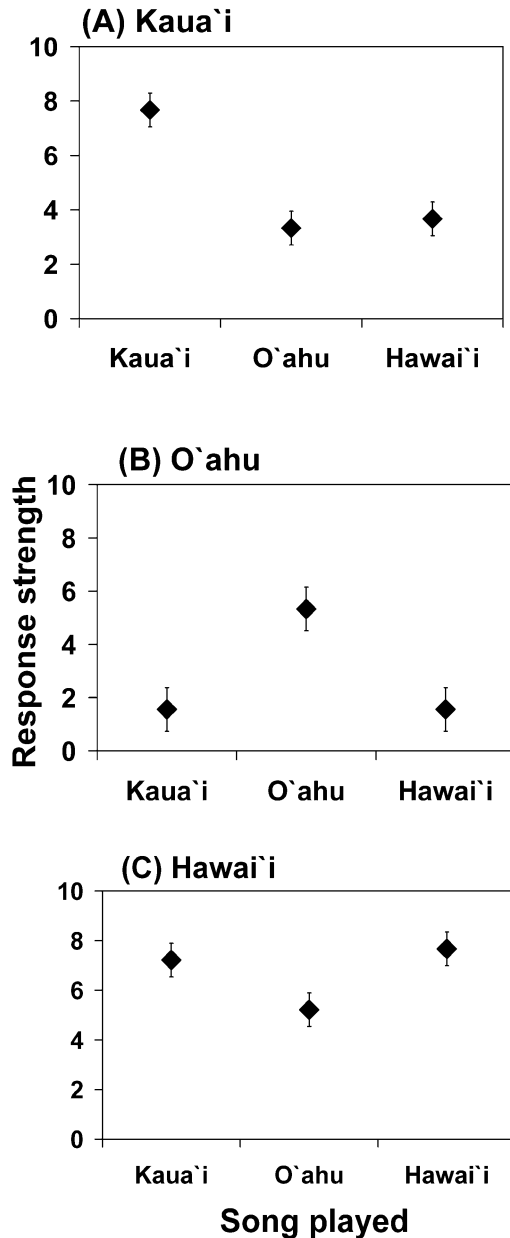


FIG. 2. Responses of male 'Elepaio on each island to songs from each island (mean \pm SE). Response strength includes number of songs, physical approach, and latency of response.

Slater 1995). Recent evidence indicates birds retain a long-lasting memory of the tutor's song that largely shapes their own song (Phan et al. 2006). Young 'Elepaio remain with their parents on the natal territory for up to 9

months (VanderWerf 2004). They learn complex foraging behaviors during this time (VanderWerf 1994) and begin to sing just prior to the onset of the next breeding season. Island-specific song dialects may have arisen through founder events and geographic isolation (Matessi et al. 2000, Wright and Dorin 2001); these local dialects may be reinforced through foreign song avoidance. 'Elepaio that emigrated to another island thus might not be recognized as potential mates based on their songs, or at least might not be preferred, leading to reproductive isolation (Balakrishnan and Sorenson 2006).

Colonization History and Timing

The stronger response by Hawai'i 'Elepaio to songs from Kaua'i than to songs from O'ahu suggests 'Elepaio on Kaua'i and Hawai'i share a more recent common ancestry and the O'ahu 'Elepaio is most divergent. The sequence of colonization events that led to the current distribution was most likely: (1) Kaua'i to O'ahu and (2) Kaua'i to Hawai'i (Fig. 3). However, the direction of colonization between Kaua'i and O'ahu cannot be inferred with certainty based on song playbacks alone.

