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Home range sizes of two Hawaiian honeycreepers: implications for proposed translocation efforts

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ABSTRACT. Prior to the reintroduction of a species, managers need an understanding of the expected behavior of the species in the new habitat. How a species uses its habitat and how much space individuals require are particularly important when conservation lands are limited. Critically endangered Maui Parrotbills (Kiwikiu, *Pseudonestor xanthophrys*) once occupied a variety of habitats on the Hawaiian islands of Maui and Moloka'i, but, due to habitat loss and disease, are now restricted to a fraction of their former range. To prevent their extinction, reintroducing parrotbills to historically occupied native, mesic forest on the leeward slopes of Haleakalā is considered a critical recovery action. Managers have selected Nakula Natural Area Reserve (NAR) as the site of translocation and restoration efforts are currently underway to support this goal. In addition, other species, including endemic Maui 'Alauahio (Maui Creeper, *Paroreomyza montana*), may recolonize these forests naturally as the habitat improves. However, estimates of the home range sizes of focal species are needed so that managers can estimate how many individuals might be able to occupy new habitats. Our objective therefore was to estimate the home range sizes of parrotbills and 'alauahio at three sites within their current ranges to provide estimates of typical habitat and space use patterns. Using resightings of color-banded birds from 2007 to 2014, we calculated home ranges using minimum convex polygons and kernel density estimators. Depending on estimation technique, parrotbill home ranges were estimated to encompass 9.29 ± 1.29 (SE) ha or 9.63 ± 1.51 ha, and pairs occupied ranges of 11.8 ha or 14.5 ha. 'Alauahio home ranges were 0.85 ± 0.09 ha or 0.87 ± 0.08 ha in size. Home range sizes varied among study sites for both species, likely reflecting the influence of local habitat attributes and quality on movement patterns and space use. Although we do not know how these species will behave in the new habitat, our estimates of home range size provide guidance for managers planning the reintroduction of parrotbills to Nakula NAR.

RESUMEN. **Ámbito hogareño de dos mieleros Hawaianos: implicaciones para esfuerzos de translocación**

Antes de la reintroducción de una especie, es necesario que los gerentes entienden el comportamiento esperado de la especie en el nuevo hábitat. Cuando las zonas de conservación son limitadas es particularmente importante a saber cómo una especie utiliza su hábitat y cuánta área se demande. El *Pseudonestor xanthophrys* es en grave peligro de extinción, y una vez ocupó una variedad de hábitats en las islas hawaianas de Maui y Moloka'i, pero, debido a la pérdida de hábitat y enfermedades, la distribución hoy en día es limitada a una fracción de su antigua área de distribución. Para evitar su extinción, reintroduciendo picolores a bosques mésico en las laderas de sotavento de Haleakalā, lo cual fueron históricamente ocupadas por los picolores, se considera una acción crítico para recuperación de la especie. Los gerentes han seleccionado Nakula Reserva Natural Area (NAR) cómo el sitio de los esfuerzos de translocación y restauración, lo cual están en curso. Además, otras especies, incluyendo la endémica especies *Paroreomyza montana*, pueden recolonizar estos bosques naturales mientras el hábitat se mejora. Sin embargo, se necesitan estimaciones de los tamaños del ámbito hogareño de especies focales para que los gerentes pueden estimar cuántos individuos podrían ser capaces de ocupar los nuevos hábitats. Nuestro objetivo, por tanto, fue a estimar el tamaño del ámbito hogareño de *Pseudonestor xanthophrys* y *Paroreomyza montana* en tres sitios dentro de sus rangos de corriente para desarrollar estimaciones de los patrones de movimiento típicos y el uso del espacio. Usamos avistamientos de aves con anillas de color, desde el 2007 hasta el 2014, para calcular las áreas de distribución utilizando polígonos convexos mínimos y estimadores de la densidad kernel. Dependiendo de la técnica de estimación, se estimaron que el ámbito hogareño de *Pseudonestor xanthophrys* fue 9.29 ± 1.29 (SE) ha o 9.63 ± 1.51 ha, y pares ocuparon rangos de 11.8 ha o 14.5 ha. El ámbito hogareño del *Paroreomyza montana* fue 0.85 ± 0.09 ha o 0.87 ± 0.08 ha. Para ambas especies, los tamaños del ámbito hogareño variaron entre los sitios de estudio, lo cual probablemente refleja la influencia de los atributos locales y la calidad del hábitat, y también de los patrones de movimiento y el uso del espacio. Aunque no sabemos cómo estas especies se comportarán en el nuevo

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hábitat, nuestras estimaciones del ámbito hogareño sirven de guía para los gerentes que planean la reintroducción de picolores a Nakula NAR.

