Estimating home range and temporal space use variability reveals age-related differences in risk exposure for reintroduced parrots

Short title: Home range and space use variability reveals risk

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Abstract

Individual-level differences in animal spatial behaviour have been identified in numerous species, which can lead to differential exposure to risk for different groups, particularly for reintroduced species in fragmented landscapes. To assess the risk-exposure of a population of kākā (*Nestor meridionalis*) reintroduced into a fenced reserve, we GPS-tracked 10 individuals and estimated their home ranges and temporal space use variability (SUV). We compared home range area (within 95% contour of utilisation distribution - UD_{95}) between individuals in relation to age, sex, and fledging origin, and assessed risk exposure by calculating the proportion of each individual's home range beyond the reserve's fence. To estimate temporal variability within each individual's space use, we used a sweeping window framework to estimate occurrence distributions of temporally overlapping snapshots of the movement trajectory. For each occurrence distribution, we calculated the proportion outside the reserve's fence to assess how risk exposure changed throughout time, and the UD_{95} area and UD_{95} centroid to assess the behavioural pattern of space

use. Home range area declined significantly and consistently with age (up to 27-fold differences), and the space use of juvenile kākā was more temporally dynamic, particularly in relation to drift of the UD_{95} centroid. The wider-ranging behaviour of younger kākā resulted in more time spent outside the reserve, which aligned with a higher number of incidental mortality observations of younger individuals. Quantifying both the home range and space use variability of populations that may encounter spatially dependent threats is an effective approach to assess risk exposure, which can provide guidance for management interventions. We also emphasise the temporal space use variability approach, which is a flexible approach that can provide numerous insights and has not been widely adopted in the literature. We provide code and data such that all the analyses in this study can be reproduced.

Keywords: dynamic, home range, risk, space use variability, spatial behaviour, telemetry, temporal variation, reintroduction

Introduction

Individual and group-level behavioural differences have been observed in a broad range of animal taxa, which represents intrapopulation diversity in physiological, behavioural, and ecological mechanisms (Bolnick et al., 2003; Dall et al., 2012; Stuber, Carlson, & Jesmer, 2022). These differences can manifest as variable foraging strategies, spatial behaviours (Stuber, Carlson, & Jesmer, 2022), and problem-solving abilities of conspecific individuals (Loepelt, Shaw, & Burns, 2016), each of which influence population dynamics (Hanski, 1998) and adaptation to environmental change. Extrinsic factors that influence behaviour include resource availability and the density of competitors, predators, prey, or conspecifics, while intrinsic factors include age, sex, and breeding status (Andreassen, Stenseth, & Ims, 2002; Reader & Laland, 2002; Loepelt, Shaw, & Burns, 2016; Lesmerises & St-Laurent, 2017; Clay et al., 2018). In birds, age is considered to influence behaviours such as those relating to problem solving and foraging efficiency, with

younger individuals being more behaviourally flexible, innovative, and able to solve novel problems (Loepelt, Shaw, & Burns, 2016; Sherratt & Morand-Ferron, 2018) whilst older individuals are typically more efficient foragers (Phillips et al., 2017; Clay et al., 2018).

In a conservation context, individual- or group-level behavioural differences that lead to variability in space use are relevant as they may lead to differential exposure to risk, which can affect the population's or species' trajectory and persistence (Merrick & Koprowski, 2017). This is especially the case for populations in conservation reserves, understood as discrete areas of habitat that undergo protection from threats and allow for the refuge and possible translocation of sensitive wildlife species that have been reduced or historically extirpated, even while the major causes of species decline persist in the wider region (Burns, Innes, & Day, 2012; Innes et al., 2019). In the case of fully-fenced conservation reserves, flighted species that 'spill-over' into the wider landscape (Tanentzap & Lloyd, 2017) may encounter a fragmented or modified landscape containing a higher number of threats, which can impose a greater mortality risk outside the fence. These effects may be further increased if the species has lost predator-avoidance behaviours (Muralidhar et al., 2019).

Assessing spatial behavioural differences that lead to variable exposure to risk can be estimated through telemetry data and space use analyses. A common measure to quantify space use is to calculate an individual's utilisation distribution (UD), which is a two-dimensional probability surface that represents the relative frequency of animal locations (Van Winkle, 1975; Kernohan, Gitzen, & Millspaugh, 2001; Kie et al., 2010). For an animal's home range, risk exposure can be quantified by calculating the overlap of an individual's UD with areas of presumed risk, which represents the proportion of time spent in these areas during the tracking period. While this approach provides valuable evidence and can indicate whether certain individuals or groups are likely to be at higher risk than others, an animal's space use may not be stable over time, and resources or climate might drive the space use of certain individuals, groups, or even the entire population to change in position or size, leading to risk-exposure that changes over time. If these

changes are predictable, they can lead to more effective and efficient decisions that manage risk-exposure for certain groups at certain times of the year, which is highly relevant in the particular case of conservation reserves.

