

LINKING AVIAN VOCAL BEHAVIORS AND RESOURCE SELECTION USING A NOVEL  
BROADCAST TRANSMITTER TECHNOLOGY

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## **Dedication**

I would like to dedicate this thesis to my grandmother, Lurette Bowen. She has always been the strongest advocate of furthering my education and one of my biggest supporters. I would not be where I am today without her love and encouragement.

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## Abstract

Most studies that explore the environmental factors that influence the distribution and abundance of species do not incorporate social behaviour into their habitat selection models. Resource selection by individuals is multifaceted and can reflect the intensity of space use in an ecosystem. For nine ‘ōma‘o (*Myadestes obscurus*), a species of thrush endemic to Hawai‘i island, I combined movement data, habitat structure features collected by an airborne light detection and ranging (lidar) system, and vocalisation data recorded with a novel broadcast transmitter to link where different types of vocalisations (*i.e.* song, call, whisper song) most frequently occur across the landscape with the underlying habitat features. At the population-level, I found the presence of song was highly variable across a landscape, while the likelihood of calls increased in the open lava matrix and whisper songs were associated with the dense interior areas of the kīpuka (*i.e.* forest fragments). In contrast, the rate of ‘ōma‘o vocalisations decreased in the open lava matrix, suggesting that ‘ōma‘o may be selecting the matrix for foraging rather than vocalising. For individuals, I found similar patterns for songs and whisper songs, but there was high intra-specific variation. The results revealed context-specific uses of vocalisations across birds’ home ranges as each vocalisation type is associated with different behaviours, including courtship, aggression, and social interactions between individuals. Moreover, the novel methodologies used to document the relationship between behaviour and resource selection can be applied to many taxa across different ecological landscapes.

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## INTRODUCTION

Studies that explore the environmental factors that influence the distribution and abundance of species usually provide information on the presence or absence of organisms, providing critical information on a species' range and conditions for suitable habitats (Brotons, Thuiller, Araujo, & Hirzel, 2004). However, these studies rarely incorporate social behaviour into their habitat selection models (Jones, 2001), nor do they explain the reasons an individual is using specific resources to maximize survival or reproductive success (Lima & Zollner, 1996). Deliberate selection of high-quality resources suggests that space use is non-random particularly when linked to the availability of food resources (Manly, McDonald, Thomas, McDonald, & Erickson, 2002). Furthermore, individuals may vary behaviours associated with resource selection patterns in response to both spatial and temporal variations in environmental factors that influence survival rates (Benson, Mahoney, & Patterson, 2015; Lewis et al., 2015), highlighting the importance of incorporating behavioural patterns into resource selection studies, which many studies currently lack. Most studies examining resource selectivity focus on foraging or breeding behaviours, but few have used vocal behaviour as a means of evaluating resource selection.

Oscine passerines, or song birds, constitute approximately half of all bird species and rely heavily on vocal communications to transmit information related to behaviours important for survival and reproduction success (Catchpole & Slater, 1995). Indian peafowls (*Pavo cristatus*) are a classic example of birds with elaborate and colorful courtship displays to relay information from one individual to another. However, visual signals can easily be obstructed (*e.g.* dense forests, tall grass) and birds could waste energy on displays that may never be seen by the target receiver (Catchpole & Slater, 1995). Conversely, acoustic signals are more effective at broadly

transmitting information because vocalisations can travel long distances and through a diverse array of environments. Therefore, acoustic signals and their underlying behavior can be used to link resource selection and habitat use with behaviors important to fitness parameters. For example, in willow flycatchers (*Empidonax traillii*), the frequency and distribution of vocalisation resource selection across the landscape was directly linked to underlying behaviours such as nesting, territory maintenance, positioning in habitat (*e.g.* perch height), and movement (Bakian, Sullivan, & Paxton, 2012). Moreover, males sang more frequently at the core of their home range, whereas females decreased vocalisations in these areas, further highlighting the benefits of using vocal behaviours as a link to understand how and why individuals select different areas within their home range. Bakian *et al.* (2012) showed that resource selection at the individual-level is a multifaceted, decision-making process that reflects the intensity of space use in an ecosystem.

In this study I developed behavioral landscape models to link space use of an endemic Hawaiian thrush, the 'ōma'ō (*Myadestes obscurus*), with vocal behaviors to further our understanding of why 'ōma'ō are selecting particular resources. Behavioural landscapes predict the occurrence of an animal's behaviour within a home range based on a given set of environmental variables and are therefore beneficial in examining the spatial distribution of behavior across the landscape (Bakian et al., 2012). 'Ōma'ō have three distinct vocalisation types (calls, songs, whisper songs) that are each associated with different behaviours, including courtship, aggression, and social interactions between individuals. The production of vocal signals has been shown to be impacted by habitat characteristics (Bakian et al., 2012; Boncoraglio & Saino, 2007) and I evaluated the impact of habitat type, vegetation density, canopy height, and the distance from a bird's core zone on the rate and type of vocalisations

produced by ‘ōma‘o. To examine the relationship between vocalizations and habitat features across the landscape I implemented one of the first field trials of a novel song broadcast transmitter (Thiebault, Charrier, Pistorius, & Aubin, 2019) to record acoustic signals of individual ‘ōma‘o in the wild. Hawaiian habitats are challenging to transverse and contain high densities of target birds. The use of broadcast transmitters mitigates these challenges by transmitting the vocalizations of only the target bird to distances over 100 m from the bird, enabling the recording of all vocalizations, including low-amplitude whisper songs.

Since different vocalisations imply different underlying behaviours, I investigated if the rate and the types of vocalisations were associated with particular landscape features. I had two main hypotheses regarding changes in vocalisation rate and type based on habitat structure parameters in a naturally fragmented landscape. First, I hypothesised a decrease in ‘ōma‘o’s vocalisation rate as they increased the distance from their core zone (*i.e.* area where bird spends over 50% of its time) to avoid detection while entering other conspecific’s territories (Morton, 2000), or to reduce predation risk from the ‘Io (Hawaiian Hawk; *Buteo solitarius*). Secondly, I hypothesized that the distribution of vocalisation types across the landscape would vary based on habitat parameters such as habitat type, vegetation density, and canopy height. I predicted that songs and whisper songs would be associated with forested areas given that both vocalisation types are often linked to courtship or territory defense, both of which are more likely to occur in a bird’s core area in the forest fragments (Catchpole & Slater, 1995; Reichard & Welklin, 2015). Conversely, I predicted calls and absence of vocalisations (*i.e.* silence) would be associated with the barren areas because they are abundant with fruiting vegetation and may only be vocalising as a way to maintain contact between individuals within the forest fragments while foraging (a behavioural trade-off to vocalising). Finally, I predicted that vegetation density and canopy

height would have an effect on where ‘ōma‘ō select to vocalise as forest structure has been documented to impact acoustic signaling in the tropics (Boncoraglio & Saino, 2007; Nicholls & Goldizen, 2006). The combination of behavioural landscapes and the data collected by the novel broadcast transmitters offer an innovative approach to evaluating resource selection by linking behaviour with underlying landscape features.

## METHODS

### *Study Site and Species*

I conducted the study on the eastern slopes of Mauna Loa Volcano on Hawai'i Island in the Upper Waiākea Forest Reserve within four naturally fragmented forest patches, termed kīpuka in Hawaiian (Fig. 1). This area experienced two lava flows in the mid- and late-1800s creating a large network of kīpuka that vary in size and isolation. The kīpuka substrate is approximately 3000-5000 years old and the forest is comprised primarily of 'ōhi'a trees (*Metrosideros polymorpha*), sparsely distributed *Acacia koa*, and a native-dominated understory (Flaspohler et al., 2010). The barren lava, hereafter referred to as the matrix, surrounding the kīpuka consists of sparse small 'ōhi'a trees (< 3m), dry grasses, and low-lying fruiting shrubs (e.g. 'ōhelo, *Vaccinium calycinum*) and vines (e.g. kūkaenēnē, *Coprosma ernodeoides*). The kīpuka system is a healthy native forest with a primarily native bird community. The endemic thrush species, 'ōma'ō is an ideal study species because of their larger size in comparison to native honeycreepers (~50g; Wakelee & Fancy, 1999), high densities in the kīpuka (Kovach, 2012) and sedentary tendencies compared to other endemic bird species (e.g. 'i'iwi, *Drepanis coccinea*). In addition, the complex and varied types of vocalisations utilised by 'ōma'ō (Fernandez, 2018) allows for the examination of how vocal behaviours vary across the landscape.

As the last functionally extant native frugivore with population estimates appearing to remain stable at around 170,000 individuals (Scott, Mountainspring, Ramsey, & Kepler, 1986), 'ōma'ō serve as a critical seed disperser for native flora (Wu, Delparte, & Hart, 2014). 'Ōma'ō's frugivorous behaviour allows them to have long potential breeding periods, depending on when fruiting vegetation is available. Previous studies have indicated that 'ōma'ō sing year-round with

the highest rates occurring during the winter months (January through May) (Wakelee, 1996). ‘Ōma‘o have three main vocalisation types: calls, songs, and whisper songs (Fig. 2). Calls and songs are considered high-amplitude signals both of which are audible at over 150m in the forest. Calls were defined as short, repetitious, single syllable vocalisations, which vary in length from 0.5 to 1.5 seconds (Fernandez, 2018), and they are typically observed with behaviours such as contact between conspecifics, predator alarms, and aggression (Wakelee & Fancy, 1999). Songs are typically complex (*i.e.* composed of multiple syllables), between 0-9 kHz, and 0.5- 5 seconds long (Fernandez, 2018). The function of song is potentially vast and can be used for mate attraction, courtship, territory establishment, and an indicator of an individual’s age and fitness (Catchpole, 1980; Derryberry, 2011; Wakelee & Fancy, 1999). Whisper songs are a low-amplitude signal that are typically less than 4Hz and require close proximity to transmit between the sender and receiver (Reichard & Welklin, 2015) which makes them difficult to detect by a person beyond 10 m from the singing target bird. While the function of whisper songs is still unknown in ‘ōma‘o, it has been documented in other species in varying social contexts including interactions between bonded pairs, aggressive behaviours, and group movement (Reichard & Welklin, 2015). The difficulty of acquiring high quality recordings of whisper songs has been the main limitation in furthering this area of research (Reichard & Anderson, 2015). However, I was able to overcome the challenges of recording whisper songs by using a novel broadcast transmitter (see field methodology section below for more details).

### *Field Methodology*

To examine movement and vocalisations of ‘ōma‘o I equipped nine individual male ‘ōma‘o with two transmitters, a very high frequency (VHF) pulse transmitter and a transmitter

that contained a miniature condenser microphone that broadcasts all sounds emitted by a bird (JDJC Corporation, Fisher, IL, USA) (Fig. 3). Birds were captured via passive mist-netting between January, 2018, and January, 2019, in two large (>10 ha) and two small (~3 ha) kīpuka, as part of a larger study that banded approximately eight days per month in the study area. All individuals were fitted with USGS aluminum bands and a unique color combination for re-sighting purposes. Adult male ‘ōma‘o were identified according to the aging and sexing guide for Hawaiian forest birds (Paxton, McLaughlin, Levins, VanderWerf & Lancaster, 2016). I attached the transmitters to the birds using a backpack harness (Rappole & Tipton, 1991), consisting of a modified leg-loop harness with a degradable rubber band ensuring the transmitter would fall off the bird within six months to a year. The VHF transmitter had a mean weight of 0.45 g with a ~28-day life span and the broadcast transmitter had a mean weight of 1.5 g and ~21-day life span. In total, the harnesses with the transmitters represented only approximately 3% of average total body mass of ‘ōma‘o to ensure there were no impediments on an individual’s flight or behaviour.

I collected high-resolution movement data using five automated radio tracking stations (ARTS; 20 m height) dispersed across a 7-km area that surrounded the four kīpuka and supplemented with hand tracking (Fig. 1). Each ARTS consisted of 6 yagi antenna oriented 60 degrees apart for 360° detection coverage. The ARTS were connected to an autonomous radio-telemetry receiving unit (JDJC Corporation, Fisher, IL, USA) that scanned each programmed transmitter frequency every two minutes and recorded signal strength (in dB), electromagnetic noise (dB), pulse width (how long a transmitter emits a beep in milliseconds; ms), and pulse interval (pulses per minute in ms) of each programmed transmitter (Celis-Murillo, Schelsky, Benson, Louder, & Ward, 2017; Zenzal, Moore, Diehl, Ward, & Deppe, 2018).

