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Movements of four native Hawaiian birds across a naturally fragmented landscape

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Animals often increase their fitness by moving across space in response to temporal variation in habitat quality and resource availability, and as a result of intra and inter-specific interactions. The long-term persistence of populations and even whole species depends on the collective patterns of individual movements, yet animal movements have been poorly studied at the landscape level. We quantified movement behavior within four native species of Hawaiian forest birds in a complex lava-fragmented landscape: Hawaiʻi ʻamakihi *Chlorodrepanis virens*, ʻomaʻo *Myadestes obscurus*, ʻapapane *Himatione sanguinea*, and ʻiʻiwi *Drepanis coccinea*. We evaluated the relative importance of six potential intrinsic and extrinsic drivers of movement behavior and patch fidelity: 1) forest fragment size, 2) the presence or absence of invasive rats (*Rattus* sp.), 3) season, 4) species, 5) age, and 6) sex. The study was conducted across a landscape of 34 forest fragments varying in size from 0.07 to 12.37 ha, of which 16 had rats removed using a treatment-control design. We found the largest movements in the nectivorous ʻapapane and ʻiʻiwi, intermediate levels in the generalist Hawaiʻi ʻamakihi, and shortest average movement for the ʻomaʻo, a frugivore. We found evidence for larger patch sizes increasing patch fidelity only in the ʻomaʻo, and an effect of rat-removal increasing patch fidelity of Hawaiʻi ʻamakihi only after two years of rat-removal. Greater movement during the non-breeding season was observed in all species, and season was an important factor in explaining higher patch fidelity in the breeding season for ʻapapane and ʻiʻiwi. Sex was important in explaining patch fidelity in ʻomaʻo only, with males showing higher patch fidelity. Our results provide new insights into how these native Hawaiian species will respond to a changing environment, including habitat fragmentation and changing distribution of threats from climate change.

Movement is a fundamental component of how animals interact with each other, key resources, and their environment (Nathan et al. 2008, Pittman et al. 2014). Movement behavior has consequences at all ecological levels from individual fitness to population persistence, gene flow, and the spatial distribution of species and communities (Knowlton and Graham 2010). Although the importance of movement ecology has long been recognized (Swingland and Greenwood 1983), the accelerating rate of habitat loss, fragmentation and degradation worldwide has highlighted the importance of understanding how animal movement might allow scientists to predict the response to such changes (Fahrig 1998, Opdam and Wascher 2004, Pittman et al. 2014). Moreover, anticipated changes in habitats due to climate change and other anthropogenic stressors (Clobert et al. 2009) will influence the benefits and risks of movement behavior with implications for individuals, populations and species. The drivers of movement behavior may be extrinsic or intrinsic, but will necessarily be context and species specific, depending on species traits, landscape configuration and composition, and the spatial and temporal distribution of resources, conspecifics and predators (Nathan et al. 2008).

We evaluated the relative importance of potential drivers of movement behavior and patch fidelity for a community of Hawaiian birds in a naturally fragmented landscape. Native forests on the Big Island of Hawaiʻi have experienced fragmentation from volcanic activity for millennia, and eruptions dating from the mid-1800s created a landscape of forest patches (henceforth kīpuka, from the Hawaiian roots meaning forest and hole) populated with native bird species belonging to different feeding guilds (Flaspohler et al. 2010). While a natural phenomenon in our context, habitat fragmentation is often implicated as a major factor inhibiting the movement of forest birds, reducing the functional connectivity of a landscape and survival of sub-populations (Cooper and Walters 2002, Brooker and Brooker 2003). Further, habitat fragmentation modifies the spatial distribution and availability of food resources, thus influencing bird movement decisions and foraging behavior (Loiselle and Blake 1991, Levey and Stiles 1992).

Another factor known to affect habitat quality and thus potentially influence movement behavior is the presence of predators. In Hawaiʻi, beginning ca 1200 ya (Lindsey et al. 2009), rats (*Rattus* sp.) were introduced and are now widespread throughout the archipelago (Atkinson 1977). Terrestrial native predators in Hawaiʻi were all birds (corvids and raptors), but most of these species are now extinct or near-extinct and no longer cause any significant mortality of adults or nests (Griffin 1985, Klavitter 2009). Rats are known to be important nest predators for at least some Hawaiian bird species (VanderWerf and Smith 2002), preying on eggs, nestlings, and even incubating adult females (VanderWerf 2012). Another potential impact of omnivorous rats is competition with birds for food resources, particularly arthropods and fruit (Lindsey et al. 2009). The presence of rats can affect movement of birds by decreasing their likelihood of nesting success which can result in reduced site fidelity (Haas 1998, Hoover 2003, VanderWerf 2009). Therefore, we expected that rats would have an influence on the movement behavior of the native birds, both through predator avoidance by the birds and by changing the quantity and distribution of resources, and that the impact of rats would vary among bird species based on their nesting and foraging behavior. Previous work in mature Hawaiian native forests suggests that rat density decreases with height above ground (Shiels 2010, VanderWerf 2012). In the kīpuka system, large kīpuka have a taller canopy and greater structural complexity than small kīpuka (Vaughn et al. 2014), such that the effects of rats might vary as a function of kīpuka size. We were able to design the first systematic test of the effect of removing rats on bird movement behavior by using a treatment-control design where rats were removed via continuous snap trapping in half of our study kīpuka. This design also allowed us to examine the interactive impacts of patch size and rat presence on bird movement behavior in a multi-species context.