The pattern of response between Kaua'i and Hawai'i was asymmetrical; Hawai'i 'Elepaio responded to songs from Kaua'i, but Kaua'i 'Elepaio did not respond to songs from Hawai'i. This suggests 'Elepaio respond more strongly to songs of their ancestors than to songs of their descendents. Such asymmetrical behavioral isolation, in which ancestral populations discriminate against courtship displays of derived populations but derived populations accept displays of their ancestors, was first described in Hawaiian *Drosophila* (Kaneshiro 1976, Kaneshiro and Giddings 1987) and has become known as the Kaneshiro hypothesis. The mechanism originally proposed for the behavioral asymmetry was loss of certain elements of the courtship display during founder events, but Ohta (1978) proposed that founder events also could involve selection for decreased female discrimination. It is not clear why only Hawai'i 'Elepaio recognized ancestral songs, since either Kaua'i or O'ahu must have been ancestral to the other. Ancestral song recognition may decrease over time due to gradual accumulation of changes in

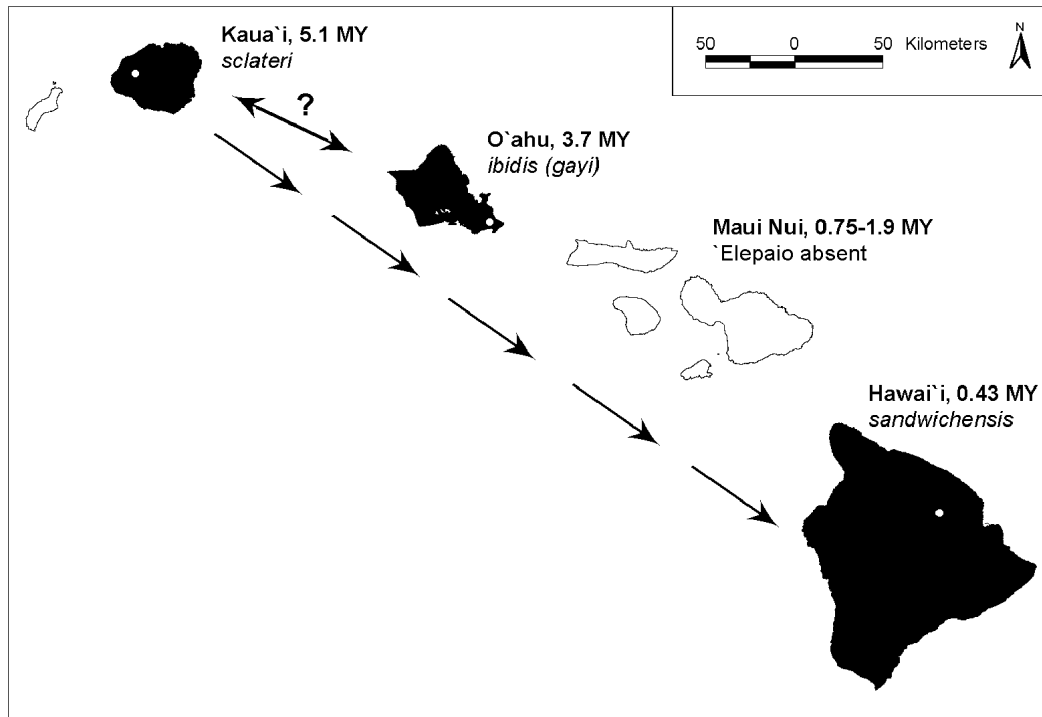


FIG. 3. 'Elepaio occur on the Hawaiian islands of Kaua'i, O'ahu, and Hawai'i, but are absent from Maui Nui (Maui, Moloka'i, Lana'i, and Kaho'olawe), even in the fossil record. Island ages in millions of years (MY) from Carson and Clague (1995). Evidence from song playbacks suggests 'Elepaio on O'ahu diverged first, but the direction of colonization is not certain, and that Hawai'i was colonized directly from Kaua'i. Study sites are marked with a dot.

song or to reversal in selection for decreased female discrimination with increasing population size. The Kaneshiro hypothesis has been demonstrated in other groups of Hawaiian *Drosophila* (Koeper and Fenster 1991) and in Hawaiian crickets of the genus *Laupala* (Shaw and Lugo 2001). If further analysis of genetic data corroborates the colonization sequence indicated by song playback experiments, this would represent the first demonstration of the Kaneshiro hypothesis in a bird. Male song represents only one aspect of courtship behavior in 'Elepaio, which also involves courtship feeding and mock chases (VanderWerf 1998); comparison of these behaviors among islands could provide additional evidence.