I recorded broadcasted vocalisations of individual ‘ōma‘o three to five days a week, weather permitting, for a two to four-hour time period between 0800 – 1600, the peak hours of ‘ōma‘o vocalisations. Additionally, because weather can affect bird behaviour, we did not record on rainy days (Jorde, Krapu, Crawford, & Hay, 1984). The broadcast transmitters can transmit sound between 100-200 m away, but the highest quality recordings, which reduce the noise to signal ratio, occur when the bird is at a distance of no more than 60 m to 80 m. All acoustic data from the broadcast transmitters were received by a 3-element yagi antenna (JDJC Corporation, Fisher, IL, USA) connected to a wide band receiver (AR8200; AOR Ltd., Tokyo, Japan) in wide band amplitude modulation (WAM) mode. The wide band receiver was connected to a Marantz PMD661 professional field recorder (Marantz America, LLC., Mahwah, NJ, USA) with a 2-second pre-record setting allowing the full vocalisations of the bird to be captured. The person recording could hear all vocalisations broadcasted by the transmitter through headphones connected to the Marantz recorder. Recordings were started as soon as a vocalisation was heard in the headphone and continued for at least two minutes after the last vocalisation. All sound files were recorded in 24-bit WAV format at 44.1 kHz sampling rate. The broadcast transmitters ensured that only the targeted individual’s vocalisations and movement sounds were recorded, omitting other species’ vocalisations and background noise. In addition, detailed notes were documented on the bird’s behaviour based on vocalisations and activity detected by sounds (*e.g.* foraging, flying, perching, counter-vocalising, silence) to maintain a continuous log of behaviour throughout the recording time period.

### *Data Processing*

To process and filter the movement data collected by the ARTS and determine the

location of individual birds I used custom R scripts. A bearing to the bird from the ARTS was calculated for data points that met the following conditions: 1) signal strength of the two strongest antennae were over -130 dB; 2) noise level of the two strongest antennae were under -130 dB; 3) two strongest signals were from adjacent antennae; 4) pulse width was  $\pm 3$  ms of the VHF transmitter's width as provided by the manufacturer; 5) pulse interval was within 50 ms of the VHF transmitter's interval or a multiple thereof (Zenzal et al., 2018). I then used LOAS (Ecological Software Solutions LLC) to calculate bi- and tri-angulations from data points with bearings calculated from multiple ARTS during the same 2-minute time interval.

The digital sound files were processed using Raven Pro 1.5 software (Bioacoustics Research Program 2014) in the form of spectrograms. All recordings were measured using a Hann window type with a DFT size of 750 samples and 50% time overlap. For each telemetry point that occurred during a period of vocal recording, all vocalisations within a one-minute time period surrounding the location point time were selected (*e.g.* if a telemetry point was at 0930, vocalisations 30 seconds before and 30 seconds after the start of that time were chosen). Telemetry points utilised were randomly distributed across the time period of observation to ensure independence (Table 1). For each selection, I identified the vocalisation type (*i.e.*, call, song, whisper song) and total length of the selection in seconds. Vocalisation types were first determined based on field observations and then verified in Raven Pro. Verification was determined based on visual and aural structure and that the signal met vocalisation type criteria set by Catchpole & Slater (1995) and Reichard & Welklin (2015). Silence was also a category when there were no vocalisations within the one-minute time period. For each one-minute time period, I calculated the vocalisation rate by calculating the total time of all vocalisations divided

by 60 seconds. For instances where more than one vocalisation type was selected within the one-minute period, the category with the largest summed vocalization time was assigned.

### *Habitat Classification*

To classify the habitat type (*i.e.*, kīpuka, matrix) associated with each telemetry point that occurred during a period of vocal recording I projected the bird locations in ArcMap 10.4 (ArcInfo, ESRI®) and overlaid polygons of each kīpuka. I also included a 27m buffer around the kīpuka edge to account for the average telemetry error (see core zone calculation section for telemetry error details). Each point's classification of habitat type based on the projected points was then verified using field notes. Points within the 27 m buffer were classified based on field notes. Any points that were found to not match the field notes and did not accurately represent the bird's location were removed.

### *Core Zone Calculations*

Core zones for individual 'ōma'ō were calculated from all locations determined by triangulation using the R package continuous time movement modelling (ctmm; Calabrese, Fleming, & Gurarie, 2016). The ctmm package integrates a broad range of continuous-time stochastic process (CTSP) models in conjunction with statistical methods to account for autocorrelated data associated with telemetry points (Calabrese et al., 2016). Autocorrelated kernel density estimations (akde) fit with Ornstein-Uhlenbeck Foraging (OUF) models were used to determine the home range and core zone for a given bird based on the triangulations. OUF models recognise that the data have both position and velocity autocorrelation along with range residency (*e.g.*, tendency to remain in a defined area; Calabrese, Fleming, & Gurarie, 2016). The

most suitable model for each 'oma' was selected based on Akaike information criterion (AIC) model selection using information from variograms and periodograms of the telemetry data.

I also incorporated telemetry error into the akde model based on the x and y variances for each point produced when calculating triangulations in LOAS. The akde function produces both a 50% and 95% kernel (Fig. 4) The 95% kernel comprises the total home range and the 50% represents the core zone. Using the R packages geosphere (Hijmans, 2019) and McSpatial (McMillen, 2013), the centroid of each 'oma's core zone was determined and then distances between the centroid and all other telemetry points were calculated.

### *Airborne Lidar*

The airborne light detection and ranging (lidar) data were collected on January 16, 2016 by the Global Airborne Observatory (GAO; formerly the Carnegie Airborne Observatory; Asner et al. 2012). The aircraft was flown at 2000 m above ground level at a speed averaging 80 m/s. Laser settings include 34hz scan frequency, 34 degree total field of view, and 30% overlap between adjacent flightlines. This combination of flight and instrument parameters yielded a laser spot density minimum of 2 points per square meter. The lidar was operated in discrete return mode, registering up to four returns per outbound laser pulse.

The metrics extracted from the lidar data were mean tree canopy height (TCH; in meters, Fig. 5), standard deviation of TCH (m), and density of vegetation between 6 and 10 m within a 20m radius of each location point to account for error in telemetry locations. Mean TCH was calculated by determining the difference between the digital elevation model (DEM) and digital surface model (DSM), calculated using the method outlined in Asner et al. (2012). The standard deviation of TCH was chosen to show the variability in canopy height surrounding telemetry

points. Lastly, vegetation density was defined as the proportional number of laser returns that interacted with vegetation (between 6 m and 10 m above ground), measure for each pixel in a 5m x 5m grid.

### *Statistical Analyses*

All statistics were calculated using R (R version 3.6.1). To examine the relationship between the rate of vocalisations and landscape features, I performed a generalised linear mixed-effects model with a gamma distribution and log link. The model evaluated the influence of distance from core zone (in meters), habitat type (kīpuka, matrix), mean TCH, standard deviation of TCH, and vegetation density on total time ‘ōma‘o spend vocalizing (in seconds). To account for multiple observations from the same individual, the unique band number of each individual was incorporated as a random effect in the model. All explanatory variables were scaled and centered to improve model performance.

I used a Bayesian framework to examine the probability of occurrence for vocalisation types based on habitat features at the population-level by combining the data for all individuals sampled. A Bayesian approach provides a coherent framework for dealing with complexity in the models (Hooten & Hobbs, 2015). Specifically, I used a resource selection function (RSF) model estimated with a logistic regression to predict the occurrence of each vocalisation type with habitat features across the landscape (Muff, Signer, & Fieberg, 2019). Resource selection models sample randomly or systematically from within an animal’s home range by pooling a single set of available locations for each individual (Manly et al., 2002). A separate RSF model was run for each vocalisation type (songs, calls, whisper songs, silence) resulting in a total of four population-level models. In each model, the presence or absence of a vocal behavior was

included as the response variable, while explanatory variables were the same set of habitat features described in the first analysis. I included an individual-specific random intercept in each model to account for repeated observations of the same individual (e.g. non-independent data) and differences in sample size among individuals (Gillies et al., 2006, Muff et al. 2019). In addition, I included individual-specific random slopes for each habitat feature (habitat type, mean TCH, SD TCH, vegetation density) to control for individual-specific differences in selection of habitat features (Gillies et al., 2006, Muff et al. 2019). As recommended by Muff et al. (2019), observations without the presence of a vocal behavior were given a weight ( $W$ ) (i.e.  $W=1000$ ) while the presence of a vocal behavior was not weighted (i.e.  $W=1$ ). Models were generated using a Bayesian approach via R-INLA (Manly et al., 2002) which utilizes integrated nested Laplace approximations (INLA) to approximate posterior marginal distributions. INLA is a popular and efficient alternative to Metropolis-Hastings Markov chain Monte Carlo (MCMC) (Rue & Martino, 2009).

For individual-level models I also used a Bayesian framework to examine the spatial distribution of specific vocal behaviors within an individual 'ōma'ō's home range and the association of vocal behaviors with landscape features. The base of the model was a logistic regression. However, for the individual-level models I added a spatial effect to the model to account for spatial autocorrelation among observations of a given individual and to assess whether vocal behaviours were spatially segregated within an individual's home range. Bubble plots indicated that there was little to no spatial autocorrelation in the data (Fig. 6).

For model specification I used the function 'spGLM' in the spBayes package (Finley, Banerjee, & Gelfand, 2015) to run generalized linear mixed models with a binomial distribution

and spatial effects (Banerjee et al. 2015). Posterior distributions of the model were generated from a MCMC algorithm. A general equation of the model is:

$$h(\mathbf{Y}(\mathbf{s})) = \mathbf{X}(\mathbf{s})\boldsymbol{\beta} + \mathbf{W}(\mathbf{s}), \quad (1)$$

where  $\mathbf{Y}$  is a vector of observations at a spatially referenced (*e.g.*, longitude and latitude) set of locations  $\mathbf{s}$ ,  $\mathbf{X}$  is the matrix of explanatory variables at locations  $\mathbf{s}$ ,  $\boldsymbol{\beta}$  is a vector of fixed effect parameters, and  $\mathbf{W}$  is a random effect capturing spatial dependency. The link function,  $h()$ , used in our model was the logit link function.  $\mathbf{W}$  was modeled as a multivariate Gaussian distribution,  $\text{MN}V(0, (\sigma^2\mathbf{R}(\phi)))$ , where  $\mathbf{R}$  specifies the spatial covariance matrix used in the model (*i.e.* exponential covariance function),  $\phi$  is the spatial decay parameter (*i.e.*, distance at which points are effectively uncorrelated), and  $\sigma^2$  is the spatial effect variance or partial sill (*i.e.*, degree of variance when points are effectively uncorrelated).

Separate hierarchical models were fit to each vocal behavior (calls, songs, whisper songs, silent) for each individual resulting in four models per individual ( $n = 16$ ). In each model, the presence or absence of a vocal behavior at each location was included as the response variable, while explanatory variables were the same set that was described in the first analysis. The model also required the specification of starting values for parameters  $\boldsymbol{\beta}$ ,  $\sigma^2$ , and  $\phi$ , and prior distributions for parameters  $\sigma^2$  and  $\phi$ . The coefficients calculated from a non-spatial logistic regression model served as the starting values for  $\boldsymbol{\beta}$  parameters in the hierarchical spatial model. To determine the starting values of  $\sigma^2$  and  $\phi$  variograms were fit to the non-spatial logistic regression model using the function ‘variog’ (spBayes package; Finley, Banerjee, & Carlin, 2007), and then an exponential spatial model without a nugget was fit to the variogram using the function ‘variofit’ (spBayes package; Finley, Banerjee, & Carlin, 2007). A variogram displays the correlation in the deviations of the observations from the mean response as a function of

distance between locations (Banerjee et al. 2015), and a spatial model fit to the variogram provides an estimate of the spatial effect variance (asymptotic point on the vertical axis) and the spatial decay (asymptotic point on the horizontal axis; Fig. 7). As recommended by Banerjee et al. (2015) and Gelfand & Banerjee (2017), prior distributions for the spatial effect variance and spatial decay parameters were an inverse-Gamma distribution, specified as  $\sigma^2 \sim \text{IG}(2,1)$ , and a uniform distribution, specified as  $\phi \sim U(3/\text{maximum distance}, 3/1)$ , respectively. The maximum distance represents the maximum Euclidean distance between pair-wise comparisons of all locations (in meters). Parameter tuning values for the model were adjusted to maintain healthy acceptance rates between 23% and 50% (Gelman et al. 2004). I generated three independent chains for each model with 100,000 MCMC iterations discarding the initial 75,000 iterations as burn-in. Therefore, posterior distributions, parameter estimates and predictions are based on 25,000 iterations. Density estimates and trace plots of the chains were produced using the spBayes package as a wrapper for the R package coda (Finley, Banerjee, & Carlin, 2007). Gelman and Rubin's convergence diagnostics (function 'gelman.diag' in coda package; Plummer, Best, Cowles, & Vines, 2006) was used to assess convergence of the three chains.