The four most abundant native bird species in this landscape are the frugivorous ʻomaʻo *Myadestes obscurus*, the Hawaiʻi ʻamakihi *Chlorodrepanis virens*, a generalist insectivore, and the largely nectarivorous ʻapapane *Himatione sanguinea* and ʻiʻiwi *Drepanis coccinea* (Banko and Banko 2009). The movement patterns of many tropical birds are shaped by their foraging preferences, and seasonal fluctuations in tropical frugivore and nectivore populations are common as they track their resources through space (Morton 1977, Stiles 1978a, b, Leighton and Leighton 1983, Feinsinger et al. 1985, Martin and Karr 1986, Loiselle and Blake 1991, Levey and Stiles 1992), whereas insectivores are considered to have a more stable food source throughout the year. In Hawaii, the main nectar source, flowering ʻōhiʻa lehua trees *Metrosideros polymorpha*, shows temporal and spatial variation in flowering peaks depending on elevation, rainfall and other factors, and does not always coincide with the native birds' breeding season (Hart et al. 2011). Past research has documented nectivorous ʻiʻiwi and ʻapapane make wide-ranging movements in search of flowering trees (Ralph and Fancy 1995). Studies of Hawaiʻi ʻamakihi and ʻomaʻo suggest that these species are more sedentary than the nectarivores (Lindsey et al. 1998) which may be related to more stable and uniformly distributed food resources, although fruiting trees in Hawaii have strong seasonal patterns (Kovach 2012). We also expected to see intraspecific differences in movement behavior, based on individual age and sex. Males and females often have different motivations for movement, such as defending a territory or nesting site, finding a mate, extrapair copulations, or finding food for nestlings (Greenwood 1980). Recently fledged birds, or juveniles, can also have different movement motivations than adults, especially if they are dispersing from their natal site and seeking a new territory or home range (Gill 1995).

Thus, in this landscape, we predicted that the main external factors driving the native birds' movement behavior are related to the fragmentation of the forest (patch size), the season or year, and the presence of an abundant invasive omnivorous predator/competitor. We also predicted that important internal factors could be species-specific foraging preference and the individual's age and sex. By summarizing and contrasting the frequency of movements and patch fidelity of four species of color-banded native birds, we provide new insights into the drivers of these species' movement behavior in a complex landscape. To our knowledge, this study is the first to examine how fragmentation and non-native predator removal influence landscape scale avian movement. Importantly, worldwide, such landscapes are increasingly becoming the norm for birds (Bregman et al. 2014). In Hawaii, where a tragic number of extinctions have occurred over the last two centuries and the majority of extant forest bird species are currently listed as endangered (Leonard 2008), it is important to understand how complex landscapes can affect movement behavior, which can strongly influence population dynamics and persistence.

Methods

Study site and rat removal

Our study took place on Hawaiʻi Island on the NE slope of Mauna Loa Volcano (19°40′N, 155°20′W, 1470–1790 m elevation), in a 5 km^2 landscape consisting of a network of native forest fragmented by historical volcanic activity. These kīpuka were formed in 1855 and 1881, when eruptions from the Mauna Loa volcano sent flows of molten lava snaking through continuous tracts of forest, leaving behind forest fragments of various shapes and sizes (Fig. 1A). The forested kīpuka consist almost entirely of native plant species, with the exception of a few kīpuka that have some non-native grass cover. The canopy of the kīpuka is dominated by the native ʻōhiʻa *Metrosideros polymorpha* (family Myrtaceae) tree with some koa *Acacia koa* (Fabaceae) as well, and the mid-story consists of native ʻōlapa *Cheirodendron trigynum* (Araliaceae), pilo *Coprosma montana* (Rubiaceae), kōlea *Myrsine lessertiana* (Primulaceae), kāwaʻu *Ilex anomala* (Aquifoliaceae) and hāpuʻu *Cibotium glaucum* (Cibotiaceae) tree fern. The native Hawaiian nectarivores feed primarily on ʻōhiʻa nectar, and the ʻomaʻo feeds on fruit from ʻōlapa, pilo, kōlea and kāwaʻu, among many others (Wakelee and Fancy 1999). The primary successional plants growing in the lava matrix are smaller and sparser than in the kīpuka forests, making the boundary between kīpuka and matrix visually obvious (Fig. 1B). This primary successional matrix plant community is composed of small trees and shrubs

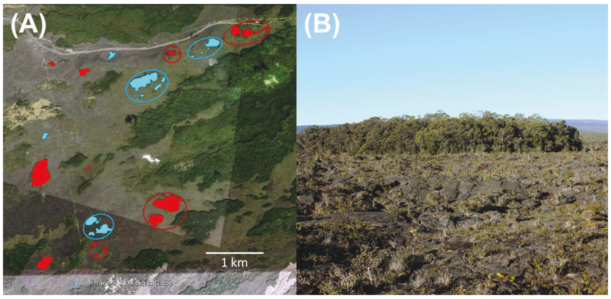

Figure 1. (A) The 34 kīpuka (forest fragments) included in this study, which were divided into 15 groups (clustered kīpuka are shown with circles around them) based on proximity and rat treatment (rat-removed = blue, un-trapped (control) = red). (B) A kīpuka (background), which stands out from the smaller and sparser plants growing in the surrounding lava matrix (foreground).

such as *Coprosma ernodeoides* (Rubiaceae), *Vaccinium* spp. (Ericaceae), and *Leptecophylla tameiameiae* (Epacridaceae), which all produce fruits eaten by ʻomaʻo; the pteridophytes, *Dicranopteris linearis* (Gleicheniaceae), *Sadleria cyatheoides* (Blechnaceae), and *Palhinhaea cernua* (Lycopodiaceae); and a sedge, *Machaerina angustifolia* (Cyperaeae). The density of plants and closed canopy of the kīpuka creates a shaded microenvironment that is cooler and moister than the surrounding lava matrix (Raich et al. 1997). The kīpuka landscape receives a mean annual range of rainfall between 2000–3000 mm (Giambelluca et al. 2013), and mean average temperatures vary spatially from 10–20°C (Wu et al. 2014). The study site is within the State of Hawaiʻi Forest Reserve System, and has remained largely undisturbed by people, although several introduced mammals besides rats are present including feral pigs *Sus scrufa*, mongooses *Herpestes javanicus*, and mouflon-domestic sheep hybrids *Ovis orientalis* × *Ovis aries*. The study site occurs at high elevations where the mean annual temperatures are below that required for the development of avian malaria parasite *Plasmodium relictum* and its vector, the mosquito *Culex quinquefasciatus* (Atkinson and LaPointe 2009), allowing for the persistence of populations of endemic birds that have been extirpated from lower elevations by malaria and other threats. The most abundant non-native birds present in the landscape are the Japanese white-eye *Zosterops japonicas* (family Zosteropidae) and kalij pheasant *Lophura leucomelanos* (Phasianidae).