We aimed to test the ability of static and dynamic space-use estimations to assess variable risk exposure in a reintroduced parrot population in a fenced conservation reserve. Kākā (*Nestor meridionalis*) are long-lived endemic parrots that are being restored through translocation to conservation reserves throughout New Zealand, where they were historically wide-spread (Recio, Payne, & Seddon, 2016; Aichele, Seddon, & van Heezik, 2021). Kākā are large-brained (Iwaniuk, Dean, & Nelson, 2005), social (Bond & Diamond, 2004), and are considered generalist, extractive foragers (Beggs & Wilson, 1987; Moorhouse, 1997). These traits typical of parrots suggest a propensity for exploration and innovation (Sol et al., 2005; Dunbar & Shultz, 2007), which has been observed particularly in juvenile kākā (Bond & Diamond, 2004; Loepelt, Shaw, & Burns, 2016). Threats to kākā in wild populations are well-understood (O'Donnell & Rasch, 1991; Wilson et al., 1998), but fragmented, semi-urban landscapes present novel threats that include human infrastructure, vehicles, cats, dogs, and traps and toxins intended for pest species. In 2008, kākā were translocated into the fully fenced semi-urban conservation reserve Ōrokonui Ecosanctuary (*Te Korowai o Mihiwaka*; 45°46´S, 170°36´E; hereafter Ōrokonui), which is within a region that kākā have been absent from for many years. Inside the fence of Ōrokonui is free of invasive mammalian predators, Ōrokonui but in recent years there has been no detectable change in the number of individuals in the population (Elton Smith, unpublished data). This stability suggests a lack of population growth despite annual juvenile reinforcement translocations and in-situ breeding. We recognised the continued presence of threats outside the reserve and hence attempted to understand to what extent movements outside the apparent safety of the fenced reserve pose a risk to the birds, and whether this differs between certain groups. To address this, we GPS-tracked a subset of the kākā of the Ōrokonui population and estimated their home ranges and temporal space use variability. We assessed the kākā's exposure to risk by estimating the proportion of their home range outside the Ōrokonui Ecosanctuary fence and described

behavioural patterns by estimating their temporal space use variability and likely risk exposure. The approach taken here has broad application for quantifying exposure to presumed risk and when this occurs, such as outside conservation reserves, within fishing grounds for marine species (Weinstein et al., 2017), and in areas with human infrastructure such as wind turbines (Bright et al., 2008).

Methods

Ethical approval

This study was conducted with approval from the University of Otago Animal Ethics Committee under the Animal Use Protocol AUP-18-237.

Study site and semi-urban kaka reintroduction programs

Ōrokonui Ecosanctuary is a 307-ha sanctuary near the city of Dunedin (South Island, New Zealand) that is completely surrounded by a 1.9-metre-high pest-resistance fence. Since the time the Ōrokonui fence was erected in 2007, the reintroduction of multiple taxa has led to positive biodiversity impacts within and beyond the fence (Bogisch, Cree, & Monks, 2016; Jarvie et al., 2016; Tanentzap & Lloyd, 2017; Aichele, Seddon, & van Heezik, 2021). The vegetation within Ōrokonui is predominately comprised of regenerating kanuka-broadleaf native forest with small areas of old growth forest, as well as stands of exotic pine forest (predominately *Pinus radiata*) and mountain ash (*Eucalyptus regnans*). Surrounding the sanctuary is a fragmented landscape of old-growth and regenerating native forest fragments, as well as exotic conifer forest, working farms for grazing livestock, and semi-urban areas. At the time of the study areas outside the fence were subject to continuous pest-control, targeting mustelids, possums (*Trichosurus vulpecula*), and rodents. Since the initial translocation of kākā in 2008, roughly 50 captive-raised kākā have been released and more than 50 individuals have fledged from local breeding (as of 2020, Elton

Smith, unpublished data). However, seasonal monitoring estimates the population to be at approximately 40-50 individuals, which has been stable for several years. Supplementary food is available to kākā at feeding stations in Ōrokonui year-round as parrot-specific pellets and sugar water.

Data collection

To gather locational data, we fitted SWIFT fix GPS devices (PinPoint 350/450, 18.4 – 19.1g, Lotek, NZ) to 10 kākā using backpack harnesses with a weak-link (Karl & Clout, 1987). The devices were set to take a location every 3 hours for the nine PinPoint 350 devices, and every 2 hours for the single PinPoint 450 device due to a larger battery. Free-ranging kākā were captured in the reserve for tagging by luring them into a baited aviary used for soft-release of captive-raised individuals during population reinforcement translocations. All kākā were weighed, subjected to a health check, and sexed by measuring the upper mandible (Moorhouse & Greene, 1995; Moorhouse et al., 2008). The GPS devices were distributed evenly between the sexes, with five females and five males, and across a range of ages from 1 – 10 years old (mean = 4.5 years). The tracked kākā were a combination of Ōrokonui-fledged and captive-raised. All but one kākā had been in the sanctuary for a minimum of 5 months, and some for up to 10 years. The remaining kākā was a 10-year-old male who was released (with his breeding partner) into Ōrokonui directly from a captive-breeding facility, and the environment was therefore novel to this individual. GPS devices recorded location data, the number of satellites, and horizontal dilution of precision (HDOP), as well as temperature, and overall dynamic body acceleration (ODBA) at 1-minute intervals. All GPS locational data was projected to New Zealand Transverse Mercator (NZTM2000 – EPSG:2193) before analysis. Prior to and during the study period kākā mortalities of tracked and non-tracked individuals were recorded during surveys by managers of the sanctuary or by GPS or VHF telemetry mortality signals. Kākā were sent to Massey University, New Zealand, for post-mortem to determine cause of death, and we recorded the approximate time and location of the mortality where possible.