## RESULTS

### *Telemetry*

From January 2018 through January 2019, nine male ‘ōma‘o were tagged with VHF transmitters and the ARTS stations collected a range of 189 to 8132 triangulations with an average of 3306 triangulations per bird between sunrise and sunset (Table 1). Home ranges, calculated from triangulations, for each individual encompassed different percentages of both habitat types. However, core zones were primarily contained within the kīpuka, with the exception of one individual (band number 253107718) who was frequently observed being chased out of the kīpuka and into the matrix by conspecifics. Because individuals spent the majority of their time in the forest, telemetry locations were biased towards the habitat type kīpuka with a sample size of 664 compared to 199 in the matrix. Home range sizes varied from 47 600 m<sup>2</sup> to 368 980 m<sup>2</sup> with an average size of 133 590 m<sup>2</sup>, while core zones ranged in size from 6 146 m<sup>2</sup> to 72 373 m<sup>2</sup> with an average size of 21 135 m<sup>2</sup> (Fig. 8a & b).

### *Vocalisation Rate*

The generalised linear mixed-effects model indicated that ‘ōma‘o decreased their rate of vocalisations in the matrix ( $t = -3.36$ ,  $p < 0.01$ ) compared to the kīpuka (Fig. 9). However, the rate of ‘ōma‘o vocalisations was not influenced by a bird’s distance from core zone ( $t = -1.29$ ,  $p = 0.2$ ) or the lidar habitat structure variables, mean TCH ( $t = -1.05$ ,  $p = 0.3$ ), SD TCH ( $t = 1.22$ ,  $p = 0.22$ ), and vegetation density ( $t = 0.58$ ,  $p = 0.55$ ). The results were based on vocalisation data that corresponded to telemetry points during periods of observation which ranged from 27 to 160 with an average of 87 data points per bird (Table 1). At the population level, 783 vocalisations points were observed with silence representing over half of the data (Fig. 10).

### *Population-level Model*

A population-level model examining the probability of occurrence of different vocalisation types found that various habitat features influenced vocalisation selection. The parameter estimates (Table 2) show that all habitat structure covariates in various combinations affect the presence or absence of vocalisation types. For example, there was high variability in where song occurs with a slight tendency towards the matrix ( $\beta = -1.838$ ; Fig. 11a). Similarly, habitat type ( $\beta = -0.929$ ) influenced the likelihood of calls with calls more likely to occur in the matrix (Fig. 11b). In contrast, whisper songs were more likely to occur in the kīpuka ( $\beta = 1.671$ ) where vegetation is denser ( $\beta = 0.369$ ) and there is less variability in tree height ( $\beta = -0.477$ ) (*i.e.* interior of the kīpuka) (Figure 11c). Whereas, silence was strongly influenced by an increased diversity of vegetation height ( $\beta = 1.089$ ) (*i.e.* small patches of habitat in the matrix or the boundary between kīpuka and matrix) in addition to a weak suggestion of less dense vegetation ( $\beta = -0.312$ ) like that found in the matrix ( $\beta = -0.366$ ; Fig. 11d).

### *Individual-level Behavioral Landscape*

To understand individual variability and the consistency of patterns found in the population-level model, I determined the probability of occurrence of each vocalisation type at the individual-level for four birds that had greater than 100 locations with observed vocalizations (Table 1).

Patterns similar to those of the population-level results were seen at the individual-level for songs and whisper songs. However, the large standard deviation for some average individual selection parameter estimates suggests intra-specific variation in the relationship between

vocalization types and habitat covariates (Table 2). Similar to the population model, covariate estimates indicated that only habitat type ( $\beta = -4.867$ ) influenced the likelihood of song with song more likely in the matrix, but there was high variability with error around the parameter estimate slightly crossing zero (Fig. 12a). Similarly, whisper songs were strongly influenced by the kīpuka habitat type ( $\beta = 9.1935$ ) with whisper songs more likely in the kīpuka as was seen at the population-level. However, at the individual-level there was more variability in the influence of other habitat covariates on the likelihood of where whisper songs occurred (Fig. 12b). At the individual-level there was a lot of variability in parameter estimates for calls and silence compared to the population model. Calls tended to be produced in the kīpuka ( $\beta = 3.30825$ ), but were highly variable and contradictory to the population-level results suggesting high intra-specific variation (Fig. 12c). Similar conflicting results were produced for silence which indicated that only the kīpuka ( $\beta = 7.868$ ) was influential (Fig. 12d). In addition, the variable “distance from core” was added to the individual-level model and proved influential for all vocalisation types. Song ( $\beta = -0.222$ ), whisper song ( $\beta = -0.068$ ), and silence ( $\beta = -0.193$ ) had a decreased probability of occurring with increasing distances from an individual’s core zone, while calls ( $\beta = 0.502$ ) had an increased probability of occurring with increased distance. Lastly, images of the behavioural landscape models that contain a spatial effect were produced for each individual (see example, Fig. 13) to visualize the results of one ‘ōma‘o to the models, which appear to be more consistent with the population-level but still showcase the amount of variability in vocalisation types across the landscape.

## DISCUSSION

I investigated resource selection through vocalisations to improve our understanding of how ‘ōma‘o are utilising areas in their environment. By linking spatial patterns to behaviour, I found that habitat structure features influence vocalisation resource selection of ‘ōma‘o at both the population and individual-level. In addition, behavioural patterns associated with different vocalisation types provided insights into “why” a bird is utilising particular areas within their overall range. For example, the amount of time ‘ōma‘o spent vocalising was dependent on habitat type with birds vocalizing less in areas farther from an individual’s core zone which are dense in low-lying fruiting vegetation but have high exposure to predators. The lack of vocalizations in these barren areas suggests utilization of areas away from a bird’s core zone are associated with behaviours such as predator avoidance and foraging. This study is one of few to use vocalisations to link resource selection with underlying behaviour based on habitat features. Furthermore, the novel broadcast transmitter technology used in this study permitted continuous recordings of all vocalisations of an individual, including high-quality recordings of ‘ōma‘o whisper (*i.e.* low-amplitude) songs, a vocalisation type that is fairly common in passerines, but much is still unknown.

Both the frequency of occurrence and type of acoustic behaviours used by ‘ōma‘o provide us with information to interpret and link behaviour with habitat and movement. Vocal communication among birds is strategic, including the decision to not vocalise (Catchpole & Slater, 1995). I found that habitat type influenced the vocalisation rate of ‘ōma‘o. Specifically, that birds vocalized less as they enter the matrix, an open area with low vegetation abundance and potential exposure to predators. Acoustic signaling can give away a bird’s location (Ward & Slater, 2005), so vocalizing less may potentially be a defence mechanism against attracting

predators such as ‘Io. Alternatively, as much of the vegetation in the lava matrix produces fruit eaten by ‘ōma‘o (*e.g.* ‘ōhelo and kūkaenēnē), the matrix may be preferentially selected for foraging rather than vocalising. Since birds cannot vocalise and forage simultaneously, there may be a trade-off between these behaviors, leading to a decreased vocalization rate in ‘ōma‘o. European robins (*Erithacus rubecula*) and willow warblers (*Phylloscopus trochilus*) also have been shown to exhibit a trade-off behaviour by decreasing the amount of time spent vocalising as foraging increases (Ward & Slater, 2005). Similarly, the probability of silence at the population-level was higher in the matrix, which supports the idea of a behavioural trade-off due to higher exposure to predators caused by decreased vegetation height and increased foraging opportunities.

By examining spatial patterns of ‘ōma‘o movement, I revealed probabilities of vocalisations across the landscape to identify behavioural resource selection within a bird’s home range. I found that the probability of song occurrence was highly variable within and among individuals. Contrary to our prediction that songs would occur more frequently in the forested kīpuka, I found a slight tendency towards song being produced more frequently in the matrix. The high variability in the probability of where songs occur indicates that either ‘ōma‘o songs are not tied to features in the landscape (*e.g.* tree height, vegetation density, habitat type) or are tied to features that were not measured in this study. The high variability in song occurrence across the landscape may be a function of the wide range of behaviours associated with song, especially territory defense and behaviours linked with reproduction (*e.g.* courtship, mate attraction and selection, mate recognition, etc.). The geography of song probability may also be affected by the presence of other birds and proximity to core zones of other birds. Similarly, the likelihood of calls increased in the matrix, but had far less variability than songs, suggesting calls

are more strongly linked with the matrix habitat. Calls are short vocalisations used in a variety of contexts from contact calls to individual identification (Fox, Roberts, & Bennamoun, 2008), and alarm signals (Templeton & Greene, 2007). For instance, monogamous passerines like zebra finches (*Taeniopygia guttata*) use contact calls to identify their mates and king penguins (*Aptemodytes patagonicus*) use contact calls to find their chicks in dense colonies (Kondo & Watanabe, 2009). Established adult ‘ōma‘o are sedentary and have high fidelity to their home ranges which primarily occurred in the forested kīpuka, so it is likely they are using calls as a way to maintain a connection with other conspecifics while in the matrix. In contrast to calls, whisper songs had a higher probability of occurring in the kīpuka, where tree canopy height is less variable and the vegetation is denser than in the matrix. The mean tree canopy height is more consistent at the center of the kīpuka where the majority of old growth ‘ōhi‘a and koa (*Acacia koa*) are found and understory vegetation is dense with species like ‘ōlapa (*Cheirodendron trigynum*), kāwa‘u (*Ilex anomala*), kōlea (*Myrsine lessertiana*), and hāpu‘u (*Cibotium glaucum*), suggesting that ‘ōma‘o prefer to whisper sing in the interior of the kīpuka. ‘Ōma‘o whisper songs are at a significantly lower frequency range than regular broadcast songs (Paxton unpublished data), and thus the signal transmission of whisper songs would be less degraded in densely vegetated areas than high frequency broadcast songs (Boncoraglio & Saino, 2007). Therefore, singing whisper songs in densely vegetated areas may be advantageous for ‘ōma‘o in maintaining signal integrity and preventing eavesdropping by non-target receivers (Boncoraglio & Saino, 2007; Vargas-Castro, Sandoval, & Searcy, 2017).

This study contributes information pertaining to the distribution of whisper songs across the landscape and overall emphasizes the benefits of broadcast transmitters to document low-amplitude songs. Whisper songs have been documented in birds, mammals, amphibians, insects

and fish, however, they are still understudied and their function is mostly unknown (Reichard & Anderson, 2015). In song sparrows, whisper or soft song is typically a predictor of aggressive behaviour or escalating aggression (Searcy, Anderson, & Nowicki, 2006), but other theories of function exist, such as avoiding detection, receiver retaliation, and signal honesty (Akçay, Anderson, Nowicki, Beecher, & Searcy, 2015). Because low-amplitude songs occur in such a variety of social settings, little is still known about the evolution, fitness benefits, and environmental settings in which they occur. The novel broadcast transmitter used in this study was central to recording whisper songs across the landscape and through time, but because visual observation was not necessary to collect data, I was not always able to connect behavior to the occurrence of whisper song. Interestingly, whisper songs were documented in the presence and absence of conspecifics and occurred throughout the entire year. Additionally, ‘ōma‘o whisper songs are highly complex, variable, and can be substantially longer than regular broadcast song (Paxton unpublished data). However, there is a lack of literature to examine the structural differences between whisper and broadcast songs using frequency, syllables, and notes, but would be an interesting area for future research (Reichard & Anderson, 2015).