Key words: demography, habitat use, Kernel density estimators, Maui ʻAlauahio, minimum convex polygon, Maui Parrotbill, reintroduction planning

As in the entire Hawaiian archipelago, the native avifauna of the island of Maui has suffered widespread extinctions and range contractions (Warner 1968, Scott et al. 1986, Pratt et al. 2009). Of more than 20 species of forest passerines known to have existed on Maui prior to the arrival of humans (James and Olson 1991), only six remain. Of these six, three are endemic to Maui and two are critically endangered (U.S. Fish and Wildlife Service 1967, International Union for Conservation of Nature 2012). The three surviving Maui endemics are Maui Parrotbills (*Pseudonestor xanthophrys*; hereafter parrotbills), Maui ʻAlauahio (Maui Creeper, *Paroreomyza montana*; hereafter ʻalauahio), and ʻĀkohekohe (Crested Honeycreeper, *Palmeria dolei*). With the exception of a small, relict population of ʻalauahio in Kula Forest Reserve (FR; hereafter Kula), populations of these species are restricted to a single strip of native forest (the largest tract remaining on Maui) on Haleakalā Volcano in east Maui above 1200 m in elevation (85 km^2, Fig. 1). Driven by habitat destruction and disease, continued range contraction is expected for these species (Benning et al. 2002, U.S. Fish and Wildlife Service 2006). Establishing a second population of parrotbills, the most critically endangered of the three, to once occupied habitat on leeward Haleakalā is considered a high priority for the long-term persistence and viability of the species (U.S. Fish and Wildlife Service 2006). Habitat quality in the leeward forests is expected to improve and the area may be recolonized by other extirpated native species, such as ʻalauahio. Although the population of ʻalauahio is much larger (>55,000, Brinck et al. 2012) than that of parrotbills, most of the population is in the same area as parrotbills and subject to the threats inherent to a species with a small range. The presence of leeward populations of parrotbills and ʻalauahio would reduce the likelihood of extinction resulting from stochastic events, and provide an additional high-elevation habitat refuge from disease-carrying mosquitos.

In 2011, the State of Hawaii established Nakula Natural Area Reserve (NAR; henceforth Nakula) in the Kahikinui region of leeward Haleakalā. This was, in part, for the protection of parrotbills, and Nakula has been designated as the future reintroduction site for the species (Fig. 1). The habitat is classified as mesic forest with a canopy dominated by koa (*Acacia koa*), ʻōhiʻa (*Metrosideros polymorpha*), and ʻaʻaliʻi (*Dodonea viscosa*). Although koa is not present in much of the current range of parrotbills, early observers of this species noted a strong affinity for koa (Henshaw 1902, Perkins 1903). Subfossils also show the species to have been historically present in the Kahikinui region (leeward Haleakalā west of the Kaupō Gap, James and Olson 1991). Unfortunately, the remaining native mesic forest has been greatly denuded as a result of heavy grazing and browsing by invasive ungulates. Restoration efforts in preparation for the reintroduction are currently in place in a 170-ha fenced area of Nakula free from invasive ungulates. This area is considered suitable for a small population of parrotbills until the forest in the surrounding area regenerates and/or is restored. However, the number of individual parrotbills that can be supported in this area is unknown.

Planning a reintroduction requires a good understanding of the expected ecology of the organism in the release site (Griffith et al. 1989, Seddon et al. 2007, International Union for Conservation of Nature 2013). An estimate of home range size (Burt 1943) is one critical element to allow conservation managers to estimate the number of individuals that could be supported in a reserve (i.e., carrying capacity). Combined with other demographic measures, habitat use may provide a benchmark for success of translocation efforts. Home range size has been used in other studies to predict space use for conservation efforts, e.g., Eurasian red squirrels (*Sciurus vulgaris*; Rodriguez and Andren 1999) and Eurasian lynx (*Lynx lynx*; Schadt et al. 2002). Although the habitat composition and structure at Nakula will likely remain different in many respects from the habitat currently occupied by parrotbills and ʻalauahio, estimates of space use in their current range can provide a