Our focal study species were the native thrush ʻomaʻo (Turdidae), and the Hawaiian honeycreepers Hawaiʻi ʻamakihi, ʻapapane and ʻiʻiwi (Fringillidae). ʻOmaʻo is the largest (mean male mass 51.0 ± 0.44 g (Wakelee and Fancy 1999), followed by ʻiʻiwi (19.9 ± 0.38 g, Fancy and Ralph 1998), ʻapapane (16.0 ± 0.20 g, Fancy and Ralph 1997), and Hawaiʻi ʻamakihi (13.4 ± 0.55 g, Lindsey et al. 1998). None of these species are sexually dimorphic, but immatures do have distinct plumages.

We studied birds in 34 kīpuka, all isolated > 0.5 km from continuous forest, ranging in size from 0.07 to 12.37 ha (mean 1.93 ha, Fig. 1A). Larger kīpuka have greater average canopy heights, larger variation in heights, and less impact from the matrix than smaller kīpuka (Vaughn et al. 2014). Beginning in June 2011, we removed rats from 16 of the 34 study kīpuka using snap traps baited with peanut butter or coconut, as part of a larger study on the interactive effects of predation and ecosystem size on arthropod food webs. We placed traps in 25 m grids within each kīpuka and every 12.5 m around kīpuka perimeters, to limit rat immigration into the kīpuka. The traps were checked and re-baited every two weeks for the duration of this study. To assess the efficacy of our baiting methods, we distributed Black Trakka™ tunnels (10 × 10 × 50 cm; Gotcha Traps, New Zealand) at 1–2 randomly selected trees in each kīpuka. Tracking tunnels were placed at the forest floor, and when the tree was sufficiently tall, also at 6 and 12 m above the forest floor. Tracking tunnels were baited and checked prior to rat removal and quarterly afterwards. Data from tracking tunnels in all kīpuka suggest that the initial trapping effort was highly successful at reducing rat abundance in the treated kīpuka (henceforth ʻrat-removed kīpukaʼ) and in greatly reducing rat recolonization (Fig. 2). The un-trapped kīpuka (henceforth ʻcontrol kīpukaʼ) show persistent pre-treatment levels of rat activity (Fig. 2).

Mist-netting

We set up 8 to 20 nylon mist-nets (32-mm mesh, 12 × 2.6 m and 6 × 2.6 m) at a given time at heights covering 1–6 m above the ground. The nets were rotated through each of the 34 study kīpuka over a period of 4 months (Feb–May) each year (2011, 2012, 2013), chosen to coincide with the peak breeding period of the native Hawaiian birds (van Riper and Scott 1979, Ralph and Fancy 1994b). We operated mist-nets 5 d per week, but did not open them on rainy or windy days. Mist-net sites were selected a-priori using Google Earth (accessed January 2011) to ensure even sampling within each kīpuka. The number of mist-nets in each kīpuka was proportional to kīpuka area, with one 12-m net per 0.25 ha for kīpuka < 10 ha, and one 12-m net per 0.75 ha for kīpuka ≥ 10 ha. We netted in each kīpuka < 10 ha for 12 h over 2 d, from 07:00 to 14:00 on the first day and 07:00 to 12:00 on the second day. In kīpuka ≥ 10 ha we netted for 19 h over 3 d, from 07:00 to 14:00 on the first 2 d and 07:00 to 12:00 on the third day. We netted for an extra day in these larger kīpuka to compensate for the lower net coverage per ha.

We fitted each captured bird with a unique combination of three plastic colored leg bands and one aluminum US

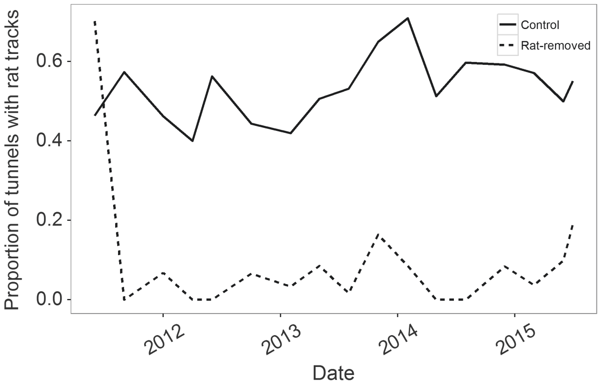

Figure 2. The proportion of all tracking tunnels with rat tracks in control and rat-removed kipuka over time (control n = 1336, rat removal n = 1004). Effect of treatment: $F_{1,33} = 23.87$, $p < 0.001$.

Federal Bird Band. We measured wing, tarsus, bill and tail length and mass of each individual. When possible ($>90\%$ of the time), we classified native birds as adult (A) or hatch year (HY) based on plumage characteristics, skull ossification and morphometric measurements (Fancy et al. 1993, Pyle 1997). We also classified adult birds by sex and breeding condition, when possible ($>90\%$ of the time), based on the presence of a brood patch or cloacal protuberance and morphometric measurements (Pyle 1997). We did not attempt to sex hatch year birds. Any birds we were unable to classify by age or sex were excluded from our analysis.