To understand intra-specific differences in the occurrence of vocalization types across the landscape I also examined patterns at an individual-level. Overall, individual-level models reflected similar patterns of distribution for songs and whisper songs, but not calls and silence. However, small sample sizes for some individuals due to unpredictable weather during the limited lifespan (*e.g.* 2-4 weeks) of the broadcast transmitter limited my ability to examine individual patterns for all birds in the study. Moreover, the small sample size for the matrix habitat type for many individuals limited my ability to understand the influence of habitat type on the occurrence of vocalization types at an individual-level. Field observations of ‘ōma‘o

behavior indicated that ‘ōma‘o often made brief visits into the matrix and therefore many trips to the matrix may have been missed during the scan schedule of the telemetry towers (once every two minutes) and limited the number of locations documented in the matrix. In addition, ‘ōma‘o primarily flew low to the ground in the matrix and this behavior may have contributed to higher error in matrix location points (*i.e.* located in wrong habitat type or far from actual matrix location), potentially due to interference with the lava as it received the bird’s signal.

Anecdotally, I observed the importance of extremely small kīpuka (<0.1 hectare) in the matrix to ‘ōma‘o that were composed of small clumps of tall trees and potentially acted as safe havens in the open landscape. Small kīpuka that occur between larger forested kīpuka, therefore, may have important management implications for ‘ōma‘o populations in the Upper Waiākea Forest Reserve. Overall, the broadcast transmitters and automated tracking towers were invaluable for tracking and recording birds, making data collection more efficient and feasible and highlights the use of innovative technologies to record and track the movement of individuals.

The individual-level models did allow me to evaluate the effect of distance from core zone on the probability of vocalisation types. The probabilities for song, whisper song, and calls met my predictions that song and whisper song decrease with increased distance from core zone and calls increase with increased distance. In contrast, silence decreased as distance from core increased. The higher amount of silence may be a function of pauses between producing songs and whisper songs as they listen for a response from conspecifics (Catchpole & Slater, 1995). The individual-level model showed that there is variation in vocalisations between individuals, yet they exhibit similar patterns to those at the population-level.

Overall, this study has allowed me to understand the distribution and frequency of vocalisations across a fragmented landscape while unveiling underlying behavioural patterns

associated with fitness, survival, and reproduction. Understanding how organisms interact with their environment in a more detailed manner is imperative to efficiently managing species and developing conservation plans. Hawai'i is home to many endemic avian species that have evolved to inhabit specialised niches. Unfortunately, the archipelago is also known as the “extinction capital of the world” due to threats such as invasive species, habitat degradation, and disease which greatly reduce population numbers (Scott et al., 1986). 'Ōma'ō are currently one of the few native forest bird species with stable populations and are therefore a viable candidate for reintroduction efforts to areas where they have been extirpated. However, selecting sites or restoring habitat for translocation requires an understanding of the species' space use and resource selection behaviours. For instance, the results of this study suggest that birds utilize resources within their home ranges for different reasons, whether it be reproduction based on song or foraging based on calls and silence. Therefore, incorporating behaviour into conservation efforts is important for maintaining behavioural diversity and enabling stability in animal populations. Here I presented an approach to link behaviour with vocal signaling using technologies that can further advance studies of resource selection and bioacoustics with methods applicable to multiple taxa and environmental conditions. As stressed by others in the field of animal behaviour (Angeloni, Schlaepfer, Lawler, & Crooks, 2008; Caro & Sherman, 2012; Cordero-Rivera, 2017; Valiente-Banuet et al., 2015) we need to consider animals as more than a gene pool because they are equally diverse in behaviour and constantly evolving. The loss of a behavior can have a cascading effect on the ecosystem and is an important characteristic that should be considered more highly in the future of conservation biology research and management.

## TABLES

Table 1. Table of summarised data for transmittered 'ōma'o (n = 9) including band number identification code, kīpuka capture site, dates tracked, total minutes observed in field, total number of triangulations used to calculate autocorrelated kernel density estimates (akde), and total number of vocalisation points used in statistical models.

Band number	Kīpuka	Dates tracked (mm/dd/yy)	Minutes observed	Number of triangulations	Vocalisation data points
93229897	K35	01/13/18 – 02/03/18	793	1 734	27
253177018	K26	02/23/18 – 03/09/18	805	5 702	46
93229914*	K40	08/03/18 – 08/20/18	1 748	1 172	130
264196188	K35	08/10/18 – 08/31/18	1 952	189	28
93229903*	K50	09/12/18 – 09/20/18	1 179	1 689	128
264196195	K35	10/20/18 – 10/29/18	861	2 471	33
264196190*	K50	11/14/18 – 11/24/18	1 062	8 132	150
264196199*	K50	01/13/19 – 01/24/19	1 088	7 365	160
93229910	K35	01/17/19 – 01/26/19	1 139	1 306	81

\* individual-level model ran for this individual

Table 2. Population-level parameter estimates, standard deviation (SD), and upper and lower quantiles for each covariate (habitat type, mean tree canopy height (TCH), SD TCH, and vegetation density) categorized by vocalisation type (call, song, whisper song and silent). Also averaged  $\beta$  and standard error (SE) values for four individuals analysed at an individual-level which included a bird's distance from its core one (cz).

Covariate	$\beta$	SD	2.5% quantile	97.5% quantile	Average $\beta$ values of individual-level parameter estimates	Average SE values of individual-level parameter estimates
<b>Call</b>						
Habitat type	-0.929	0.206	-1.328	-0.519	3.308	3.77
Distance cz*	-	-	-	-	0.502	0.091
Mean TCH	0.019	0.122	-0.219	0.259	-1.139	1.418
SD TCH	-0.031	0.126	-0.029	-0.024	-0.075	0.432
Veg density	0.059	0.118	-0.173	0.294	0.883	-0.102
<b>Song</b>						
Habitat type	-1.838	1.111	-4.072	0.184	-4.867	5.388
Distance cz	-	-	-	-	-0.222	0.075
Mean TCH	-0.059	0.265	-0.621	0.436	-0.144	0.95
SD TCH	0.012	0.336	-0.692	0.639	1.073	0.466
Veg density	0.076	0.285	-0.476	0.659	-0.101	0.537
<b>Whisper Song</b>						
Habitat type	1.671	0.554	0.709	2.898	9.194	4.178
Distance cz	-	-	-	-	-0.068	0.043
Mean TCH	-0.108	0.196	-0.504	0.275	-0.093	0.353
SD TCH	-0.477	0.248	-0.976	0.013	-0.453	0.65
Veg density	0.369	0.369	-0.085	0.754	0.266	0.613
<b>Silent</b>						
Habitat type	-0.366	0.462	-1.149	0.683	7.868	5.372
Distance cz	-	-	-	-	-0.193	0.085
Mean TCH	-0.032	0.599	-1.221	1.171	0.006	0.731
SD TCH	1.089	0.529	0.061	2.169	-0.1	0.627
Veg density	-0.312	0.331	-1.009	0.309	0.243	0.511

\* Distance variable not used in population model



*Figure 1. Geographical location of four study kīpuka in the Upper Waiākea Forest Reserve on Hawai'i Island. Five automated radio tracking stations (ARTS) used to obtain individual bird locations are indicated by yellow stars.*

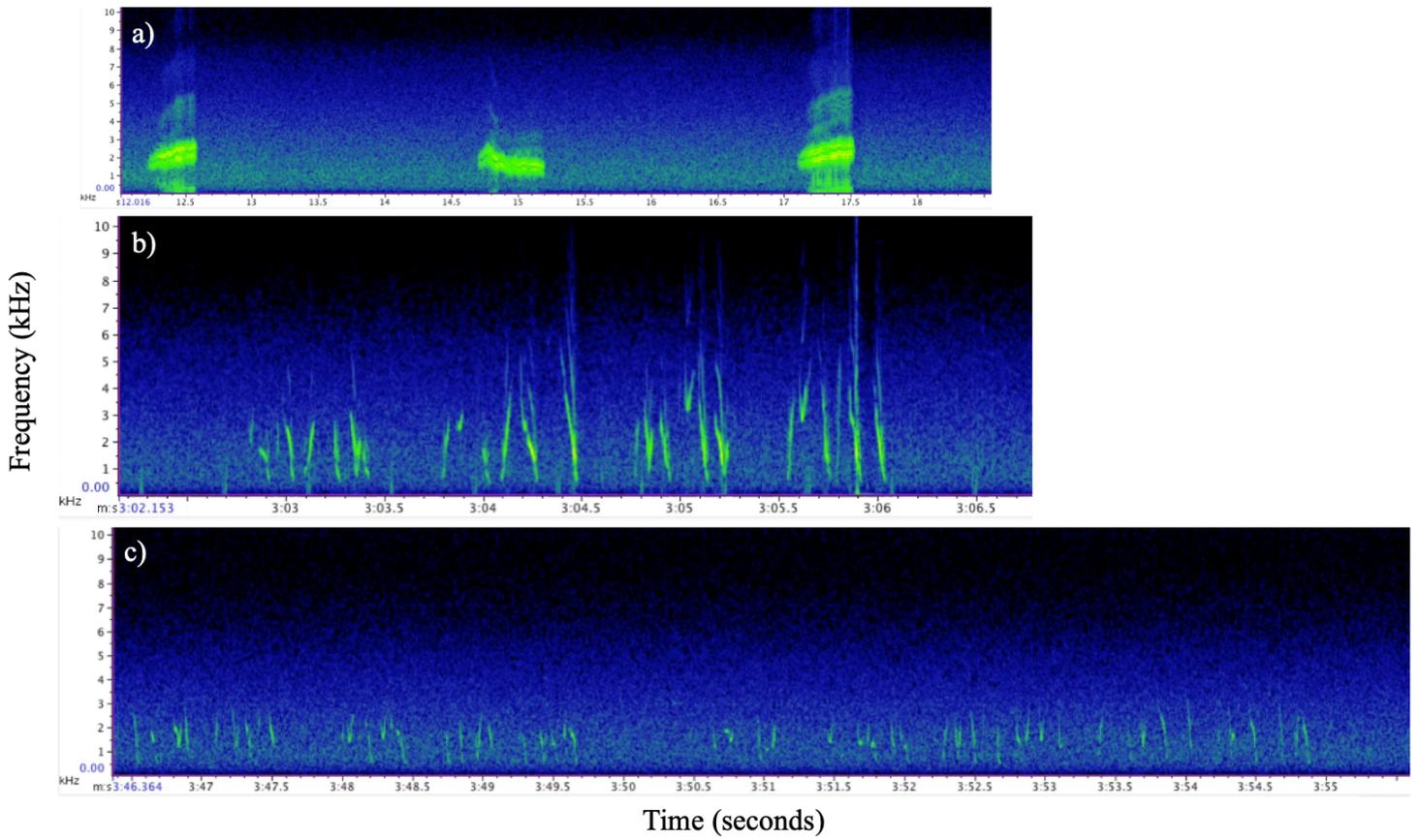


Figure 2. Spectrograms of 'ōma'ō vocalisations produced in Raven Pro: (a) three calls; (b) one song composed of three syllables; (c) one whisper song.