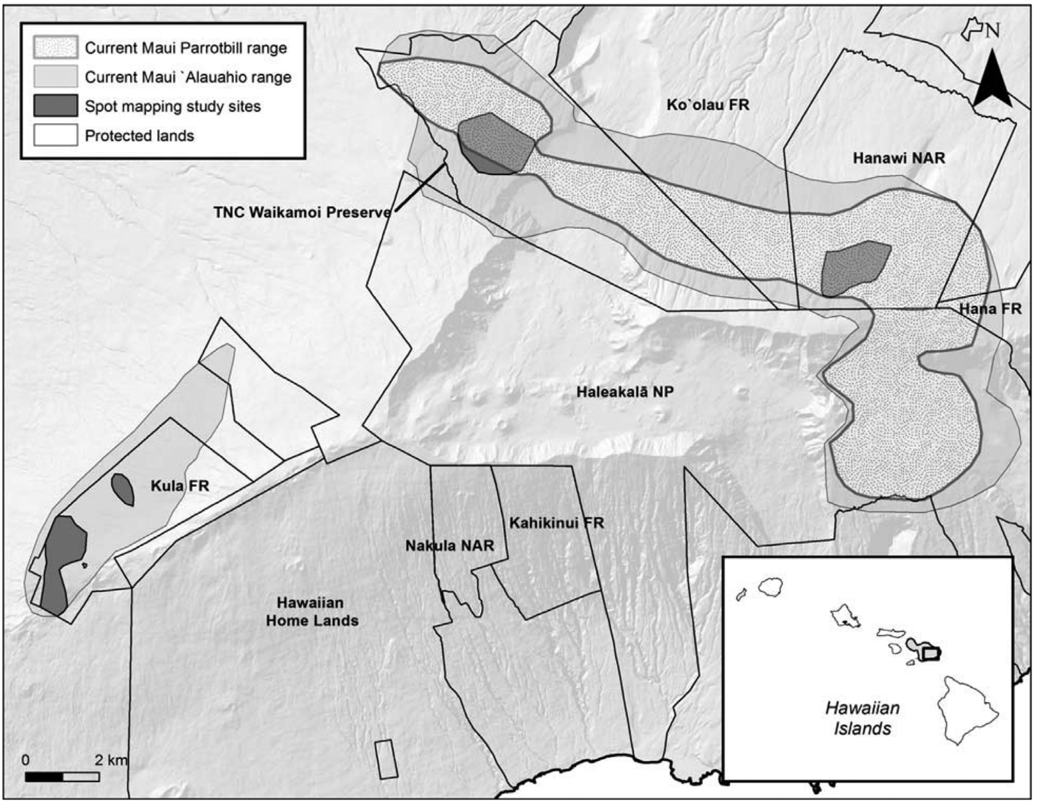

Fig. 1. Study sites where home ranges of Maui Parrotbills and Maui ʻAlauahio were examined as well as protected lands for future populations of both species.

baseline estimate of the amount of area required per individual.

The total population of parrotbills has been estimated at 500–600 individuals (590 ± 208 [95% CI], Camp et al. 2009) and occurs at low density compared to sympatric species throughout their range (Scott et al. 1986, Camp et al. 2009, Brinck et al. 2012). Estimates of overall population size have remained relatively constant since first estimated in 1980 (Scott et al. 1986, Camp et al. 2009). However, because of the large confidence intervals associated with all estimates, conclusions regarding population trends are not possible and the precision of these estimates is low (Camp et al. 2009, Gorresen et al. 2009). If the population is indeed stable, this may indicate that the available habitat is saturated and overall population size may only be increased by expansion of their range. This is one of the primary justifications for the planned reintroduction to Nakula.

Little is known about how much area is required for individual parrotbills to survive and reproduce (Simon et al. 1997). Using the best data available at the time, Pratt et al. (2001) estimated the home range size (area) of parrotbills to be 2.26 ha based on a limited sample size ($N = 7$ parrotbills) at one study site (Hanawi NAR; also included in the present study). We used similar methods over a 7-yr period and at a second study site at the western edge of the species' range. Although the entire range of parrotbills is ~50 km^2 on the windward slopes of east Maui (Simon et al. 1997), genetic variation within their range (Mounce et al. 2015) combined with variation in habitat and climate across the species' range suggests that the biology of the species may also vary spatially.

We also estimated the home range sizes of ʻalauahio, another insectivore that shares foraging substrates and moves in mixed flocks with parrotbills. Although the population on windward Haleakalā may be increasing (Camp et al. 2009), the species is also restricted to high-elevation forest, much of which is shared with parrotbills. Home ranges are reported to be 1–2 ha in size on windward Haleakalā (Baker and Baker 2000). ʻAlauahio were likely extirpated from the Kahikinui region sometime before 1980 and no definitive contemporary records exist for the species in this region. However, as with parrotbills, subfossil evidence shows the species to have been historically present (James and Olson 1991). Few surveys have been conducted in the leeward region and the status and distribution of the species outside of the range (Fig. 1) remains unknown. The abundance of ʻalauahio in the small, disjunct population in Kula is unknown, but this represents the closest known population of the species to the restoration areas of Kahikinui (~4 km). The habitat between Kula and existing Kahikinui forest is largely native shrubland, a habitat where ʻalauahio are sometimes found. This, combined with the relatively close proximity of the Kula population, suggests that the species might recolonize the Kahikinui region naturally (Scott et al. 1986). The nearest parrotbill population, by contrast, is ≥9 km of unsuitable habitat (e.g., grassland and exposed rock) away and no corridor exists for birds to move into Kahikinui naturally.

Prior to designing a reintroduction program, managers need information concerning the total number of parrotbills that could potentially occupy the release site and the greater area where birds may disperse. The intact native wet forest and the introduced mesic forest of Kula differ from the denuded native mesic forest of Nakula in many ways. However, parrotbills are only found in the intact forests and, as such, data are only available from these sites. This precludes the use of habitat attributes in the current range to predict abundance in the new habitat. Additionally, little to no upper elevation intact, native mesic forest remains on Maui and neither species occupies habitat similar to the habitat expected in the Kahikinui region after the area has been restored. Our objective was to estimate home range sizes of parrotbills and ʻalauahio in their current ranges to serve as an estimate of typical movement patterns and space use. These estimates are designed to be used by managers to predict the amount of space that might be required by translocated individuals and the number of individuals to be released at Nakula.