Resighting

To re-encounter color banded birds over time across the 34 kīpuka, 1–3 observers conducted resighting surveys in each kīpuka during a one month period 4 times a year (Aug, Nov, Feb, May), from Aug 2011 through May 2013 for a total of 8 resighting periods, 4 within the breeding season (February and May) and 4 outside of the breeding season(August and November) (van Riper and Scott 1979, van Riper 1987, Ralph and Fancy 1994a, b). Using Google Earth (accessed July 2011), we delineated straight-line transects spaced 40 m apart through each kīpuka >1 ha. We then used a compass and GPS to walk these transects at a slow, steady pace (approximately 30 min per 100 m), and wrote down the species of every bird we visually observed, whether or not it was banded, and the unique color-band combination if it was banded. We did not record birds if we were unable to see their legs. For kīpuka <1 ha, we did not use transects but walked systematically through the kīpuka for 30 min to 1 h based on kīpuka size. Our standardized resighting effort among kīpuka of different sizes resulted in approximately one hour of resighting effort for every 0.75 ha of kīpuka area.

Statistical analyses

For our analyses, we grouped kīpuka into patches based on proximity and rat treatment (i.e. kīpuka of the same treatment type <200 m from one another were grouped), for a total of 15 groups (henceforth 'kīpuka group', Fig. 1A). We did this because the rats and birds are unlikely to view distances <200 m as significant barriers to movement (Shiels 2010), and these kīpuka cannot be considered fully independent. First, we compiled data on movement distances for each species, using resightings and recaptures of individually marked birds. Distances were calculated from the specific capture location of each bird to their subsequent resight or recapture location. We used a Kruskal–Wallis test with Mann–Whitney U tests for nonparametric pairwise comparisons to test for differences in distances moved between species, including by age and sex (sex unknown for HY birds). To test for differences in proportions of individuals of each species, age and sex moving from the kīpuka group in which they were banded, we used chi-square tests of independence.

To understand factors that may influence movement patterns, we used a logistic regression to model patch fidelity versus movement. We use the term 'patch fidelity' instead of 'site fidelity' because the latter is often associated with fidelity to a home range or nesting site across seasons and years (Schlossberg 2009). Here, patch fidelity refers to the reencounter probability of an individual in a patch from one census period to the next. To account for multiple observations of the same individuals over different sampling periods we used a generalized estimating equation (GEE) with a binomial probability distribution and a logit link function (Liang and Zeger 1986, Hardin and Hilbe 2003). Thus, with a separate GEE model for each species, we determined if the patch fidelity of an individual to a patch ($0=$ patch faithful (i.e. if an individual was only resighted in the same patch and never outside of that patch), $1=$ was resighted in more than one patch), was influenced by season (breeding or nonbreeding, pooled across years), the individuals' age (adult or hatch year), sex (male or female), or rat treatment and kīpuka group size. We tested only those 2-way interactions that we believed biologically reasonable: rat treatment × kīpuka size, rat treatment × bird age, rat treatment × season, rat treatment × sex, and season × sex of the bird. We compared model fit using the quasi-likelihood information criterion, corrected for small sample sizes (QICC). The models with ΔQICC values <2 were considered the best-approximating models over the competing models (Burnham and Anderson 2002). All statistical tests were conducted in SPSS (IBM 2014). The values reported in the Results section are means ± SE.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.p9s05> (Knowlton et al. 2017).

Results

Interspecific differences in movement behavior and patch fidelity

We banded 1702 individuals of the 4 focal species over 3 yr (2011–2013). Over the course of 8 resighting surveys and 2 mist-netting periods (Aug 2011–May 2013), we resighted or recaptured 612 individuals at least once. We resighted the nectarivorous ʻapapane and ʻiʻiwi the least frequently (24 and 39% of banded individuals were reencountered, respectively), and, for those birds that moved from where they were banded, ʻapapane moved the farthest average distance (1578 ± 159 m), followed by ʻiʻiwi (1380 ± 189 m, Table 1). We resighted the frugivorous ʻomaʻo the most frequently (55% of banded individuals), and that species moved the shortest average distance (772 ± 146 m, Table 1). For those birds that moved, ʻapapane moved significantly farther than Hawaiʻi ʻamakihi ($U=5224$, $\mathrm{DF}=3$, $p=0.001$) and ʻomaʻo ($U=1548$, $\mathrm{DF}=3$, $p=0.002$), but not ʻiʻiwi. ʻIʻiwi also moved significantly farther than Hawaiʻi ʻamakihi ($U=2421$, $\mathrm{DF}=3$, $p=0.002$) and ʻomaʻo ($U=685$, $\mathrm{DF}=3$, $p=0.001$). However, all species exhibited movement across the study area and among the many kīpuka (Fig. 3).

Influence of sex and age on movement behavior and patch fidelity

Of those birds that moved from where they were banded, females moved longer distances than males in

Table 1. Total individuals and percentages of each species (ʻapapane, Hawaiʻi ʻamakihi, ʻiʻiwi and ʻomaʻo), age (HY = hatch year) and sex (M = male, F = female) banded, resighted, moved to a different kīpuka group, and total average and maximum distances moved for those birds that did move from the kīpuka in which they were banded over the two years of the study.

Species	Total banded (F, M, HY)	Total resighted (F, M, HY)	Percent resighted (F, M, HY)	Percent moved to a different kīpuka group (F, M, HY)	Ave. distance moved (only birds that moved) (m ± SE) (F, M, HY)	Max distance moved (m) (F, M, HY)
ʻApapane	843 (190, 527, 126)	200 (39, 136, 25)	24 (20, 26, 20)	33^{a}, 23^{b}, 20	1578 ± 159 (2080, 1372, 1764)	4835 (4209, 4835, 4035)
Hawaiʻi ʻamakihi	387 (108, 196, 83)	199 (52, 123, 24)	51 (48, 63, 29)	$27^{c,e}$, $21^{d,f}$, $67^{e,f}$	938 ± 90 (1108, 757, 1484)	5195 (4063, 5195, 3608)
ʻIʻiwi	293 (89, 162, 42)	114 (26, 77, 11)	39 (29, 48, 26)	15, 21, 18	1380 ± 189 (765, 1745, 1496)	4698 (3159, 3791, 4698)
ʻOmaʻo	179 (38, 120, 21)	99 (27, 63, 9)	55 (71, 53, 43)	$22^{a,c}$, $10^{b,d}$, 33	772 ± 146 (1058, 727, 480)	4874 (4874, 3866, 1580)

*Superscript letters indicate significant differences across species and kīpuka group (within the same column only) based on chi-square tests of independence.