*Figure 3. Backpack harness on a male 'ōma'ō. Harness carries a very high frequency (VHF) transmitter to provide location data and a broadcast transmitter that emits acoustic data live in the field.*

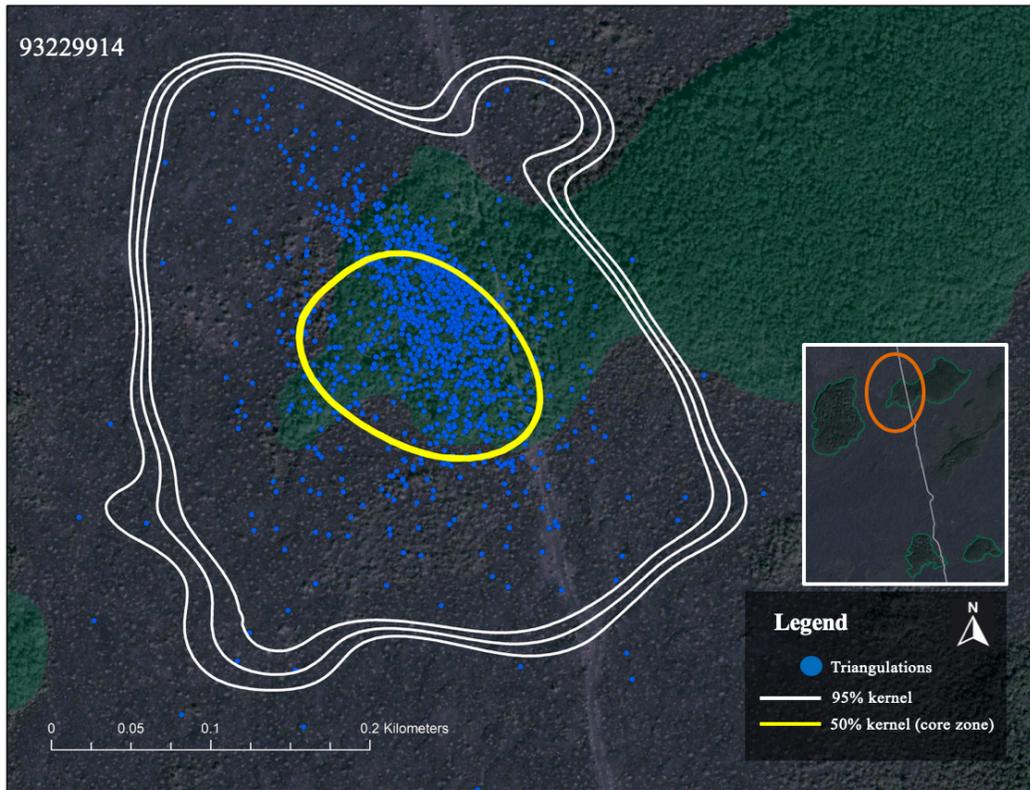
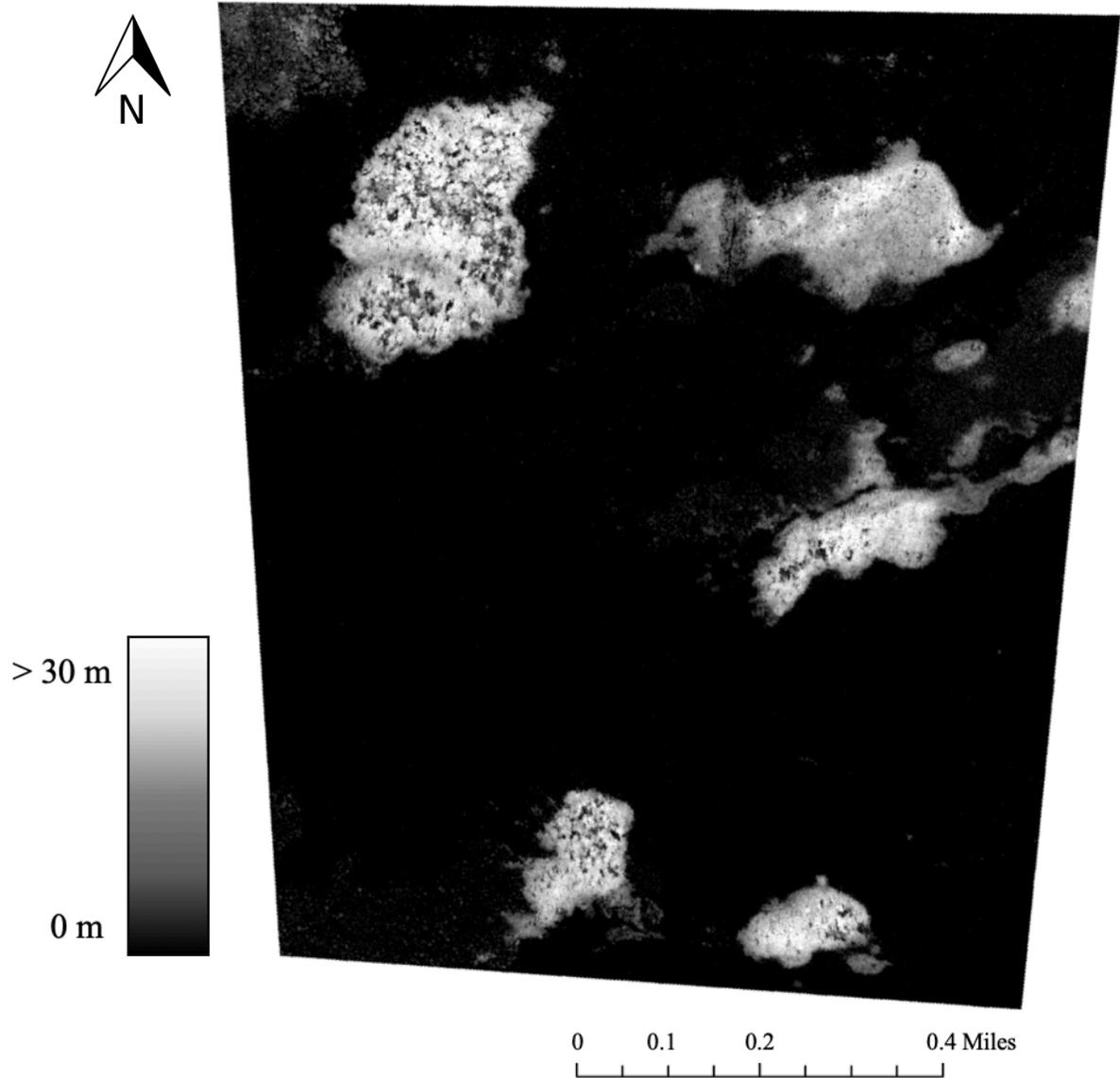


Figure 4. Automated kernel density estimates (akde) for bird 93229914 using the R package ctmm. Blue dots represent triangulations used to calculate akde. The middle white contour lines express the home range area (95% kernel) and the two surrounding contour lines are the confidence ranges. The yellow lines represent the core zone (50% kernel).



*Figure 5. Map of study site using imagery computed from lidar data collected in 2016. The brightness gradient indicates canopy height, which clearly shows the contrast between forested kipuka and the lava matrix. UTM Zone 5N, Datum = WGS84*

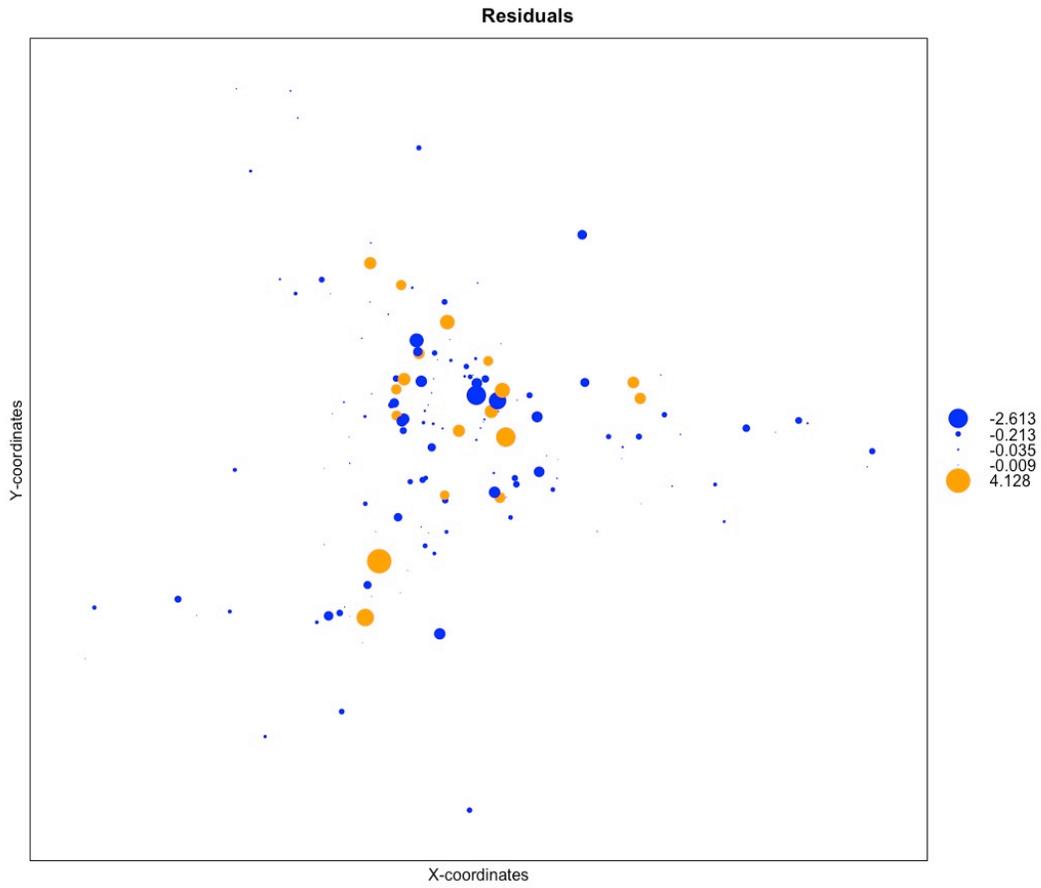


Figure 6. Bubble plot of the spatial effect for an individual, which show little spatial autocorrelation of the vocalisation data. If there was spatial autocorrelation, “bubbles” would be large and clustered together.

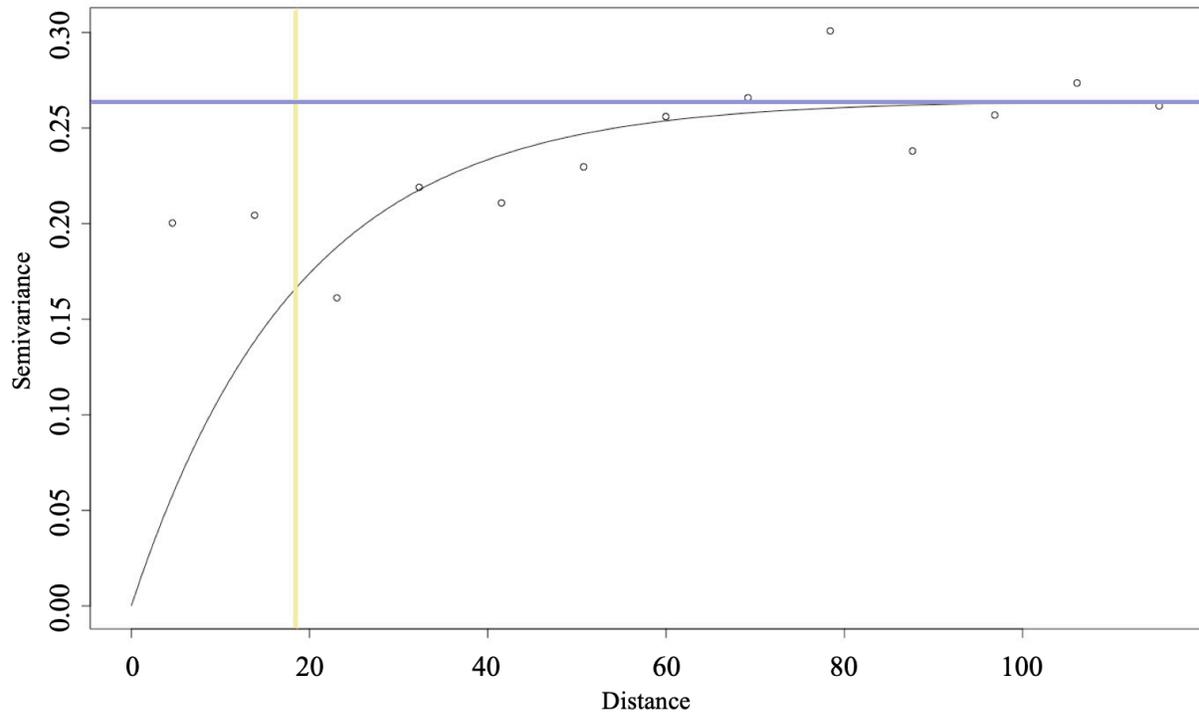


Figure 7. Example of a semi-variogram plotting spatial autocorrelation for a vocalisation type using modelled data where the blue line represents  $\sigma^2$  (i.e. partial sill) and the yellow line shows  $\phi$  (i.e. spatial decay). The x-axis represents the distance between telemetry locations and the y-axis is semi-variance.