METHODS

Study sites. We studied parrotbills and ʻalauahio at two and three study sites, respectively, at Hanawi NAR (henceforth Hanawi; 20°44′N, 156°7′W), The Nature Conservancy's Waikamoi Preserve (henceforth Waikamoi; 20°46′N, 156°13′W), and Kula (26°42′N, 156°18′W) in east Maui, Hawaii, U.S.A. (Fig. 1). Both Hanawi and Waikamoi contain some of the most pristine remaining native forest on Maui, primarily dense, montane rainforests dominated by ʻōhiʻa and ʻōlapa (*Cheirodendron trigynum*; Jacobi 1989). Kula, in contrast, is dominated by non-native tree species, including various conifers (Families Pinaceae and Cupressaceae), eucalyptus (*Eucalyptus* spp.), Black Wattle (*Acacia mearnsii*), and tropical ash (*Fraxinus uhdei*). Rainfall was greatest at Hanawi (≥10,000 mm/yr), moderate at Waikamoi (≥2000 mm/yr), and comparatively low at Kula (~900 mm/yr) (Giambelluca et al. 2013).

Observations. Personnel from the Maui Forest Bird Recovery Project (MFBRP) conducted intensive spot mapping surveys (Verner 1985, Bibby et al. 1992) for parrotbills and ʻalauahio annually from 2007 to 2011 in Hanawi, from 2012 to 2014 in Waikamoi, and from 2013 to 2014 in Kula. At each site, birds were captured and fitted with unique combinations of colored leg bands. An effort was made to capture and band all parrotbills at each site each year using both targeted (using playback) and passive mist-netting in areas where unbanded parrotbills were observed. ʻAlauahio were among the most commonly captured species using both methods to capture parrotbills. Targeted and passive methods were also used at Kula for ʻalauahio.

Each year from 1 February to 1 July, three to seven observers systematically searched study sites and recorded locations of all color-banded individuals encountered using handheld Global Positioning System (GPS) units in Universal Transverse Mercator coordinates. The difficulty in traversing the terrain and the sensitivity of the forest to disturbance forced observers to stay largely on established trails at Hanawi and Waikamoi. Extensive trail systems allowed for comprehensive coverage of each site. Observers were not as limited to trails in the non-native forests at Kula. However, spot mapping was concentrated in areas with the highest densities of banded ʻalauahio. Areas covered included 184 ha at Waikamoi, 133 ha at Hanawi, and 220 ha at Kula. Survey effort was similar across all three study sites and averaged 2504.7 ± 480.5 survey hours per year (2010–2014).

Home range metrics. Despite the high survey effort, the sample size of resight points per individual per year was low for estimating home ranges (parrotbills = 7.2 ± 0.9 resights/bird/year, and ʻalauahio = 5.4 ± 0.5 resights/bird/year). Because the number of observations per individual could influence the size and shape of home ranges, we used two methods to delineate home ranges, minimum convex polygons (MCPs; Mohr 1947, Hayne 1949) and kernel density estimators (KDEs; Worton 1989).

Both MCP and KDE use a set of repeated observations to estimate a home range area. These methods predict areas where an animal was likely to have occurred during the survey period based on proximity to observed locations (Bibby et al. 1992). Each observation is used as an index of the movement patterns of an individual. Outlying points (i.e., resighting points separated from the main cluster) may represent: (1) an individual travelling outside its core range, or (2) an artifact of uneven survey effort in the localized area (e.g., an insufficient number of trails for adequate sampling).

Comparing the two methods, KDE limits the impact of outlying points on the metrics of a given home range by weighting contours by frequency of occurrence thereby targeting the core area(s) of a home range. In contrast, an MCP for the same individual would incorporate all points and the space between them as part of the home range, accounting for potential missed observations in the interstitial space between the apparent main cluster of observations and an outlier due to uneven survey effort. We estimated home range sizes using both MCP and KDE to obtain two estimates to take potential biases into account.

We first restricted estimation of home ranges to individuals with ≥10 resights per year (28.7% of resighted parrotbills and 20.8% of resighted ʻalauahio) based on Pratt et al. (2001). However, this resulted in some dubiously small home range sizes for both species. In addition, we found a significant positive linear (t = 2.4, P = 0.02) and logarithmic effect (t = 2.8, P = 0.007) of the number of resights on the size of parrotbill home ranges using the MCP method (Fig. 2). No asymptote was reached and could therefore not be used to assign a minimum number of observations to use (Haines et al. 2009). This relationship suggested that a minimum of 10 resights included under-sampled birds, resulting in inaccurate home range estimation. The minimum number of resights for which this relationship no longer existed was 13 (linear: t = 1.0, P = 0.31, logarithmic: t = 1.4, P = 0.18). This indicated that the addition of more observations beyond 13 did not significantly influence the size of estimated home ranges. Thus, we selected 13 observations as the minimum cutoff for analysis of home range area. No effect of the number of resights per individual per year was found for parrotbill home ranges estimated using KDE or ʻalauahio home ranges using either method. However, for consistency, all home ranges included in these analyses for either species were of individuals resighted a minimum of 13 times per year.