Data Analysis

Location filtering

To remove unrealistic locations that are unlikely to represent the true location but are instead due by GPS-related error, we used a filtering method which is based on the maximum observed speed of each individual (Shimada et al., 2012, 2016). We calculated the maximum observed speed (Vmax) between successive locations for each individual, based on the locations from six or more satellites (average of 51.4% of locations were from ≥ 6 satellites per individual). As 95% of SWIFT-fix GPS locations are considered to be within 19.0m from 6 satellites (Forrest, Recio, & Seddon, 2022), we expected these observed maximum speeds to reflect the maximum speed dictated by the particular individual's behaviour, rather than due to measurement error. The individual Vmax values were then applied to all locations for that individual, and locations that had a speed exceeding the Vmax before and after the location were removed from further analyses. The location filtering analysis was conducted using the R package 'SDLfilter' (Shimada et al., 2012).

Home range behaviour and presumed risk exposure

To estimate each individual's space use for the full tracking period (which we term home range), we used the dynamic Brownian bridge movement model (dBBMM) (Kranstauber et al., 2012). With this estimator we accounted for the information contained in the temporal structure of GPS data while quantifying the home range based on the animal's movement path rather than individual points (Horne et al., 2007). A benefit of the dBBMM is that it calculates the Brownian motion variance parameter depending on the characteristics of the local movement trajectory, which allows for robust space use estimation when there are behavioural changes (Kranstauber et al., 2012). We opted for an occurrence distribution estimator (Alston et al., 2022) as we were answering the question of where did the animal go during a specified period of time, which was more applicable for assessing risk in this case. The dBBMM method requires the user to input a

window size, which is the number of locations that characterise the local movement behaviour, and a margin size where no behavioural breakpoints can be estimated but that is required to calculate the likelihood. We used 3 locations for the margin size and 15 for the window size. For inference, we considered 50% isopleths (UD_{50}) to represent areas of core use, and 95% isopleths (UD_{95}) as the home range when using the tracking data for the entire study period (Börger, Dalziel, & Fryxell, 2008; Kie et al., 2010; Kranstauber et al., 2012; Stark et al., 2017). As the UD is a distribution describing the probability of an individual being in a particular location during the period used for estimation, portions of the probability distribution can be summed to approximate the time spent in a specified area. With this in mind, we calculated a proxy of presumed risk exposure by calculating the proportion of the utilisation distribution that was outside the Ōrokonui Ecosanctuary fence, as the majority of threats to kākā (introduced predators and human-based threats such as infrastructure and vehicles) exist only outside the fence.

Comparison of home range area between individuals

To identify differences between individual's space use, we assessed the influence of age, sex, and origin (Ōrokonui-fledged or captive-fledged) of individuals on home range area (area contained within the UD_{95} isopleth of the full study period, which ranged from 111 to 168 days) using a multi model-selection and model-averaging approach. We proposed different alternative models combining age, sex, and origin and predictors and home range area as the dependent variable using generalised linear models (GLM) with Gamma distributions and logarithmic link functions to account for the non-negative, continuous and right-skewed data (Burnham, Anderson, & Huyvaert, 2011; Bartoń, 2020). As all three predictors were considered to be biologically important, all possible combinations of the predictors were used to construct a set of competing models, which we ranked by AICc due to the small sample size of individuals (Johnson & Omland, 2004). Model coefficients were averaged in proportion to their Akaike weight, using the full model average calculation to prevent biasing the coefficients away from zero (Burnham, Anderson, & Huyvaert, 2011). Model fit was assessed using a likelihood-ratio based on pseudo-

R-squared for each model (Bartoń, 2020). Dispersion (φ), Pearson residuals and quantiles were checked for model fit (Dunn & Smyth, 2014).

Temporal space use variability (SUV)

To assess how the space use of each individual changed throughout time we employed a simple, non-statistical framework to use in conjunction with a statistical home range estimator, which we termed temporal space use variability (SUV). Our approach was to estimate occurrence distributions for temporally overlapping snapshots of the movement trajectory for each individual, resulting in many temporally overlapping utilisation distributions (UDs). This is similar to the approach of (Schlägel et al., 2019), who used a sweeping window approach to estimate interactions between individual animals. We adopted a similar sweeping window approach but calculated summary statistics such as the area, centroid, and overlap of each snapshot UD, which we tracked throughout time and compared between individuals.