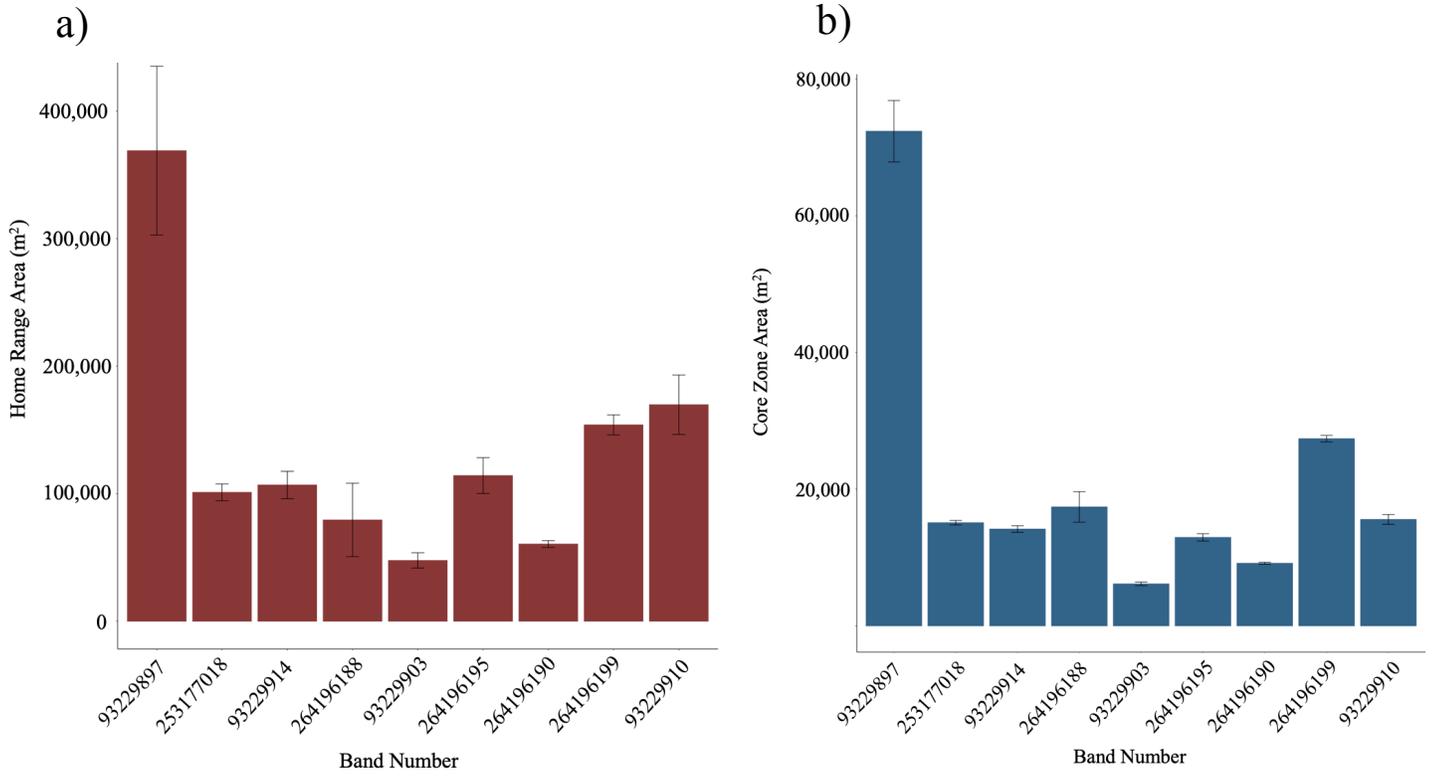


Figure 8. Barplot of a) home range size(m<sup>2</sup>) for all nine 'ōma'o individuals with error bars representing confidence ranges calculated by the automated kernel density estimates (akde) and b) core zone sizes (m<sup>2</sup>) for each individual.

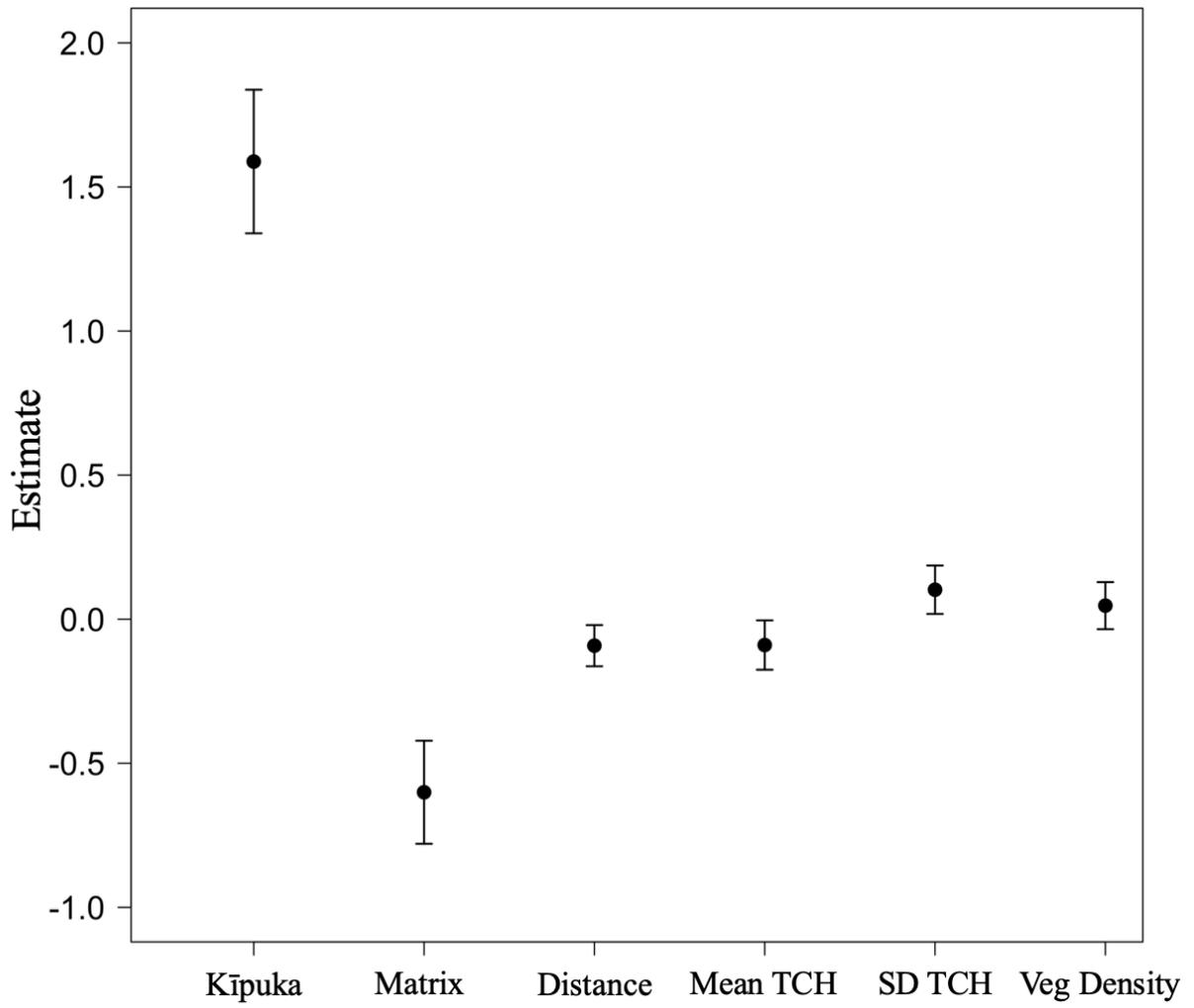


Figure 9. Point plot of model estimates for each habitat variable (kīpuka, matrix, distance from core, mean tree canopy height (TCH), standard deviation of TCH, and vegetation density) with standard error bars.

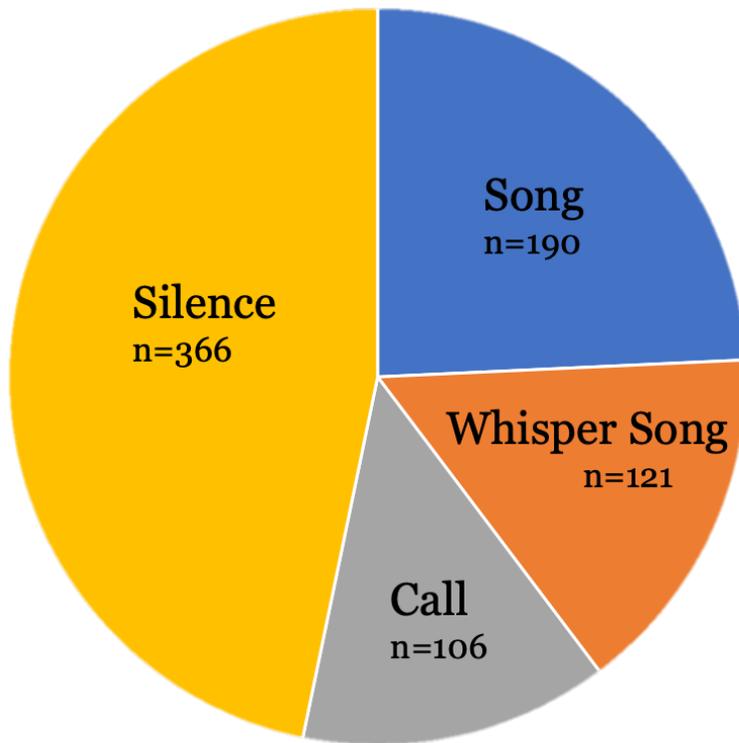


Figure 10. Pie chart depicting the distribution of vocalisation type data for call ( $n = 106$ ), whisper song ( $n = 121$ ), song ( $n = 190$ ), and silence ( $n = 366$ ).

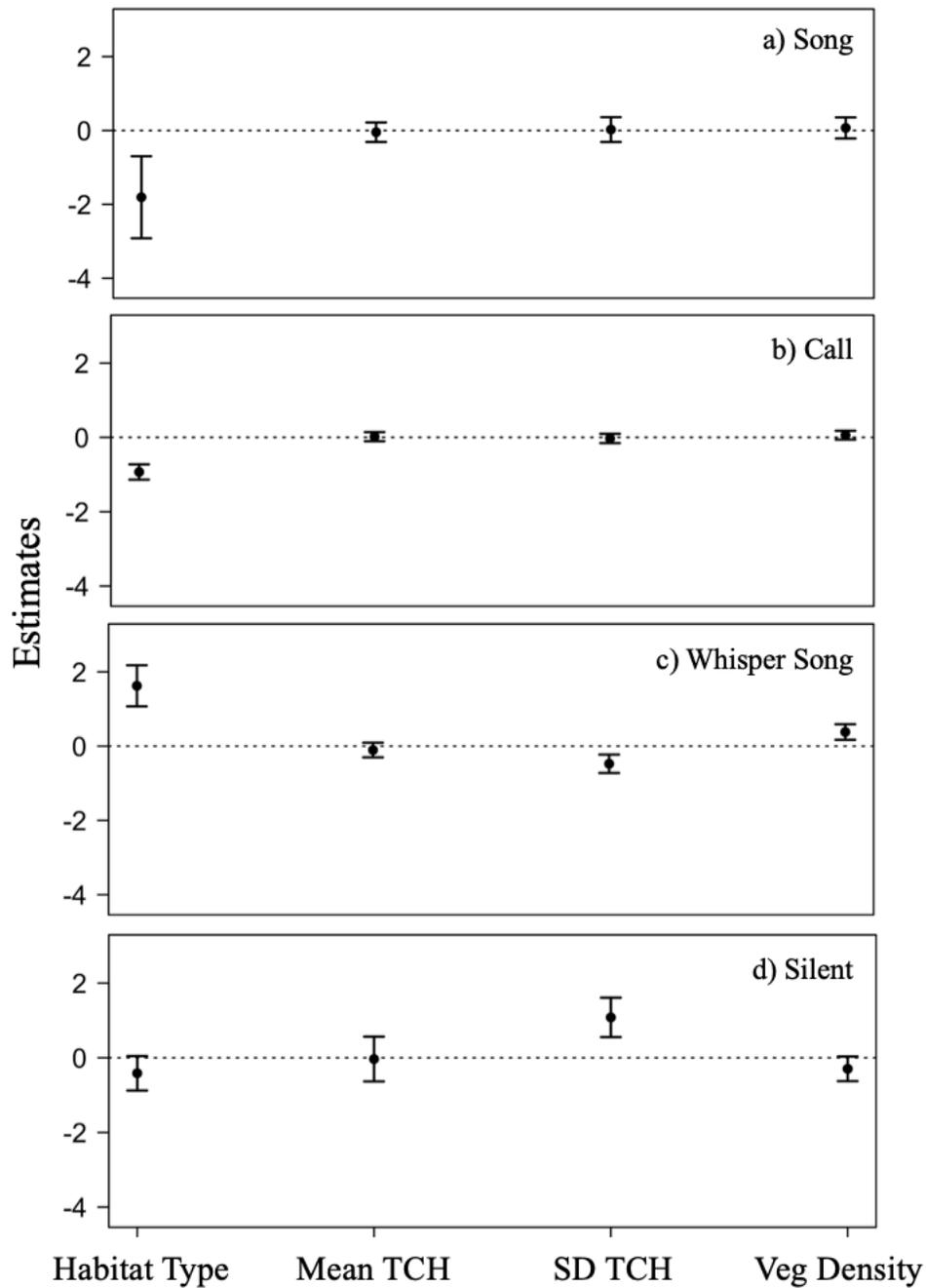


Figure 11. Point plot of population-level parameter estimates for each model covariate (habitat type: kīpuka or matrix; mean TCH: mean tree canopy height; SD TCH: standard deviation of tree canopy height; and vegetation density) by vocalisation type ((a) song; (b) call; (c) whisper song; and (d) silent). Points represent the  $\beta$  for each covariate and the error bars indicate the standard error.  $\beta$  values above zero for habitat type indicate an influence by the kīpuka and below indicates matrix.