Some individuals were resighted more than once in a given day and these were only included if the bird was resighted ≥15 min after and/or was seen ≥50 m between consecutive points. To reduce the influence of single days on the size of home ranges, we also restricted our analyses to individuals resighted on a minimum of 3 d. In rare cases (N = 10 of 162), a single outlying resight point was excluded from construction of ʻalauahio home ranges because these points were clearly the result of a GPS error or a band misidentification resulting in a point distantly disjunct (i.e., >1 km) from the main cluster of resight points for an individual (e.g., outside the study site). No parrotbills that met the minimum resight number were excluded from analyses.

We estimated MCP and KDE home ranges of both species in Geospatial Modeling Environment version 0.7.2.0 (Beyer 2012) using the “genmcp” and “kde” tools (Supplemental Table S1). We used smoothed cross validation to estimate bandwidth and a raster cell size of 10 (Beyer 2012). We estimated 100% MCP home ranges rather than eliminating a certain

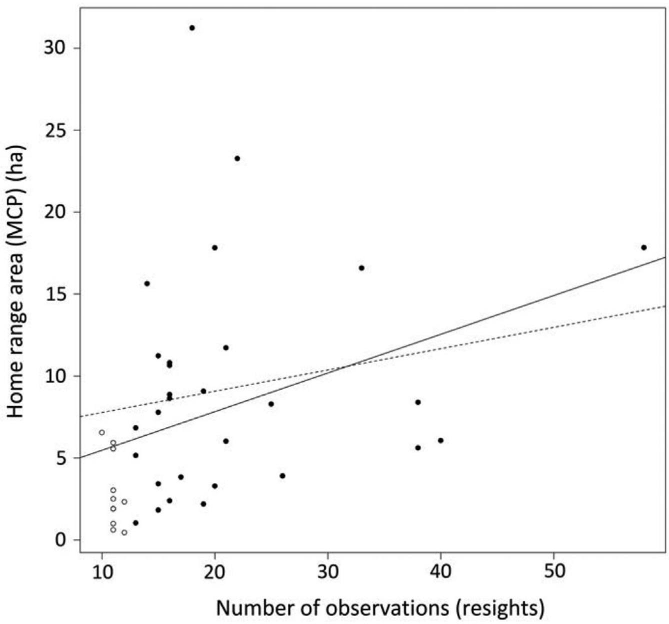

Fig. 2. The number of observations (resights) versus the area (ha) of estimated home ranges (minimum convex polygons [MCPs]) for Maui Parrotbills. Open circles represent estimated size of home ranges of parrotbills. Filled circles indicate the home range sizes estimated from ≥13 observations that were included in analyses. Trend lines indicate the linear relationship between observation number and home range area for all individuals (solid) ($t = 2.4$, $P = 0.02$) and only those above the cutoff (dashed) ($t = 1.0$, $P = 0.31$).

proportion of outer points because we were interested in an estimate of the entire area that an individual used during the study period. We delineated 50%, 75%, and 90% KDE isopleths (contour intervals) for each individual. The isopleths contained a percentage of the volume of the contour raster created by the KDE.

Pair home ranges. Because parrotbills are known to be socially monogamous (Simon et al. 1997), an estimate of the area used by a mated pair may be more appropriate than individual home range size for conservation planning. This follows the assumption that a mated pair would occupy a smaller amount of habitat than the sum of two unrelated individuals. We compared home ranges between paired individuals and estimated a combined home range for each known pair for each year. Pairing status and identity was recorded for all banded parrotbills at each study site each year. We compared home range sizes and overlap between known paired individuals where both individuals were resighted ≥13 times within a year. This analysis was not conducted for ʻalauahio because pairing status was not recorded for this species.

To estimate the size of pair home ranges, we clipped ("Clip" tool in ArcMap 10.0 [ESRI 2011]) the MCP and 70% KDE home range polygon of each individual of a pair by their respective mate's home range polygons. We then added the shared (overlapped), male- and female-only areas of each pair to estimate a collective pair home range. From this result, we calculated the area and proportion of overlap among pairs' home ranges. We then compared the sizes of the pair home ranges to the home ranges of the same paired individuals independent of their mates. Estimating home range size for pairs provided a way to adjust mean home range size for all individuals as if we had been able to measure home range for all mated pairs. Although pairing status was not always established for all individuals within a site each year, few unpaired adult parrotbills were observed during spot mapping surveys (MFBRP, unpubl. data). All parrotbills for which home range size was estimated in our study were known to be paired with either a banded or unbanded bird. This justified adjusting individual home range sizes to pair home ranges.