ʻapapane ($U = 386$, DF = 1, p = 0.033) and Hawaiʻi ʻamakihi ($U = 1430$, DF = 1, p = 0.05), although male ʻiʻiwi moved farther than females ($U = 90$, DF = 1, p = 0.009, Fig. 4). The only significant age-related difference in movement was in Hawaiʻi ʻamakihi where hatch years moved farther than adults ($U = 708$, DF = 1, p < 0.001, Fig. 4). Species-specific

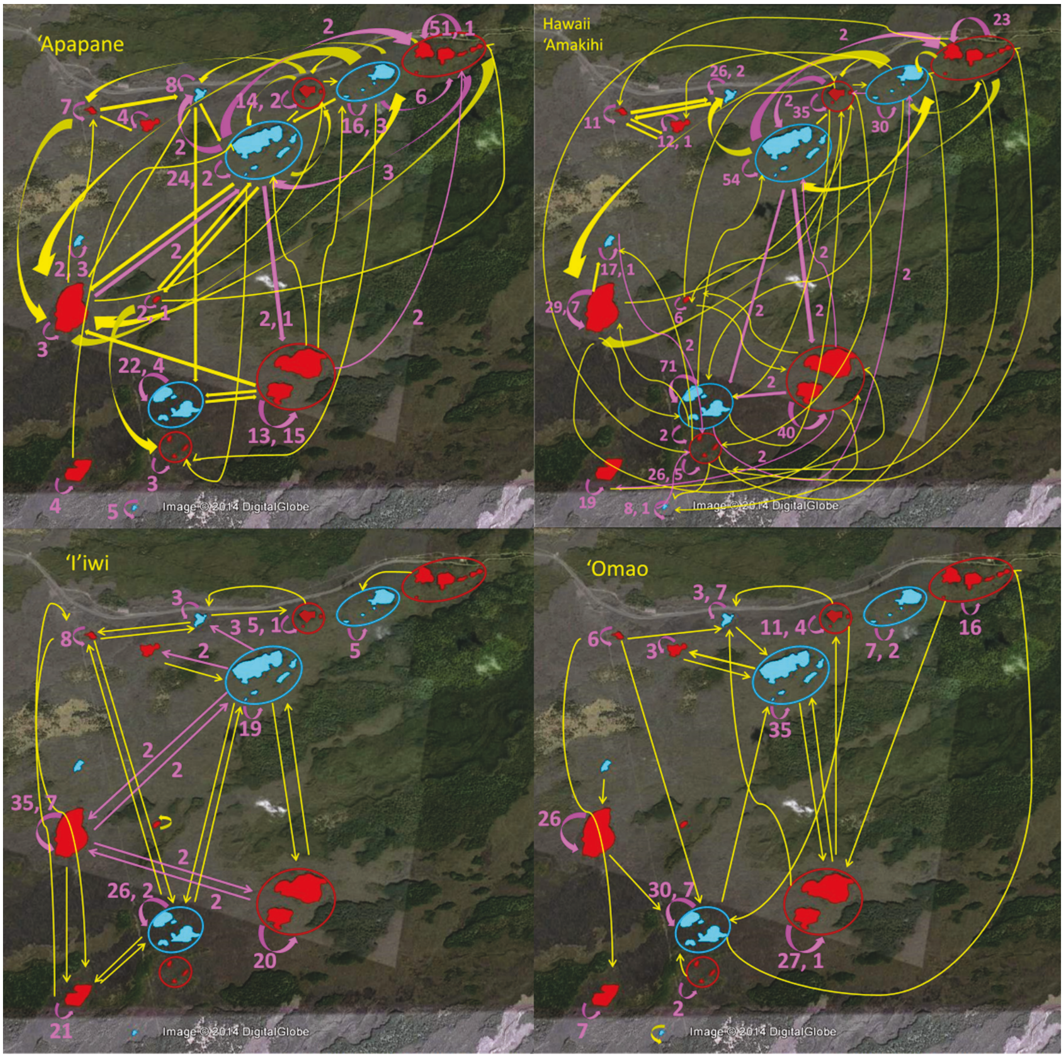

Figure 3. Maps of individual movements of adult (first number) and hatch year (second number) birds across the kīpuka landscape, for each species. Numbers indicate movement events, not individuals. Yellow arrows indicate a single movement, while purple arrows indicate multiple movements and the number of movements is listed next to the arrow (adults, hatch year). If no second number is shown no hatch year birds were recorded. Arrows that loop back to the same kīpuka indicate birds resighted in the same kīpuka where they were banded. Red fragments are control kīpuka (no rats were removed), and blue fragments are rat-removed kīpuka.

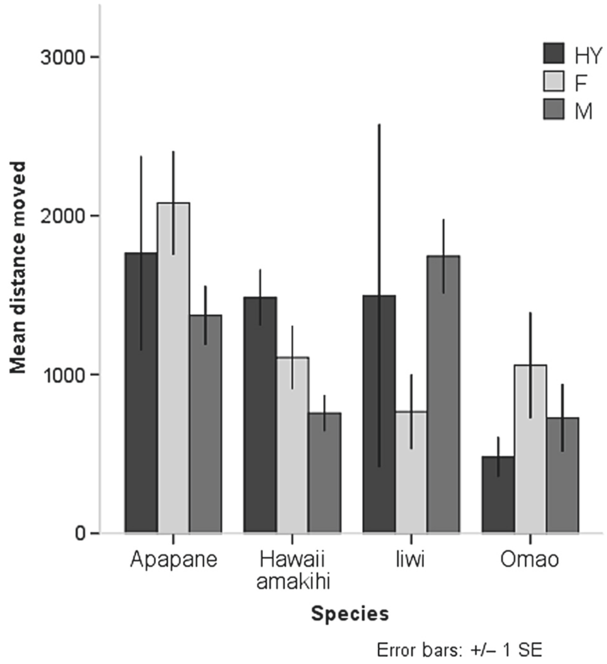

Figure 4. Distances moved (mean ± SE) by adult males (M), females (F), and hatch year (HY) ‘apapane, Hawaiʻi ‘amakihi, ‘i‘iwi and ‘oma‘o birds that moved from the kīpuka where they were banded. For HY birds sex is unknown.