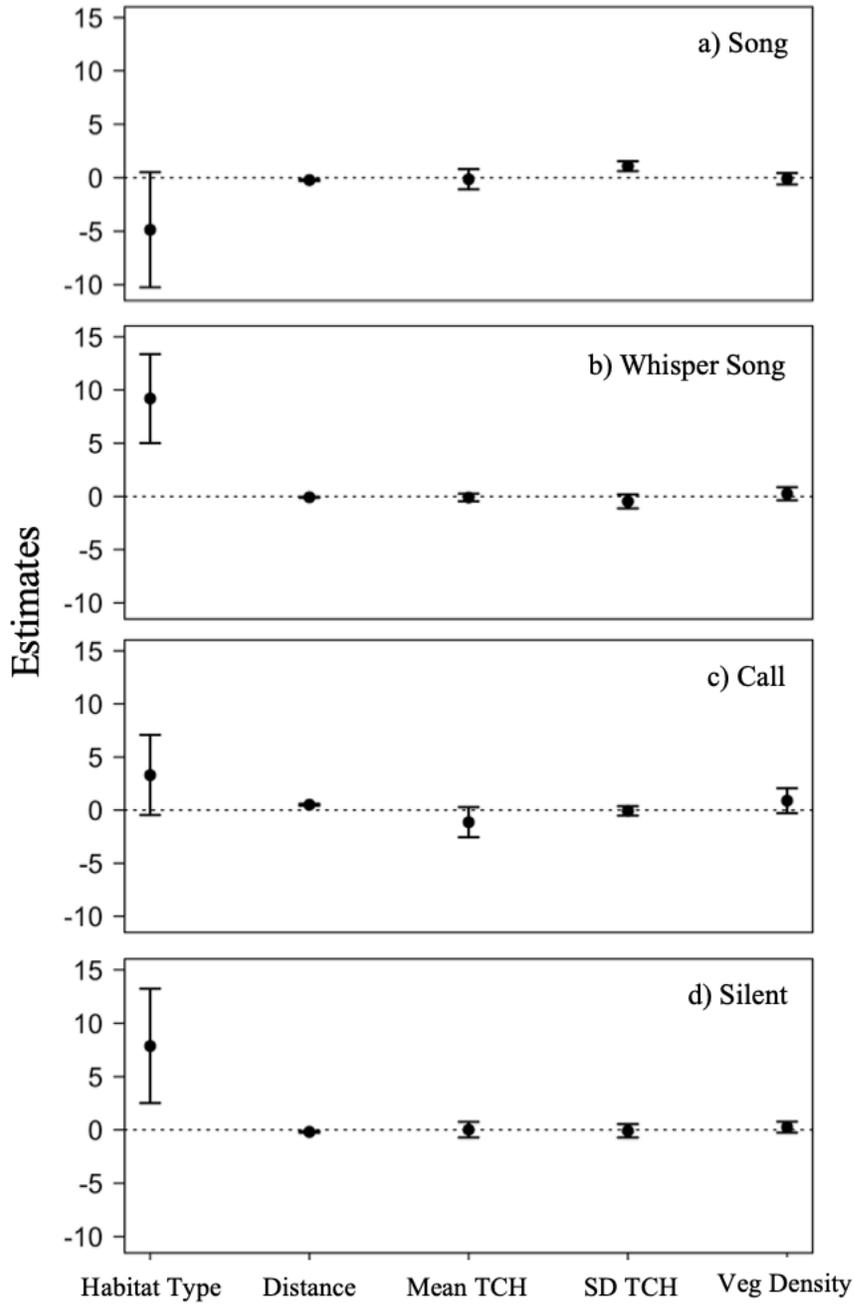


Figure 12. Point plot of averaged individual ( $n = 4$ ) parameter estimates for each model covariate (habitat type: kīpuka or matrix; distance from core zone (m); mean TCH: mean tree canopy height; SD TCH: standard deviation of tree canopy height; and vegetation density) by vocalisation type ((a) song; (b) whisper song; (c) call; and (d) silent). Points represent the  $\beta$  for each covariate and the error bars are the standard error.  $\beta$  values above zero for habitat type indicate an influence by the kīpuka and below indicates matrix.

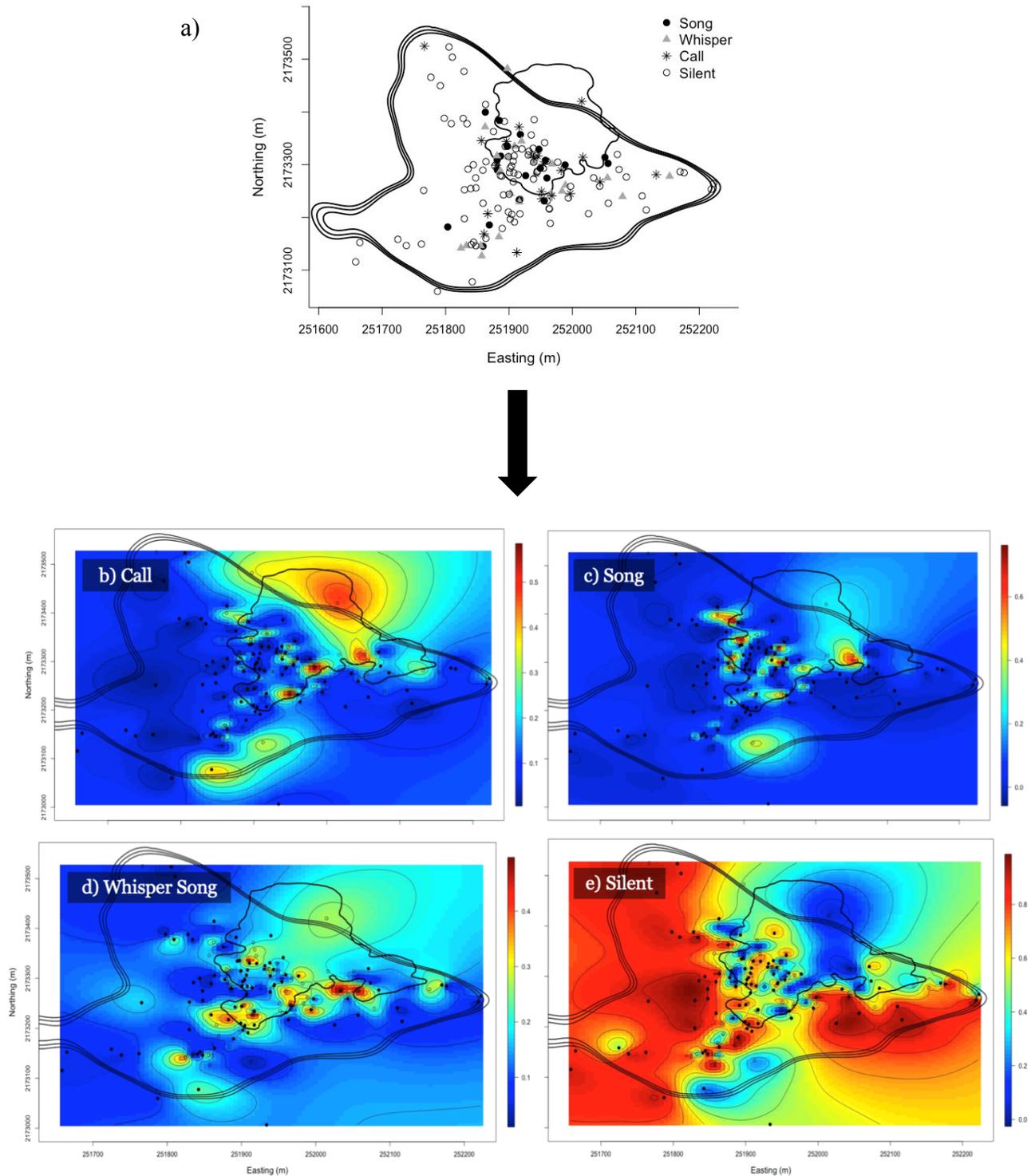


Figure 13. Each map (a – e) has a central polygon representing the kīpuka and three black contour lines (triangular shape) which indicate the home range (95% akde) for a single individual (band number 264196199). (a) Map shows the presence of each vocalisation type associated with telemetry locations represented by a different symbol (solid circle: song; hollow triangle: whisper song; asterisk: call; hollow circle: silent). Behavioural landscape models for individual 264196199 showing the probability of occurrence of vocalisation types ((b) call; (c) song; (d) whisper song; (e) silent). The probability of occurrence for each vocalisation type is on a scale from 0.0 (dark blue) to 0.9 (dark red) with blue indicating a low probability of occurrence and red a high probability.

## Appendix

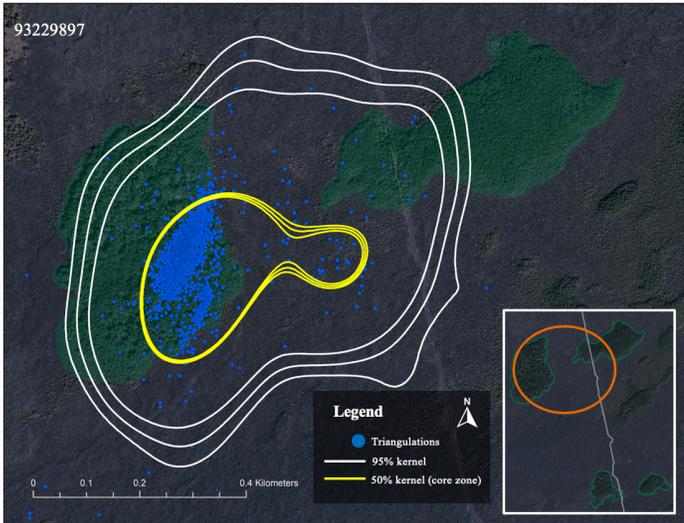


Figure 1. Autocorrelated kernel density estimations (akde) for bird 93229897 created in ctmm. Blue dots represent triangulations used to calculate akde. The middle white contour lines express the 95% home range area and the two surrounding contour lines are the upper and lower 95% confidence intervals. The yellow lines represent the core zone (50% kernel) with 95% confidence intervals.