Within the SUV sweeping window framework, there are two parameters, one determining the width of the window to estimate the behavioural snapshot, and another that determines the increment that the window is moved along the track by (Figure 1). In this case, we used the dBBMM approach to estimate UDs separately for each temporal snapshot, although other methods that estimate utilisation distributions may also be used. We used a window containing 240 locations of the movement trajectory, which is approximately one month at 3-hour fix intervals, which was swept along at increments of 6 locations, which is 18 hours. The temporal window and increment widths can be freely chosen and should depend on the frequency of telemetry locations and questions being asked. Shorter window widths will capture changes in space use that are shorter in duration, but for persistent changes in the pattern of space use to be identified then the animal should ideally visit all of its home range within the window duration. The increment size changes the resolution with which to assess changes and should be small relative to the window size. In this study, the fix-success rate (proportion of attempted GPS fixes that were successful) averaged 78.1% for all individuals, and therefore the actual window width

will be wider than one month, and the increment may be greater than 18 hours. We kept the number of locations, rather than the time period, consistent to ensure that space use was estimated for a consistent number of locations. A consistent time period can also be used. To prevent confusion, although the window and increment parameters of the SUV framework are similar to the window and margin parameters of the dBBMM, they are separate and are both specified by the user.

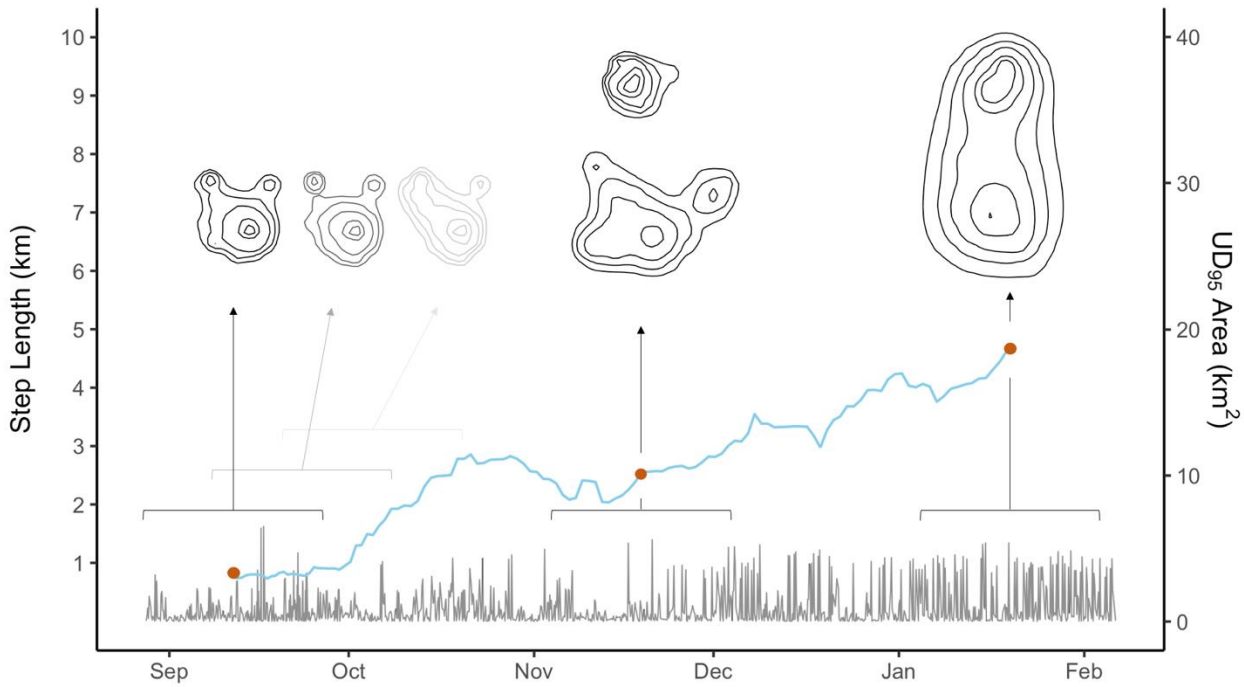

Figure 1: Concept plot of the Space use variability (SUV) method, based on data from this paper (kākā ID 08). Utilisation distributions were estimated for temporal snapshots of a fixed window width of 240 locations, which was swept along the movement track at a fixed increment of 6 locations. For this individual this resulted in 169 temporally overlapping space use snapshots. The kākā's movement trajectory is represented by step lengths (black line – left y-axis), and the resulting UD_{95} areas that were calculated for each temporal snapshot are shown by the blue line (right y-axis). Several example UDs (all on the same scale) are shown to illustrate the gradual evolution of space use, which in this example the large increases in UD_{95} were due to the inclusion of a new core area to the geographical north in the central and right UDs. This is also reflected in the step lengths for the latter part of the tracking period, with longer steps on average as this individual moved between core areas.