GEE model comparisons for patch fidelity showed the highest support for models including age and sex for Hawaiʻi ‘amakihi, and sex for ‘oma‘o (Table 2). Overall, male ‘oma‘o had the highest patch fidelity, with 90% of resighted individuals resighted in the kīpuka group where they were banded, and hatch year Hawaiʻi ‘amakihi had the lowest patch fidelity, with only 33% of resighted individuals resighted in the kīpuka group where they were originally banded (Table 1).

Influence of season on movement behavior and patch fidelity

Although all species tended to move farther during the non-breeding season than the breeding season (Fig. 5), these differences were significant only for ‘i‘iwi ($U = 130$, $DF = 1$, $p = 0.014$) where non-breeding movement averaged 900 m greater than the breeding season. In terms of patch fidelity, species-specific GEE model comparisons indicated seasonal differences for ‘apapane and ‘i‘iwi only (Table 2).

Influence of patch size and invasive rats on site fidelity

For all species, more individuals were resighted repeatedly in larger patches compared to smaller patches (67 vs 32%, respectively), although Hawaiʻi ‘amakihi also had high resight frequency in small patches (41% of individuals; Fig. 3). However, the effect of patch size on patch fidelity ranked high only for ‘oma‘o (Table 2). In response to rat treatment, only Hawaiʻi ‘amakihi was more likely to be faithful to patches from which rats had been removed (68% of resighted individuals remained in or moved to rat-removed kīpuka) (Table 2). For ‘apapane, ‘i‘iwi and ‘oma‘o, 42, 36 and 53% of resighted individuals remained in or moved to rat-removed kīpuka, respectively.

Discussion

Our study is among the first to describe detailed spatially-dynamic movement behavior among a community of birds within a fragmented landscape, with measures of the strength of some key extrinsic and intrinsic drivers of these behaviors. Overall, many weak forces as opposed to one or a few strong forces appear to collectively shape

Table 2. Model selection results for site fidelity, by species, using generalized estimating equation quasi-likelihood information criterion, corrected for small sample sizes (QICC) values. Rats = rat treatment, size = kīpuka group size. $^+$Indicates a significant parameter ($p < 0.10$).

Species	Model	QICC	ΔQICC
‘Apapane	Intercept	247.87	–
	Season	249.06	1.19
	Season, age, sex	249.97	2.10
	Season, age, sex, rats, size	254.75	6.88
	Rats × size, rats × age, rats × season, rats × sex, season × sex	258.69	10.82
Hawaiʻi ‘Amakihi	Sex	358.75	–
	Sex, rats, age	360.01	1.26
	Intercept	360.18	1.43
	Sex, rats, age, season, size	364.71	5.42
	Rats × size, rats × age, rats × season, rats × sex, season × sex	370.39	11.64
‘I‘iwi	Season$^+$	159.53	–
	Season, rats	160.23	0.70
	Intercept	161.59	2.06
	Season, rats, sex, size	164.92	5.39
	Season, rats, sex	165.25	5.72
	Rats × size, rats × age, rats × season, rats × sex, season × sex	170.43	10.90
‘Oma‘o	Size$^+$, sex$^+$	108.48	–
	Sex	109.95	1.47
	Size, sex, season	110.46	1.98
	Intercept	111.8	3.32
	Size, sex, season, age, rats	112.32	3.84
	Rats × size, rats × age, rats × season, rats × sex, season × sex	117.86	9.38

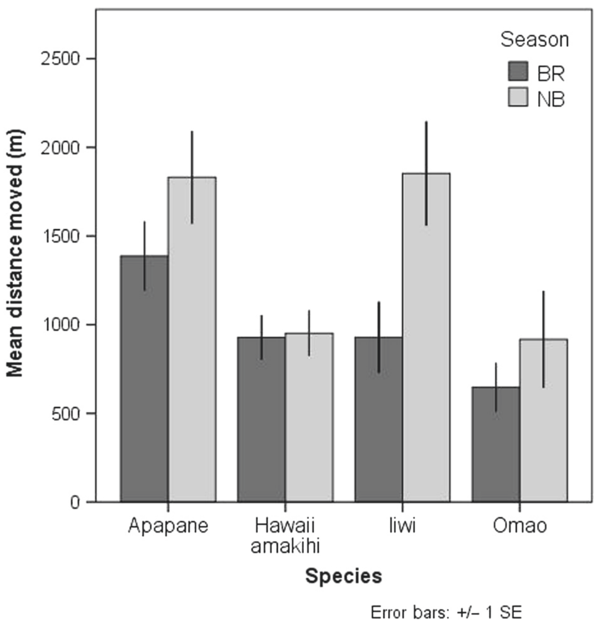

Figure 5. Distances moved (mean ± SE) by ʻapapane, Hawaiʻi ʻamakihi, ʻiʻiwi and ʻomaʻo during the breeding (BR, Jan–June) and non-breeding (NB, July–Dec) seasons for those birds that moved from the kīpuka where they were banded.

birds' movement behavior, with the more intrinsic drivers of movement behavior – species, sex, age and season, being more important than the extrinsic drivers of patch size and invasive rats. These results help to clarify dynamic and species-specific patterns of movement behavior by four native species with different dietary resource requirements. This is consistent with the notion that the interactions of different species with their landscape, and perhaps each other, are complex and are shaped by multiple factors including resource quantity (kīpuka size), and resource distribution (spatial arrangement of kīpuka and seasonal variation). Some recent studies have suggested that including species-level behavioral movement information is critical to understanding the extinction risk to populations (Fordham et al. 2014). Few bird communities on Earth have experienced as dramatic a loss to extinction as those in Hawaii (Pratt et al. 2009), and therefore, the need for accurate, biologically sound information on species traits that can be used to help forecast extinction risk is paramount.