A combination of genetic and geological evidence indicates ancestral 'Elepaio arrived in the Hawaiian Islands 1.5–1.9 million years (myr) ago. Mitochondrial DNA analysis indicates the 'Elepaio lineage is at least 1.5 myr

old (Filardi and Moyle 2005). O'ahu and western Moloka'i were connected about 1.9–2.2 myr ago, forming the larger island of O'ahu Nui, but the saddle connecting the volcanoes on these islands was submerged due to island subsidence and rising sea level (Price and Elliott-Fisk 2004). If 'Elepaio existed on O'ahu when it was connected to Moloka'i, they presumably would have occupied both islands. This apparently was not the case, indicating the 'Elepaio lineage is less than 1.9 myr old. Given the age of each island (Fig. 3), either Kaua'i or O'ahu could have been the first island colonized, but Hawai'i could not.

'Elepaio and other Pacific island monarchs are non-migratory and quite sedentary (Sanders et al. 1995, VanderWerf 2004), and it is unlikely that 'Elepaio deliberately flew between islands. Natal dispersal distances of 'Elepaio are usually less than a kilometer (VanderWerf 1998) and breeding dispersal

distances of adults are usually only a few hundred meters (VanderWerf 2004), although some longer distance dispersal may occur rarely (Burgess 2005). It is more likely that 'Elepaio were carried to new islands by strong winds during rare storm events and made landfall on the first island in their path. Hawai'i can be reached from Kaua'i without passing directly over O'ahu or Maui Nui because Hawai'i is slightly south of the line formed by the other islands (Fig. 3). If Hawai'i had been colonized from O'ahu, birds would have passed directly over or very close to Maui Nui, making their absence more difficult to explain. Similar disjunct distributions, in which sister taxa occur on non-neighboring islands, are known in several other Hawaiian groups, including picture-winged flies (Drosophilidae), yellow-faced bees (Colletidae), and numerous plants (K. Y. Kaneshiro, K. R. Wood, and Karl Magnacca, pers. comm.). Most of these cases involve Kaua'i and one or more younger islands.

Have 'Elepaio Become Extinct on Maui Nui?

Several lines of evidence indicate 'Elepaio have not become extinct on Maui Nui. The most compelling evidence against extinction is that 'Elepaio are absent in the fossil record on all four islands in Maui Nui, but occur in the fossil record on all three islands they currently inhabit (Olson and James 1982, James and Olson 1991, Burney et al. 2001). The adaptability of 'Elepaio also suggests it is unlikely 'Elepaio became extinct on Maui Nui or were excluded by the presence of competing species. 'Elepaio are flexible in habitat selection (VanderWerf 1993), use a wide range of foraging behaviors, forage at all heights and on many substrates (VanderWerf 1994), prey on a variety of invertebrates (VanderWerf 1998), and have adapted to a wide range of forest types including lowland wet forest, montane cloud forest, dry subalpine shrubland, small pockets of forest isolated by recent lava flows (kipukas), and disturbed forest dominated by alien plant species (Conant 1977, van Riper 1995, VanderWerf 1998, VanderWerf and Smith 2002, VanderWerf 2004). 'Elepaio also have greater immunity than many Hawaiian forest birds to alien diseases that have decimated the endemic avifauna

(van Riper et al. 1986, Atkinson et al. 1995, VanderWerf 2001). Finally, Maui is a large island that has retained extensive areas of native forest and still supports several Hawaiian honeycreepers (Drepanidinae) that are much more sensitive to disturbance and disease than 'Elepaio (Pratt et al. 2001, Groombridge et al. 2004). It is possible that too few 'Elepaio reached Maui Nui to establish a breeding population, but it is unlikely that 'Elepaio have become extinct on Maui Nui. If extinction is ruled out, the biogeography of 'Elepaio does not follow the typical stepping stone pattern found in other Hawaiian bird taxa (Freed et al. 1987, Fleischer et al. 1998).