To visually assess the pattern of space use changes throughout the tracking period we constructed a similarity matrix of Bhattacharyya's Affinity (BA), which calculates the similarity between all the snapshot UDs for each individual (Fieberg & Kochanny, 2005; Kranstauber et al., 2020). For each individual, this indicates times when the UDs were dissimilar and can be used to identify space use patterns, such as in (Kranstauber et al., 2020). We opted for BA as it is computationally efficient and all snapshot UDs for each individual at least partly overlapped; if each individual's snapshot UDs did not overlap then earth mover's distance may be more appropriate as it considers distance between separate UDs (Kranstauber, Smolla, & Safi, 2016). To quantify expansion and contraction of space use for each individual throughout time we calculated the UD_{95} area for each temporal snapshot, and to assess positional shifts in space use we calculated the location of the UD_{95} centroid. To compare positional changes of space use between individuals and groups, we calculated the distance between successive centroid locations and took the overall average for each individual, which we termed space use drift. The centroid for multimodal UDs was taken to be the overall UD_{95} centroid, rather than the centroid of the largest UD_{95} area. This is to appropriately represent the inclusion of new areas of space use, and to prevent artificial 'jumps' of the centroid if there were two modes of the UD that were similar in size but fluctuated as the largest in area. To statistically compare space use drift between kākā, we fitted a generalised linear model with a Gamma distribution and logarithmic link function and conducted the same model diagnostics as above. The recorded timestamp of each UD was midway between the first and final locations. As in the home range estimation the margin and window parameters within the dBBMM model were 3 and 15 locations, respectively.

Results

Data collection

The GPS unit data collection ranged from 111 to 168 days (mean ± SD = 147 ± 17 days), gathering between 725 to 1727 successful fixes for each individual (mean ± SD = 1087 ± 257 successful fixes). GPS fix-success rate of varied from 63.6% – 90.2% (mean ± SD = 78.1 ± 8.7%), resulting in a total of 10,868 successful location fixes for all individuals. The Vmax from 6 or more satellites ranged from 0.247 to 1.937 km/hr between individuals (mean ± SD = 0.948 ± 0.58 km/hr), resulting in between 0.23% to 3.29% (mean ± SD = 1.13 ± 0.93%) of locations being removed for each individual (Table S.1). During an 18-month period prior to and included tracking period seven kākā were recorded to have died, and five of these deaths occurred within the study period, three of which were located with either a VHF or GPS transmitter's mortality function. Six kākā were of known age, which were all 3-years or younger for an average age of 1.8 years. Confirmed causes of mortality included brodifacoum poisoning and toxoplasmosis and suspected but unconfirmed causes included electrocution via powerlines (Table S.2). No mortalities or adverse effects were attributed to the GPS or other telemetry devices or the attachment harnesses.

Static space use: home range area and comparison between individuals

Individual home range area (UD_{95} area) varied widely, from 0.57 km^2 to 15.4 km^2, with a mean ± SD = 6.54 ± 5.41 km^2 (n = 10 individuals) (Figure 2 and Table S.1), and all kākā home ranges overlapped with Ōrokonui at least partially (mean ± SD proportion of UD outside Ōrokonui = 0.43 ± 0.34 across individuals) (Figure 1 and Figure 3B). There was no significant trend of UD_{95} area in relation to sex or origin (Table S.3, Table S.4 and Figure S.4) but there was a significant negative correlation between UD_{95} area and age ($F_{1,8}$ = 23.5, P = 0.001, R^2 = 0.78 – Figure 3A). The average home range size for kākā 3 years and younger was 9.70 km^2 (n = 6), whereas the average home

range size for kākā 5 years and older was 1.81 km^2 (n = 4) (Figure 2). Similar to home range area, the proportion of each individual's UD that was outside of the Ōrokonui Ecosanctuary fence also decreased significantly with age ($F_{1,8}$ = 41.0, P < 0.001, R^2 = 0.85 – Figure 3B).