Interspecific differences in movement behavior

There was a high degree of movement among all species, but the two nectarivores, ʻapapane and ʻiʻiwi, had the longest movements (1578 and 1380 m, respectively) which may be related to foraging requirements. Nectarivores in Hawaiʻi were thought to have moved long-distances historically in search of flowering trees (Perkins 1903, Carpenter 1987, Kuntz 2008), a resource that is variable over space and time (Hart et al. 2011). In fact, such long distance movements are believed to have contributed to the extinction of some endemic Hawaiian birds by speeding the exposure and spread of introduced diseases such as avian pox and malaria (Samuel et al. 2011). It is almost certain that some nectarivores banded at our study area moved outside of our resighting area, and also that many of the birds we banded originated from other areas. The majority of banded nectarivores were never resighted (76% of ʻapapane and 61% of ʻiʻiwi, compared to 49% of Hawaiʻi ʻamakihi and 45% of ʻomaʻo), suggesting that most nectarivores captured were either transiting through the kīpuka landscape to forage or had home ranges larger than the study area. Ralph and Fancy (1995) obtained similar results during a six year study across four contiguous forest sites on Hawaiʻi Island, where 78% of ʻapapane and 82% of ʻiʻiwi were not resighted. Our result that Hawaiʻi ʻamakihi and ʻomaʻo appear to be more sedentary in the kīpuka landscape than the nectarivores is consistent with other studies (Ralph and Fancy 1994a), that observed a similar high rate (56%) of banded, re-encountered ʻomaʻo at their continuous forest and cattle-grazed study sites on the Big Island of Hawaiʻi. The non-nectarivorous species may be more sedentary because they are able to consistently use the food resources in the matrix – the Hawaiʻi ʻamakihi because they are more generalist, and ʻomaʻo because many low stature matrix plants, such as pūkiawe *Leptecophylla tameiameiae*, bear edible fruits.

Influence of patch size on movement behavior

Many studies have found a positive effect of habitat patch size on species richness and abundance (Mazerolle and Villard 1999, Watling and Donnelly 2006, Prugh et al. 2008). One important mechanism shaping the relationship between patch size and biodiversity is the influence of movement patterns, which can affect species persistence through metapopulation dynamics (Moilanen and Hanski 1998). In our kīpuka study system, Flaspohler and colleagues (2010) observed a positive relationship between patch size and species richness of native Hawaiian birds. We expected that, within species, most birds fledged in small kīpuka would fly out to forage in larger kīpuka, whereas birds fledged in large kīpuka would be more site faithful to that kīpuka. ʻOmaʻo was the only species more site faithful in larger kīpuka than in smaller kīpuka. The affinity for larger kīpuka may stem from the frugivorous diet of the ʻomaʻo and the nesting habits of this species. ʻOmaʻo nest in the cavities of large trees more often than the other focal species (Ralph and Fancy 1994a), and larger kīpuka have larger trees and more potential nest sites (Vaughn et al. 2014). Larger kīpuka also have more fruit-bearing plant species, and thus may provide a more stable resource base for the ʻomaʻo (Kovach 2012). Although ʻomaʻo are more site-faithful in large kīpuka, they are obviously not averse to using the matrix. In fact, we observed all four focal species using the matrix to a limited extent for foraging and even nesting. In a detailed radio-tracking study of nine adult (unsexed) ʻomaʻo in the kīpuka landscape, Wu et al. (2014) found that, during the observation periods, 6 of 9 tracked individuals travelled to neighboring kīpuka and spent up to 50% of their time in the matrix.

In contrast to ʻomaʻo, we found no evidence that ʻapapane, ʻiʻiwi, and Hawaiʻi ʻamakihi are more site faithful to larger kīpuka. None of the study kīpuka are > 500 m from another forest patch, and ʻapapane, ʻiʻiwi and Hawaiʻi ʻamakihi appeared able to freely travel between these patches. Interestingly, our results differ from movement behavior documented in continental Neotropical forest birds, where many species are averse to crossing gaps in forest > 100 m (Moore et al. 2008, Ibarra-Macias et al. 2011). However, the matrix in this study is populated with small shrubs and trees, making it much more hospitable to forest birds than the bare pasture or roads that formed the matrix in other studies. The high degree of movement documented in the ‘apapane, Hawaiʻi ‘amakihi, and ‘iʻiwi suggests that these native forest birds on the Island of Hawaiʻi may be well-adapted to a fragmented landscape at the small to medium landscape-scale, perhaps because these birds have evolved with an almost continuous history of volcanic activity that continually re-fragments forests. The degree to which the high mobility of movement across the kīpuka fragmented landscape scales up to mobility across larger anthropogenically-fragmented landscapes will require further study at larger spatial scales.