This study demonstrates there is lack of recognition of foreign songs among male 'Elepaio indicating birds from other islands are not recognized as potential competitors for mates (Balakrishnan and Sorenson 2006). Demonstration of foreign song avoidance by females would provide important additional evidence of reproductive isolation, although this may prove difficult in a field setting. Further investigation of molecular genetic divergence among and within 'Elepaio populations on each island would aid examination of their phylogeography and taxonomy. Finally, quantitative examination of vocal characters would help corroborate the results of this study.

ACKNOWLEDGMENTS

I thank H. D. Pratt and T. K. Pratt for valuable discussion about playbacks and avian systematics, and K. Y. Kaneshiro, K. R. Wood, and Karl Magnacca for information about biogeography of Hawaiian insects and plants. Valuable comments on the manuscript were made by H. D. Pratt, R. C. Fleischer, A. M. Kilpatrick, and an anonymous reviewer. This research was conducted while I was supported by a graduate fellowship at the University of Hawaii from the John D. and Catherine T. MacArthur Foundation.

LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 2000. Forty-second supplement to the American Ornithologists' Union Check-list of North American birds. Auk 117:847-858.
- ATKINSON, C. T., K. L. WOODS, R. J. DUSEK, L. SILEO, AND W. M. IKO. 1995. Wildlife disease and conservation in Hawai'i: pathogenicity of avian malaria (*Plasmodium relictum*) in experimentally infected Iiwi (*Vestiaria coccinea*). Parasitology 111: S59-S69.
- BALAKRISHNAN, C. N. AND M. D. SORENSON. 2006.