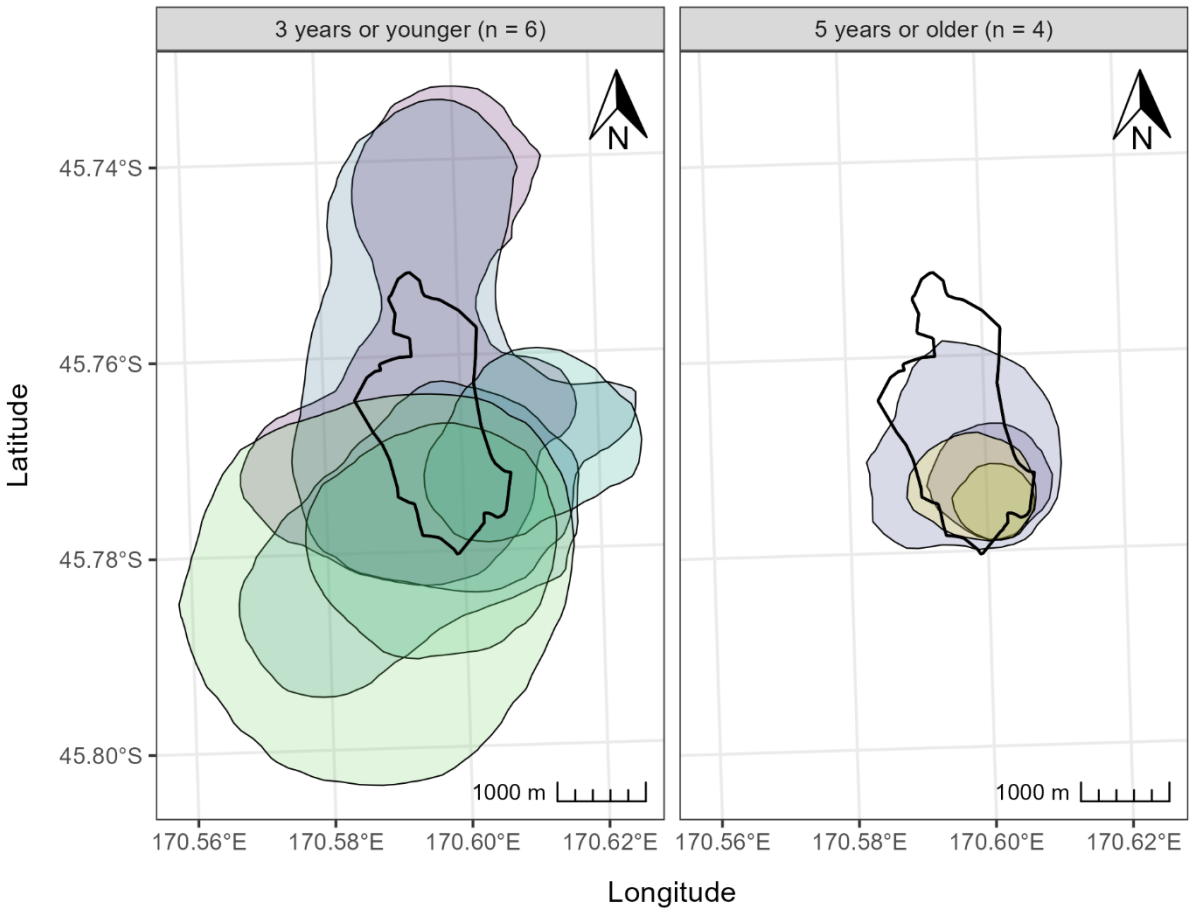

Figure 2: Examples of 95% utilisation distributions (UD_{95}) for each individual estimated from GPS tracking and dynamic Brownian Bridge Movement Modelling (dBBMM). The left plot shows the UD_{95} isopleths for individuals 3 years or younger, and the right plot shows the UD_{95} isopleths of individuals 5 years or older. The fence of the Ōrokonui Ecosanctuary is shown as the thicker black line in the centre of each plot. The scale is the same for both plots to highlight the differences between UD_{95} areas of younger and older individuals.

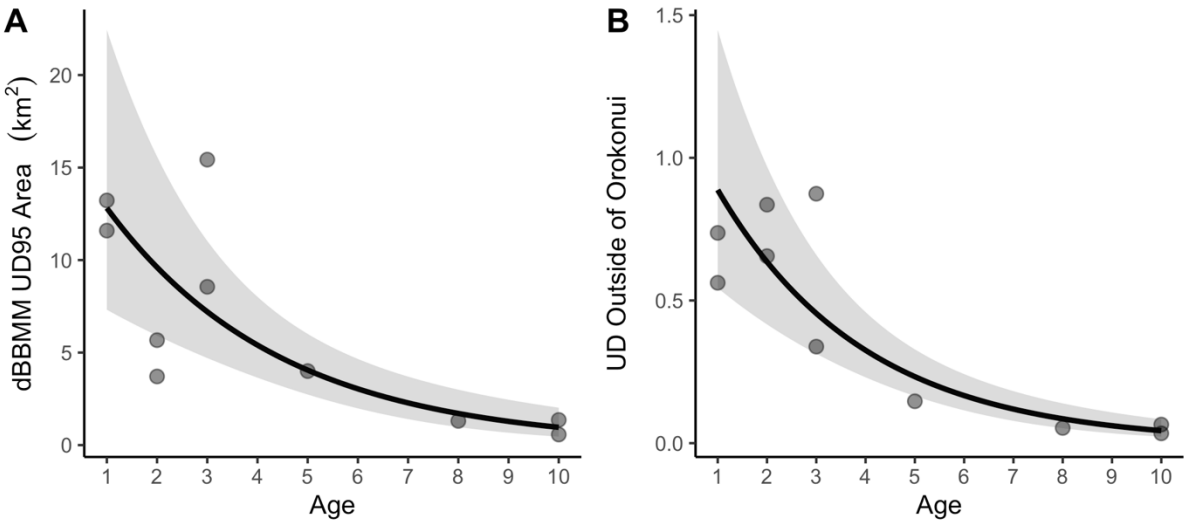

Figure 3: A) Home range area (UD_{95} area) as a function of age for 10 kākā GPS tracked at Ōrokonui Ecosanctuary, New Zealand. Generalised linear model using Gamma distribution with log link was fit with age as a predictor, ribbon is the 95% confidence interval. Pseudo-R^2 based on likelihood ratio = 0.78. B) Proportion of individual utilisation distributions (UD) of kākā that were outside of the Ōrokonui Ecosanctuary fence, as a function of kākā age. Generalised linear model using Gamma distribution with logarithmic link was fit with age as a predictor, ribbon is the 95% confidence interval. Pseudo-R^2 based on likelihood ratio = 0.85.