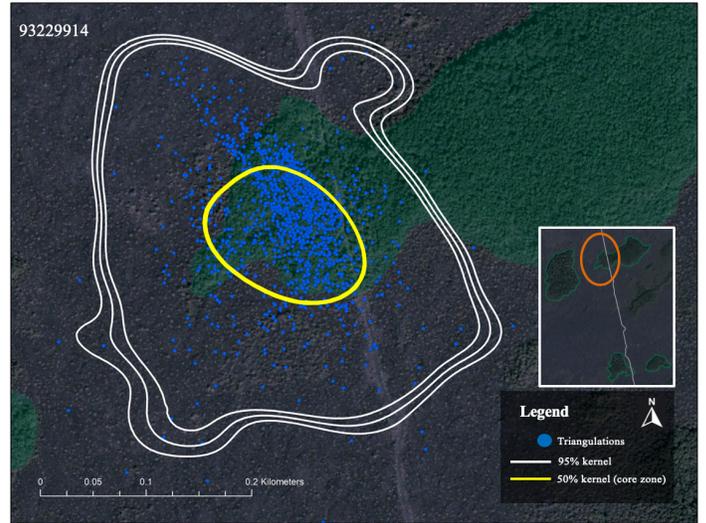


Figure 2. AKDE for bird 93229914 using ctmm. Blue dots represent triangulations used to calculate AKDE. The middle white contour lines express the 95% home range area and the two surrounding contour lines are the 95% confidence interval. The yellow lines represent the core zone (50% kernel) with 95% confidence intervals.

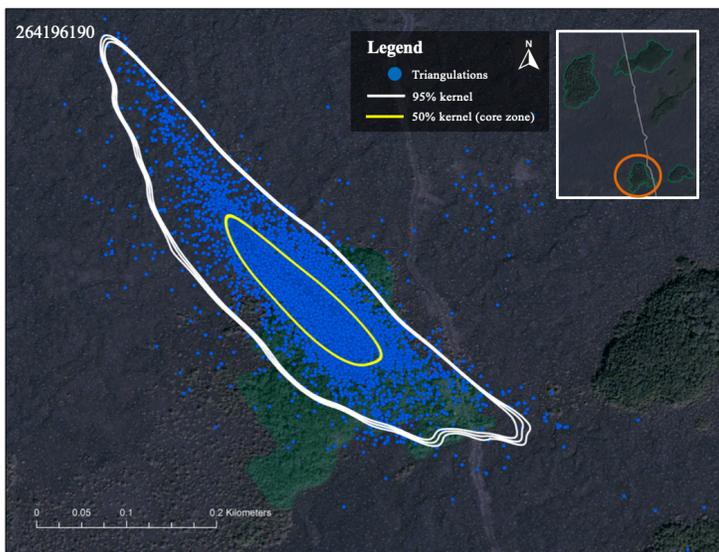


Figure 3. AKDE for bird 264196190 using ctmm. Blue dots represent triangulations used to calculate AKDE. The middle white contour lines express the 95% home range area and the two surrounding contour lines are the 95% confidence interval. The yellow lines represent the core zone (50% kernel) with 95% confidence intervals.

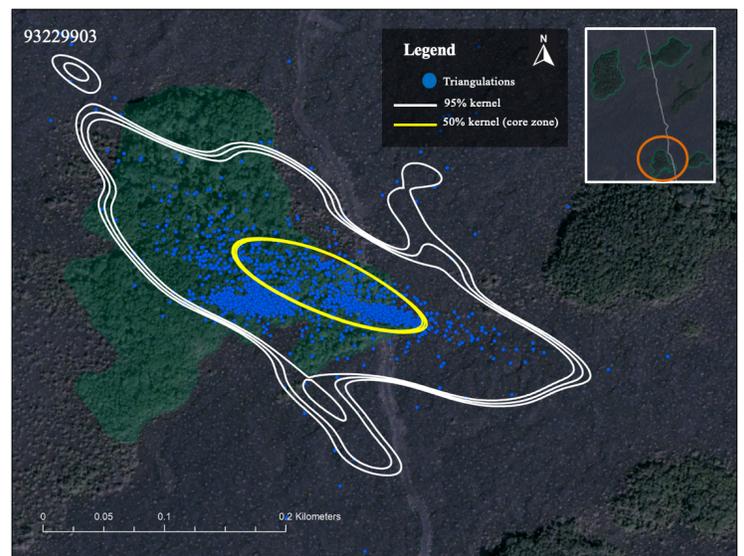


Figure 4. AKDE for bird 93229903 using ctmm. Blue dots represent triangulations used to calculate AKDE. The middle white contour lines express the 95% home range area and the two surrounding contour lines are the 95% confidence interval. The yellow lines represent the core zone (50% kernel) with 95% confidence intervals.

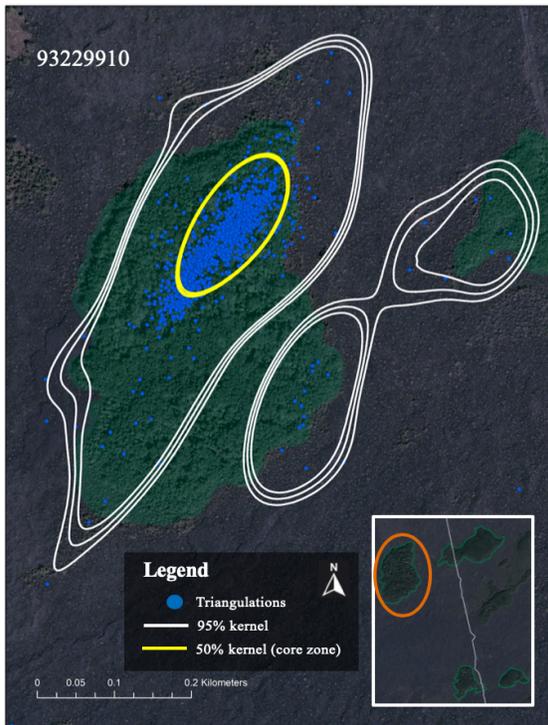


Figure 5. AKDE for bird 93229910 using ctm. Blue dots represent triangulations used to calculate AKDE. The middle white contour lines express the 95% home range area and the two surrounding contour lines are the 95% confidence interval. The yellow lines represent the core zone (50% kernel) with 95% confidence intervals.

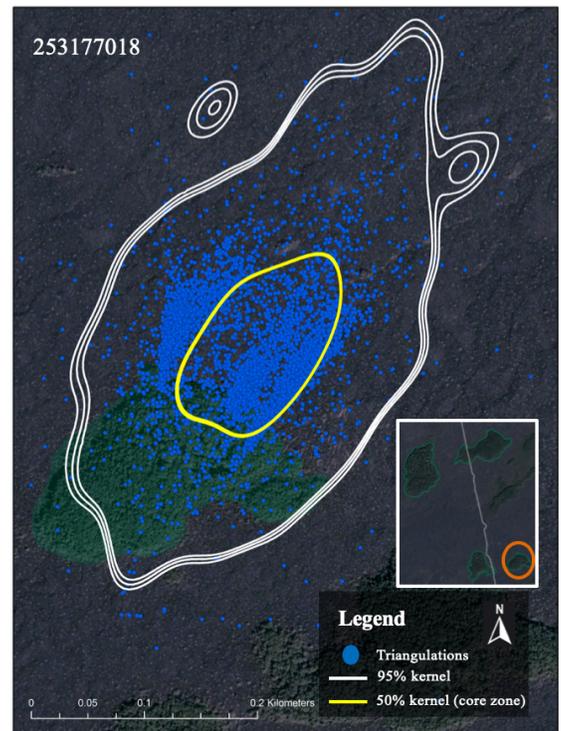


Figure 6. AKDE for bird 253177018 using ctm. Blue dots represent triangulations used to calculate AKDE. The middle white contour lines express the 95% home range area and the two surrounding contour lines are the 95% confidence interval. The yellow lines represent the core zone (50% kernel) with 95% confidence intervals.

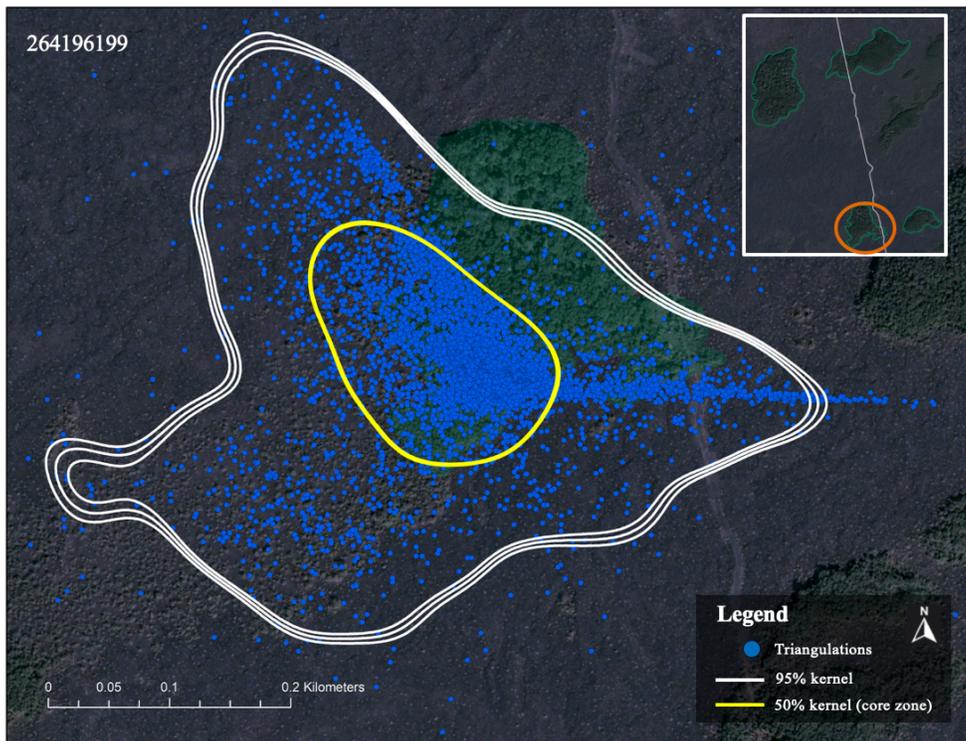


Figure 7. AKDE for bird 264196199 using ctm. Blue dots represent triangulations used to calculate AKDE. The middle white contour lines express the 95% home range area and the two surrounding contour lines are the 95% confidence interval. The yellow lines represent the core zone (50% kernel) with 95% confidence intervals.

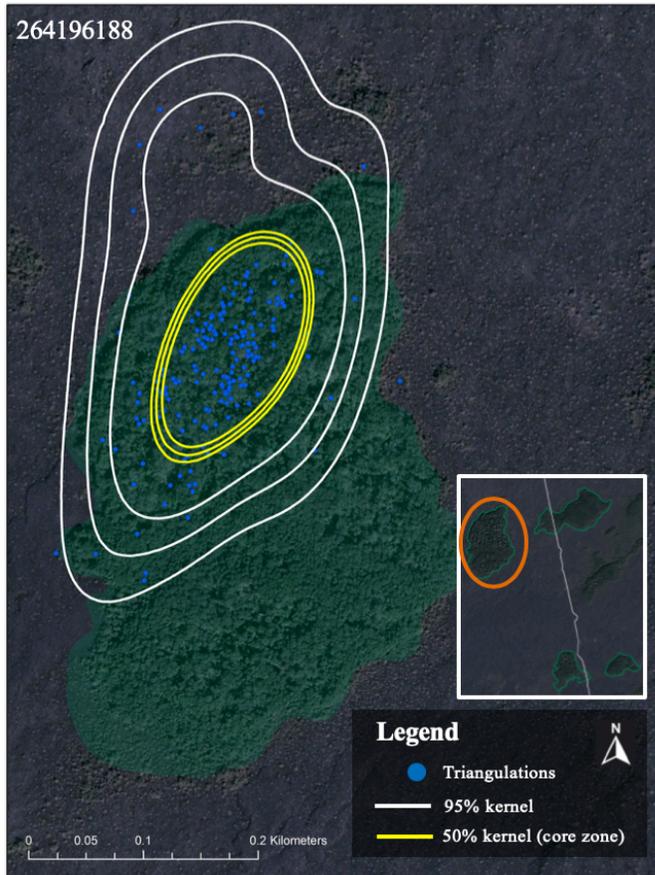


Figure 8. AKDE for bird 264196188 using *ctmm*. Blue dots represent triangulations used to calculate AKDE. The middle white contour lines express the 95% home range area and the two surrounding contour lines are the 95% confidence interval. The yellow lines represent the core zone (50% kernel) with 95% confidence intervals.

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