Statistical analysis. To test for variation in home range size between study sites, we performed separate repeated measures analyses of variance (ANOVA) for each species. We did this using linear mixed effects modeling blocking for individual bird ID using the "lme" function in the "nlme" package (Pinherio et al. 2013) followed by Type III ANOVA using the "car" package (Fox and Weisberg 2011) in R 3.0.1 (R Core Team 2013). For analysis of parrotbill home ranges, we included site and sex as fixed factors. Determining sex of ʻalauahio is not possible in the field unless birds are in breeding condition. As a result, only a subset of individual ʻalauahio were of known sex, and sex was not included as a factor in our analyses. Only site was included as a fixed factor in the ʻalauahio models. We used a two-tailed *t*-test to compare the percent home range overlap between parrotbill mates. Values are presented as means ± SE, unless otherwise noted.

RESULTS

Of 223 parrotbills and 1287 ʻalauahio banded from 1992 to 2014, 93 (51.5%) and 730 (56.7%), respectively, were resighted between 2007 and 2014. After excluding individuals with <13 observation points/year and <3 observation dates, we analyzed the home range sizes of 25 parrotbills (14 males and 11 females) and 100 ʻalauahio (sexes undetermined). We estimated home range sizes for an average of 4.1 ± 2.4 (SD; range = 0 [2010] to 9 [2011]) parrotbills and 16.3 ± 14.7 (range = 5 [2012] to 48 [2014]) ʻalauahio per year. We estimated home range sizes of 15 parrotbills from Hanawi and 10 from Waikamoi. We estimated home range sizes of 54, 38, and 38 ʻalauahio from Hanawi, Waikamoi, and Kula, respectively. Minimum known age of individuals included in analyses ranged from 2 to 10 yr old for parrotbills and 1 to 10 yr old for ʻalauahio. Seven parrotbill pairs were available for analysis of pair home ranges.

Of the 25 parrotbills analyzed, we repeatedly measured (i.e., more than 1 yr) home range sizes in a subset of three individuals (12%) and one of these individuals was measured in three separate years. Repeatedly measured ʻalauahio accounted for 21% of individuals ($N = 21$), and 7% of individuals ($N = 7$) were measured more than 2 yr. We estimated a home range size for a single individual ʻalauahio at Hanawi in five separate years (2007–2011).

Maui Parrotbill home range size and overlap. Mean MCP home range size for parrotbills was 9.29 ± 1.29 ha (range = 1.04–31.23 ha, median = 8.28 ha) across all years and study sites (Fig. 3A). Mean KDE home range of parrotbills was 5.28 ± 0.89 ha (median = 3.45 ha) among 50% isopleths and 18.71 ± 2.81 ha (median = 13.01 ha) among 90% isopleths. Of the 70% isopleths, mean home range size was 9.63 ± 1.51 ha (median = 6.13 ha). This contour level captured the most resight points while also minimizing the amount of "extrapolated" area beyond the cluster of observation points. Outlier home ranges (>2 × SD) using all methods were rare (3–7% of home ranges). Parrotbill home ranges were larger at Waikamoi (Fig. 3A), but did not vary by sex among MCPs and all KDE contour levels (Table 1).

Parrotbill pairs shared home ranges an average of 77.6 ± 9.4% (MCP) or 64.5± 7.1% (KDE) with their mate's home range. Males and females overlapped their mate's home ranges to the same degree (MCP: $t = 0.2$, $P = 0.83$; KDE: $t = 0.8$, $P = 0.44$). The mean home range size of pairs was 13.9 ± 10.5 ha (MCP) and 17.8 ± 12.3 ha (KDE, Fig. 3A). The mean area of the additive pair home range was between 26.7% (MCP) and 50.8% (KDE) larger than the mean home range size of the individuals included in the pair analysis. The adjusted pair home range size of parrotbill pairs using data from all individuals was 11.8 ha (MCP) and 14.5 ha (KDE).

Home range size of Maui ʻAlauahio. Mean home range size of ʻalauahio was 0.86 ± 0.09 ha (range = 0.05–9.08 ha) based on the MCP method across all years and study sites (Fig. 3B). Mean KDE home range of ʻalauahio was 0.48 ± 0.04 ha among 50% isopleths and 1.70 ± 0.16 ha among 90% isopleths. Among 70% isopleths (the contour producing home ranges most similar in size to MCP), mean home range size was 0.87 ± 0.08 ha (range = 0.07 to 5.78 ha; Fig. 3B). As for parrotbills, outlier home ranges were rare (4%). Home range sizes of ʻalauahio varied among study sites based on the MCP method and all KDE contour levels (Table 1). Using the MCP method, ʻalauahio home ranges were significantly larger at Hanawi