Temporal space use variability

Space use was most variable for the two juvenile kākā (1-year old), with Bhattacharyya's Affinity (BA) reaching as low as 0.43 and 0.38, whereas the minimum BA of all remaining individuals was 0.76 (Figure 4 and Figure S.5). The large dissimilarities in BA for the juvenile kākā were predominately due to positional changes of the UD_{95} centroid rather than changes in UD_{95} area. The area of every kākā's UD_{95} varied throughout the study period, with differences of 70.4% below average to 120% above average (Figure 5), which led to variable risk exposure through time (Figure S.6). There was also some synchrony as to when UD_{95} area varied within the male and female groups, with females expanding their UD_{95} areas in September before contracting after October, and males expanding their UD_{95} areas after October (Figure 5).

The centroids of the UD_{95} drifted farthest on average for the two juvenile kākā, with average drift distances of 32.3 m and 26.5 m, which decreased significantly with age, reaching a minimum of 4.87 m for a 10-year-old individual ($F_{1,8} = 38.52$, $P < 0.001$, pseudo-$R^2 = 0.81$ – Figure 6 and Figure S.7). There was no discernible population-level trend of space-use drift that might have related to seasonality (Figure 6B).

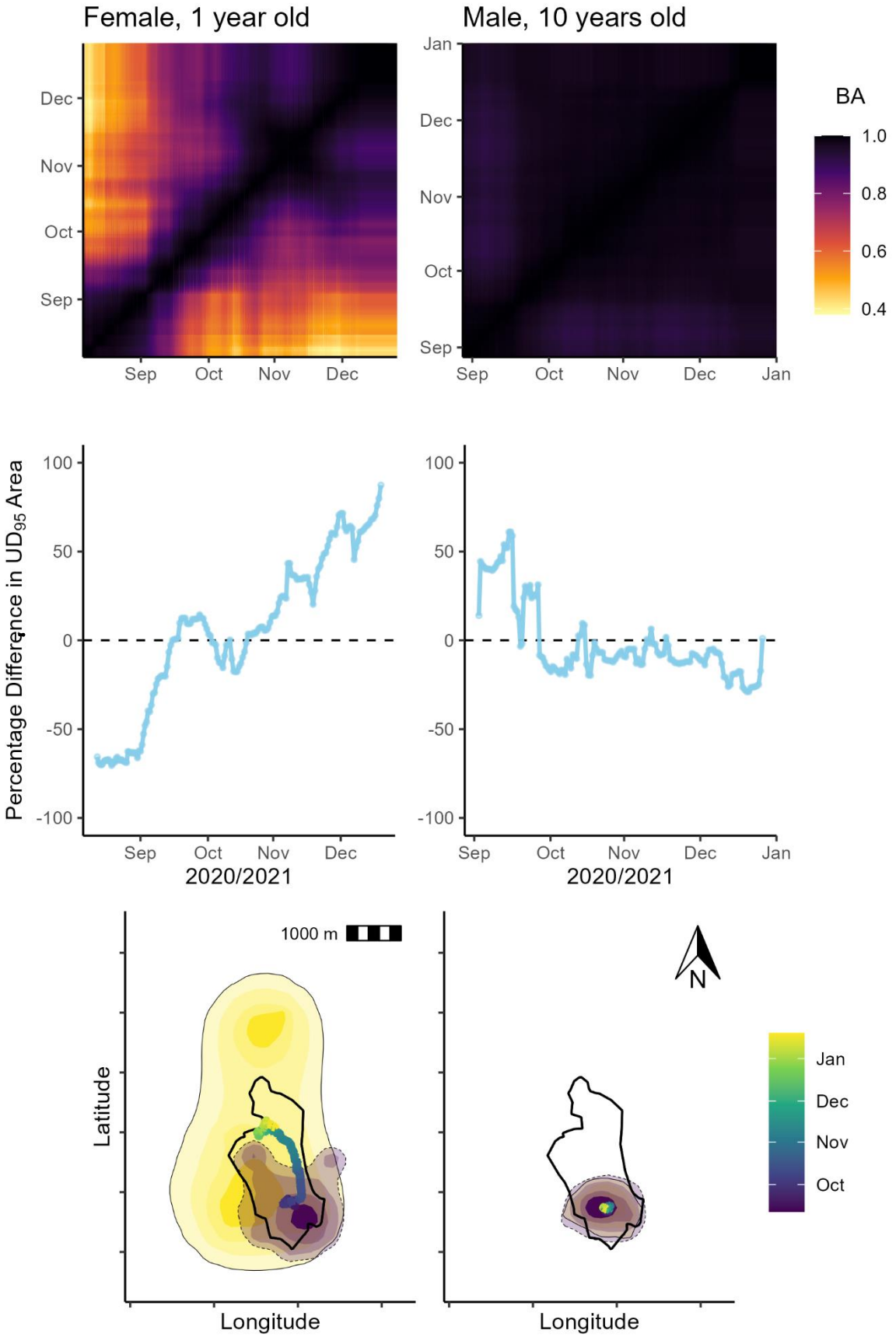
Female, 1 year old
Male, 10 years old
Dec
Nov
Oct
Sep
Jan
Sep
Oct
Nov
Dec
Jan
BA
1.0
0.8
0.6
0.4
Percentage Difference in UD95 Area
100
50
0
-50
-100
2020/2021
1000 m
N
Latitude
Longitude
Jan
Dec
Nov
Oct