Impacts of invasive rats on movement behavior

Invasive black rats are highly omnivorous, and are documented nest predators of native Hawaiian birds (Lindsey et al. 2009). Adult birds usually show high levels of patch fidelity to locations where they breed successfully, and low patch fidelity to locations where they fail to fledge young (Greenwood and Harvey 1982, Haas 1998, Hoover 2003), while hatch year birds generally show low fidelity to their natal sites (Schlossberg 2009). There is some evidence that nest predation on the native birds in the kīpuka is lower in rat-removed kīpuka (J. L. Knowlton pers. comm.), which we hypothesized would lead to higher patch fidelity in those sites. Competition between rats and native birds for food resources could be another reason for native birds to show higher patch fidelity to rat-removed sites. However, out of the four native birds species we studied, only Hawaiʻi ‘amakihi had higher patch fidelity in rat-removed patches after two years of rat-removal. The effects of rat-removal may take longer than a few years to manifest themselves in bird behavior, and may occur through differential survival over generations, not through learning by individual birds. For example, the nest height of O‘ahu ‘elepaio *Chasiempis ibidis* has increased over time as an adaptation to avoid rat predation, and this has occurred through rapid evolution, not learning (VanderWerf 2012). However, VanderWerf and Smith (2002) found that patch fidelity of female ‘elepaio on Oʻahu was much higher in sites with rat-removal (0.93, n = 14) than without (0.33, n = 9), although male ‘elepaio patch fidelity was unaffected.

Although rats have a wide-ranging diet and can compete with native Hawaiian birds for food resources (Scott et al. 1986, Banko and Banko 2009, Lindsey et al. 2009), conclusive evidence of strong population level effects of food competition is lacking. Because rats are primarily nocturnal, and the kīpuka arthropod community includes diurnal and nocturnal species, one possibility is that there is little overlap in nocturnal arthropod prey base of the rats and the largely diurnal arthropod prey base of the birds. Moreover, several studies have shown that although the diet of the black rat in Hawaiʻi does include nectar and arthropods, the majority (> 80%) of food appears to be fruit and seeds (Shiels et al. 2013, 2014). Given the complexity of the birds' movement behavior and the short duration of our study, that we found even a weak effect of rat-removal might suggest that a longer-term study would reveal a much larger effect.

Impacts of age and sex on movement behavior

We found species-specific differences in movement behavior between hatch year and adult birds within a species, as well as between males and females. Generally, we were more likely to re-encounter adult male ‘apapane, ‘iʻiwi, and Hawaiʻi ‘amakihi than female or hatch year birds. As with most passerines, hatch year birds in the kipuka landscape have lower survival rates than adults (J. L. Knowlton pers. comm.), which could contribute to the lower resight rate of the young birds. Further, male birds are more vocal and usually have higher survival rates than female birds (Payevsky et al. 1997), increasing their chance of being resighted. In contrast, adult ‘oma‘o females were resighted more frequently than male or hatch year birds, possibly because unlike other passerine species, female ‘oma‘o also sing and defend their nests (van Riper and Scott 1979). Of the resighted birds, females of ‘apapane and Hawaiʻi ‘amakihi, but not ‘iʻiwi or ‘oma‘o, traveled longer distances and showed lower kīpuka group fidelity than males of the same species. In contrast, ‘iʻiwi males traveled much farther than females, perhaps due to their much larger body mass than females (average of 19% greater, Fancy and Ralph 1998), leading to greater energy requirements. For most passerines, males often stay near the nesting site to defend their territory while females forage for food for the young (Greenwood 1980). However, both sexes of ‘apapane, Hawaiʻi ‘amakihi, ‘oma‘o and ‘iʻiwi participate in feeding nestlings and fledglings (Woodworth and Pratt 2009).

Seasonal differences in movement behavior

Tropical birds, which are generally considered non-migratory resident species, can have spatial distributions that differ substantially between breeding and non-breeding seasons for many reasons. Seasonal fluctuations in the distribution and availability of food resources may reward active resource tracking behavior, and the need to defend a breeding territory or tend to a nest may require more sedentary behavior during the breeding season (Holbrook and Smith 2000). All focal species have protracted and somewhat variable breeding and non-breeding seasons compared to temperate mainland birds (Woodworth and Pratt 2009). Consequently, although they are year-round residents, we expected that the native Hawaiian birds would be less site faithful and move longer distances in the non-breeding season than in the breeding season. As expected, ‘apapane, ‘oma‘o and ‘iʻiwi did move farther on average during the non-breeding than breeding seasons, and the nectarivores (‘apapane and ‘iʻiwi) had significantly higher patch fidelity during the breeding season. Kuntz (2008) also found that seasonal movement patterns in ‘iʻiwi were associated with breeding/non-breeding seasons, where ‘iʻiwi would move long distances (> 12 km) in search of flowering resources following their breeding season. However, some small populations of ‘apapane and ‘iʻiwi may remain at a particular location throughout the year (Perkins 1903, Baldwin 1953, Ralph and Fancy 1995), and studies that tested for a positive relationship between

ʻapapane and ʻiʻiwi densities and ʻōhiʻa flowering suggested that this relationship is not straightforward; it appears to depends on site, season, flowering intensity, and spatial scale (Carpenter 1987, Ralph and Fancy 1995, Hess et al. 2001, Hart et al. 2011). In this study we did not quantify bird densities or flowering or fruiting patterns, which may have influenced birds' movement patterns. However, bird densities often change on seasonal and yearly time scales, and are themselves influenced by many factors such as fragment size and resource levels (Kovach 2012). In the same kīpuka landscape before rat-removal, Kovach (2012) found that fragment size and ʻōhiʻa flowering were the best predictors of ʻiʻiwi density, while fruit density was the best predictor of ʻomaʻo density. Further, ʻapapane densities were best explained by elevation rather than flower density, and Hawaiʻi ʻamakihi density was best explained by the level of connectivity of the kīpuka (Kovach 2012). Hawaiʻi ʻamakihi and ʻomaʻo are believed to be more site faithful throughout the year than the nectarivores (Lindsey et al. 1998), likely corresponding to more stable food resources. To the degree that movement is driven by resource distribution, with some resources changing seasonally or stochastically, species responses to changes in forest quality will be tied to feeding guild as well as age and sex. Further, with forest quality linked in part to kīpuka size (Vaughn et al. 2014) and modified by the presence of omnivorous rats, it is clear that the forces that mold movement behavior are varied and interrelated.

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