- Song discrimination suggests premating isolation among sympatric indigobird species and host races. *Behavioral Ecology* 17:473–478.
- BRYAN JR., E. H., AND J. C. GREENWAY JR. 1944. Check-list of the birds of the Hawaiian Islands. *Bulletin of the Museum of Comparative Zoology* 94:92–140.
- BURGESS, S. L. 2005. Phylogeography and conservation genetics of the Elepaio. Dissertation. University of Hawaii, Manoa, USA.
- BURNEY, D. A., H. F. JAMES, L. P. BURNEY, S. L. OLSON, W. KIKUCHI, W. L. WAGNER, M. BURNEY, D. McCLOSKEY, D. KIKUCHI, F. V. GRADY, R. GAGE II, AND R. NISHEK. 2001. Fossil evidence for a diverse biota from Kaua'i and its transformation since human arrival. *Ecological Monographs* 71: 615–641.
- CARSON, H. L. AND D. A. CLAGUE. 1995. Geology and biogeography of the Hawaiian Islands. Pages 14–29 in *Hawaiian biogeography: evolution in a hot-spot archipelago* (W. L. Wagner and V. A. Funk, Editors). Smithsonian Institution Press, Washington, D.C., USA.
- CATCHPOLE, C. K. 1989. Pseudoreplication and external validity: playback experiments in avian bioacoustics. *Trends in Ecology and Evolution* 4: 286–287.
- CATCHPOLE, C. K. AND P. J. B. SLATER. 1995. Bird song: biological themes and variations. Cambridge University Press, Cambridge, United Kingdom.
- CONANT, S. 1977. The breeding biology of the O'ahu 'Elepaio. *Wilson Bulletin* 89:193–210.
- CONANT, S., H. D. PRATT, AND R. J. SHALLENBERGER. 1998. Reflections on a 1975 expedition to the lost world of the Alaka'i and other notes on the natural history, systematics, and conservation of Kaua'i birds. *Wilson Bulletin* 110:1–22.
- CORNELL LABORATORY OF ORNITHOLOGY. 2004. Raven 1.2. Cornell Laboratory of Ornithology, Bioacoustics Research Program, Ithaca, New York, USA.
- FILARDI, C. E. AND R. G. MOYLE. 2005. Single origin of a pan-Pacific bird group and upstream colonization of Australasia. *Nature* 438:216–219.
- FLEISCHER, R. C. AND C. E. MACINTOSH. 2001. Molecular systematics and biogeography of the Hawaiian avifauna. *Studies in Avian Biology* 22:51–60.
- FLEISCHER, R. C., C. E. MACINTOSH, AND C. L. TARR. 1998. Evolution on a volcanic conveyor belt: using phylogeographic reconstruction and K-Ar based ages of the Hawaiian Islands to estimate molecular evolutionary rates. *Molecular Ecology* 7:533–545.
- FREED, L. A., S. CONANT, AND R. C. FLEISCHER. 1987. Evolutionary ecology and radiation of Hawaiian passerine birds. *Trends in Ecology and Evolution* 2:196–203.
- GRANT, B. R. AND P. R. GRANT. 2002. Lack of premating isolation at the base of a phylogenetic tree. *American Naturalist* 160:1–19.
- GROOMBRIDGE, J. J., J. G. MASSEY, J. C. BRUCH, T. MALCOLM, C. N. BROSIUS, M. M. OKADA, B. SPARKLIN, J. S. FRETZ, AND E. A. VANDERWERF. 2004. An attempt to recover the Po'ouli by translocation and an appraisal of recovery strategy for bird species of extreme rarity. *Biological Conservation* 118:365–375.
- GROTH, J. G. 1993. Evolutionary differentiation in morphology, vocalizations, and allozymes among nomadic sibling species in the North American Red Crossbill (*Loxia curvirostra*) complex. *California Publications in Zoology* 127:1–143.
- HENSHAW, H. W. 1902. The Elepaio of Hawaii. *Auk* 19:221–232.
- ISLER, M. L., P. R. ISLER, AND B. M. WHITNEY. 1998. Use of vocalizations to establish species limits in antbirds (Passeriformes: Thamnophilidae). *Auk* 115:577–590.
- JAMES, H. F. AND S. L. OLSON. 1991. Descriptions of 32 new species of birds from the Hawaiian Islands. Part II. Passeriformes. *Ornithological Monographs* 46:1–88.
- KANESHIRO, K. Y. 1976. Ethological isolation and phylogeny in the *planitibia* subgroup of Hawaiian *Drosophila*. *Evolution* 30:740–745.
- KANESHIRO, K. Y. AND L. V. GIDDINGS. 1987. The significance of asymmetrical sexual isolation and the formation of new species. Pages 29–43 in *Evolutionary biology* (M. K. Hecht, B. Wallace, and G. T. Prance, Editors). Plenum Publishing, New York, USA.
- KOEPFER, H. R. AND E. J. FENSTER. 1991. Asymmetrical mating patterns between geographic strains of *Drosophila mercatorum*: a test of the Kaneshiro Hypothesis. *Evolution* 45:455–458.
- KROODSMA, D. E. 1989. Suggested experimental designs for song playbacks. *Animal Behavior* 37: 600–609.
- MARTENS, J. 1996. Vocalization and speciation of Palearctic birds. Pages 221–240 in *Ecology and evolution of acoustic communication in birds* (D. E. Kroodsma and E. H. Miller, Editors). Cornell University Press, Ithaca, New York, USA.
- MATESSI, G., T. DABELSTEEN, AND A. PILASTRO. 2000. Responses to playback of different subspecies songs in the Reed Bunting *Emberiza schoeniclus*. *Journal of Avian Biology* 31:96–101.
- MELEMIS, S. M. AND J. B. FALLS. 1982. The defense function: a measure of territorial behavior. *Canadian Journal of Zoology* 60:495–501.
- OHTA, A. T. 1978. Ethological isolation and phylogeny in the *grimshawi* species complex of the Hawaiian *Drosophila*. *Evolution* 32:485–492.
- OLSON, S. L. 1989. Two overlooked holotypes of the Hawaiian Flycatcher *Chasiempis* described by Leonhard Stejneger (Aves: Myiagrinae). *Proceedings of the Biological Society of Washington* 102: 555–558.
- OLSON, S. L. AND H. F. JAMES. 1982. Prodrum of the fossil avifauna of the Hawaiian Islands. *Smithsonian Contributions to Zoology* Number 365. Washington, D.C., USA.