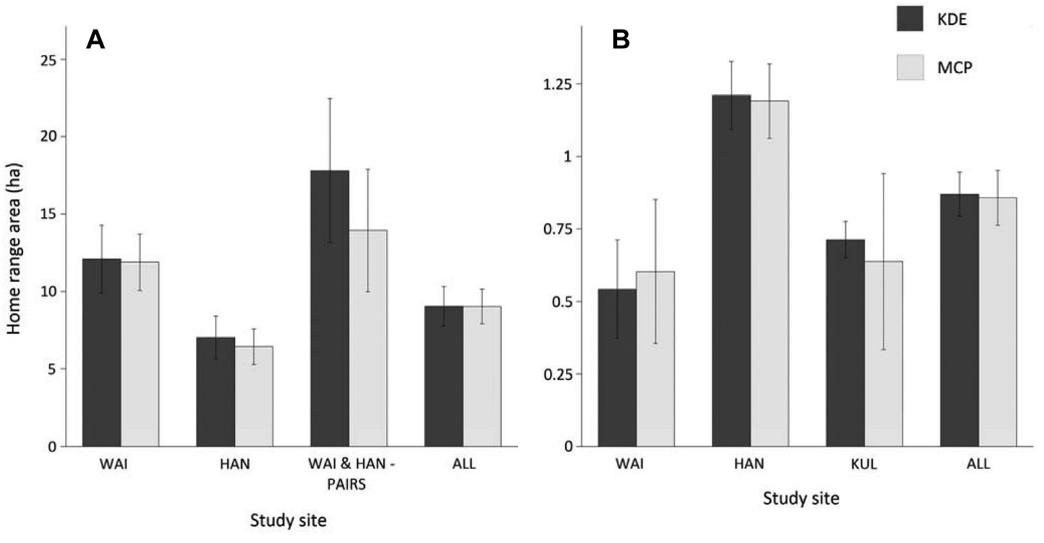

Fig. 3. Mean 70% kernel density estimator (KDE) and minimum convex polygon (MCP) home range areas (ha) at each study site. (A) Mean home range size of Maui Parrotbills at TNC Waikamoi Preserve (WAI, $N = 10$), Hanawi Natural Area Reserve (HAN, $N = 15$), pairs at both sites (PAIRS, $N = 7$), and all individuals estimated (ALL, $N = 25$). (B) Mean Maui ʻAlauahio home range size at WAI ($N = 31$), HAN ($N = 40$), Kula Forest Reserve (KUL, $N = 29$), and all sites ($N = 100$). Axes differ between panels.

Table 1. Analysis of variance type III results for Maui Parrotbill and Maui ʻAlauahio. Fixed factors included were site for ʻalauahio and site and sex for parrotbill. Results are given for kernel density estimator (KDE) and minimum convex polygon (MCP) home ranges.

	Maui Parrotbill									Maui ʻAlauahio		
	Site			Sex			Site × Sex			Site		
	F	*P*	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*	df
50% KDE	3.8	0.052	1,1	0.01	0.93	1,1	1.2	0.28	1,1	17.9	<0.001	1,2
70% KDE	4.3	0.039	1,1	0.01	0.97	1,1	1.3	0.26	1,1	16.2	<0.001	1,2
90% KDE	4.5	0.035	1,1	<0.01	0.98	1,1	1.2	0.28	1,1	12.7	0.002	1,2
MCP	4.1	0.044	1,1	0.01	0.92	1,1	0.6	0.45	1,1	9.3	0.009	1,2

than at the other two sites (Waikamoi: $t = -2.6$, $P = 0.01$; Kula: $t = -2.5$, $P < 0.014$; Fig. 3B). Home ranges sizes at Waikamoi and Kula did not differ ($t = -0.1$, $P = 0.89$).

DISCUSSION

The Kahikinui region of Maui has been identified as an area in need of conservation and restoration for both watershed health and the preservation of threatened and endangered species for decades (Scott et al. 1986, Division of Forestry and Wildlife 2010). Preparation for the planned reintroduction of parrotbills to the area has provided the impetus for significant restoration efforts in Nakula NAR. Concurrently, large sections of contiguous areas in Hawaiian Home Lands and Kahikinui FR that border Nakula have been fenced (or soon will be) and restoration actions are underway. Together, these areas contain most of the remaining forest on leeward Haleakalā, providing a large area for translocated or dispersing Hawaiian Honeycreepers to occupy. Although much remains unknown about how these species will behave in these new habitats, our estimates of home range size provide conservation managers with important metrics to be used in combination with other demographic and genetic data in designing the reintroduction plan. The space use patterns presented here were designed to help managers predict the amount of area translocated individuals will require and may help them determine the number of individuals to release.

Parrotbill home ranges were larger at Waikamoi (11.8 ± 1.82 ha [MCP]) than at Hanawi (6.4 ± 1.16 [MCP]); up to 45% larger on average based on MCP. Although both sites were dominated by the same native tree species, the structure and composition of the plant community differed between the two sites and Hanawi receives significantly more annual rainfall than Waikamoi (Giambelluca et al. 2013). Thus, differences in home range size between sites suggest that variation in parrotbill space use may be influenced by habitat variation. The forest understory, where parrotbills and ʻalauahio frequently forage, is very dense and diverse at Hanawi as a result of ungulate removal efforts in the 1980s and 1990s. Ungulates were removed from upper Waikamoi later than from Hanawi and the forest is still recovering in many areas. As a result, the food resources may be more widely distributed at Waikamoi, e.g., lower density of understory food plants, and individuals may be forced to forage over a larger area. It is also possible that parrotbill food resources at Waikamoi have recovered to pre-human-contact levels and the resulting home range sizes reflect optimal resource availability in this forest type. If so, parrotbill home ranges may be naturally larger in drier forests. Given that Nakula is drier and more open than Waikamoi and/or Hanawi, parrotbill home ranges at Nakula could be even larger than the estimates presented here.