- PAYNE, R. B. 1986. Bird songs and avian systematics. *Current Ornithology* 3:87–126.
- PHAN, M. L., P. L. PYTTE, AND D. S. VICARIO. 2006. Early auditory experience generates long-lasting memories that may subserve vocal learning in songbirds. *Proceedings of the National Academy of Science* 103:1088–1093.
- PRATT, H. D. 1979. A new subspecies of the 'Elepaio *Chasiempis sandwichensis*, from the island of Hawai'i. *Bulletin of the British Ornithologists' Club* 99:105–108.
- PRATT, H. D. 1980. Intra-island variation in the 'Elepaio on the island of Hawai'i. *Condor* 82:449–458.
- PRATT, H. D., P. L. BRUNER, AND D. G. BERRETT. 1987. A field guide to the birds of Hawai'i and the tropical Pacific. Princeton University Press, Princeton, New Jersey, USA.
- PRATT, T. K., J. C. SIMON, B. P. FARM, K. E. BERLIN, AND J. R. KOWALSKY. 2001. Home range and territoriality of two honeycreepers, the 'Ākohekohe and Maui Parrotbill. *Condor* 103:746–755.
- PRICE, J. P. AND D. ELLIOTT-FISK. 2004. Topographic history of the Maui Nui complex, Hawai'i, and its implications for biogeography. *Pacific Science* 58:27–45.
- SANDERS, K. H., E. O. MINOT, AND R. A. FORDHAM. 1995. Juvenile dispersion and use of habitat by the endangered Kakerori *Pomarea dimidiata* (Monarchinae) on Rarotonga, Cook Islands. *Pacific Conservation Biology* 2:167–176.
- SHAW, K. L. AND E. LUGO. 2001. Mating asymmetry and the direction of evolution in the Hawaiian cricket genus *Laupala*. *Molecular Ecology* 10:751–759.
- VANDERWERF, E. A. 1993. Scales of habitat selection by foraging 'Elepaio in undisturbed and human-altered Hawaiian forests. *Condor* 95:980–989.
- VANDERWERF, E. A. 1994. Intraspecific variation in foraging behavior of 'Elepaio in Hawaiian forests of different structure. *Auk* 111:917–932.
- VANDERWERF, E. A. 1998. 'Elepaio (*Chasiempis sandwichensis*). *The birds of North America*. Number 344.
- VANDERWERF, E. A. 2001. Distribution and potential impacts of avian poxlike lesions in 'Elepaio at Hakalau Forest National Wildlife Refuge. *Studies in Avian Biology* 22:247–253.
- VANDERWERF, E. A. 2004. Demography of Hawai'i 'Elepaio: variation with habitat disturbance and population density. *Ecology* 85:770–783.
- VANDERWERF, E. A. AND L. A. FREED. 2003. 'Elepaio subadult plumages reduce aggression through graded status-signaling, not mimicry. *Journal of Field Ornithology* 74:406–415.
- VANDERWERF, E. A. AND D. G. SMITH. 2002. Effects of rodent control on demography of the O'ahu 'Elepaio, an endangered Hawaiian forest bird. *Pacific Conservation Biology* 8:73–81.
- VAN RIPER III, C. 1995. Ecology and breeding biology of the Hawaii Elepaio (*Chasiempis sandwichensis bryani*). *Condor* 97:512–527.
- VAN RIPER III, C., S. G. VAN RIPER, M. L. GOFF, AND M. LAIRD. 1986. The epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecological Monographs* 56:327–344.
- WAGNER, W. L. AND V. A. FUNK. 1995. Hawaiian biogeography: evolution on a hot spot archipelago. Smithsonian Institution Press, Washington, D.C., USA.
- WALKER, G. P. L. 1990. Geology and volcanology of the Hawaiian Islands. *Pacific Science* 44:315–347.
- WRIGHT, T. F. AND M. DORIN. 2001. Pair duets in the Yellow-naped Amazon (Psittaciformes: *Amazona auropalliata*): responses to playbacks of different dialects. *Ethology* 107:111–124.