The relative abundance of ʻalauahio within much of their range masks the threats that the species faces. As with parrotbills, limited behavioral and demographic information is available for ʻalauahio and their overall distribution beyond the range described here remains in question. Our estimate of the home range size of ʻalauahio was ~0.85 ha, similar to the 1–2 ha reported by Baker and Baker (2000). However, whereas these authors reported smaller home ranges in wet native forest, we found the opposite, i.e., home ranges were largest at our wettest native forest site. Rainfall amounts generally decrease from east to west in the area encompassing these three study sites (Giambelluca et al. 2013). Home ranges were larger at Hanawi than at Waikamoi, although both are dominated by native forest, whereas home ranges at the non-native-dominated Kula site were similar in size to those at Waikamoi. Therefore, heterogeneity in the size of the home ranges of ʻalauahio may be influenced more by variation in climate than by any apparent habitat gradient. Waikamoi and Kula may provide more favorable conditions, allowing individuals to maintain smaller home ranges.

The habitat on leeward Haleakalā differs from the habitat that either species currently inhabits in a number of ways (e.g., koa- rather than ʻōhiʻa-dominant canopy), and no information is available about habitat use by these species outside their current ranges. If managers are to use our estimates of home range size as a baseline to predict potential abundance in conservation areas at Kahikinui, a number of important factors that can influence home range size must be taken into account. Primary among these is the impact of habitat variation. We tested this indirectly by sampling both species at multiple study sites throughout their ranges. Although we found some variation, the habitat that both species currently occupy on the windward slopes of Haleakalā is largely homogenous. Variation in the occupied windward habitats is dwarfed by the differences between the windward and leeward slopes. Even after complete restoration, the habitat at Nakula will likely remain different. Estimating home range sizes at more locations throughout the species' ranges may allow researchers to better evaluate variation in space use as a function of habitat variation. However, measuring home range sizes is time intensive and without knowledge of how these species behaved in the full range of conditions, they were exposed to historically, predicting how they may respond to habitat cues at Nakula would still be difficult.

Another important variable potentially affecting the density and abundance of these species at Nakula that was not examined in our study is home-range overlap. Home ranges of both species clearly overlap, but to an unknown degree. To estimate total home range overlap, and therefore the amount of unshared area required by an individual, a minimum number of resights (e.g., 13) of all individuals at a given site would be needed. This was not possible for these often cryptic species in our study. We found parrotbill home ranges overlapped that of a single neighbor by an average of 24.2 ± 13.0% in a subset of 11 parrotbill individuals included in this study. However, these data do not indicate the total amount of home range overlap when all neighbors are taken into account. In addition, because pair information was not collected for ʻalauahio, home range overlap was not estimated. Because an increase in home range overlap would result in increased density, any prediction about abundance in an area without considering such overlap would be conservative.

Home range sizes in the leeward habitat will undoubtedly be driven in part by food availability (Schoener 1971). Both parrotbills and ʻalauahio are primarily insectivorous, gleaning or extracting insects from tree and shrub branches (Simon et al. 1997, Baker and Baker 2000). Although arthropod density and diversity per stem at Nakula is similar to or greater than at Hanawi and Waikamoi, stem density is lower at Nakula, thereby reducing food availability (Peck et al. 2015). Additionally, historic observations of the parrotbill's preference for koa as a foraging substrate (Henshaw 1902, Perkins 1903) suggest a possible qualitative benefit to a habitat dominated by koa. Home range sizes at Nakula may be similar to that in the current range, particularly if qualitative differences in food resources ("preferred" habitat) compensate for the reduction in quantity of resources (stem density).

Although the habitat across the Kahikinui region varies in quality and is in various stages of restoration, this region has perhaps the greatest potential for increasing the range and population size of many of the rarest species on Maui (U.S. Fish and Wildlife Service 2006). Based on the sizes of restoration areas, the size of the parrotbill range may increase by >30% if the leeward areas are fully occupied. Of most concern to the preservation of all native passerines on Maui, global climate change is predicted to allow disease-carrying mosquitos to breed at higher elevations, thereby reducing the current ranges of these species (Benning et al. 2002). To mitigate loss of habitat due to a rising "mosquito line," more habitat must be restored at higher elevations outside the current ranges of these species. If enough habitat is restored at high elevations around Haleakalā Volcano, theoretically, parrotbills may be able to maintain a similar range and population size as exists today well into the future regardless of the climate-change-influenced habitat contractions. Establishing new populations of these species at Kahikinui is the first step toward protecting them. Given the time scale of habitat loss due to disease prevalence and the time it takes to fully restore forested habitats, attention should also be given to restoring additional available lands at high elevations beyond Kahikinui, particularly the western slopes of Haleakalā.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Table S1. Geospatial modelling code.