Figure 4: The left column represents the temporal space use variability (SUV) of an individual female kākā of age 1 year, and the right column represents the SUV of a 10-year-old male kākā. The upper panels show the similarity matrices of Bhattacharyya's Affinity (BA) throughout the study period. The middle panels show the percentage difference in UD_{95} area compared to each individual's average UD_{95} area for the full study period. The lower panels show the drift of UD_{95} centroid on the same scale, with the colour relating to the time of year (purple to yellow), with the fence of Ōrokonui Ecosanctuary represented as the black outline. The lower panels also show the initial (purple with dashed line) and final (yellow with solid line) UDs for each individual. The scale bar is in 200m increments and is 1000m in total.

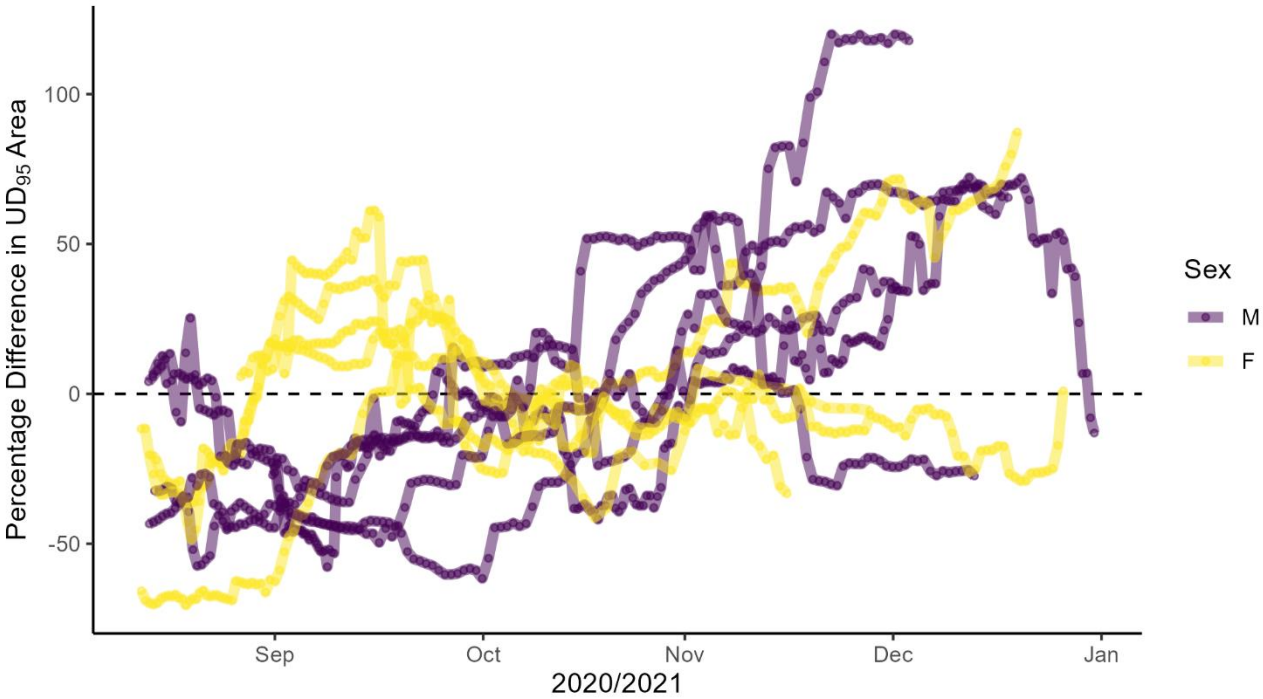

Figure 5: Percentage difference in UD_{95} area compared to average UD_{95} area for each individual kākā tracked at Ōrokonui Ecosanctuary. Positive values are above average UD_{95} area compared to the average UD_{95} area for that individual, whereas negative values are below average. Note the synchrony between females and males as they collectively expanded and contracted their space use, respectively, prior to October. This observed pattern may relate to breeding, which begins to occur around this time for this population.

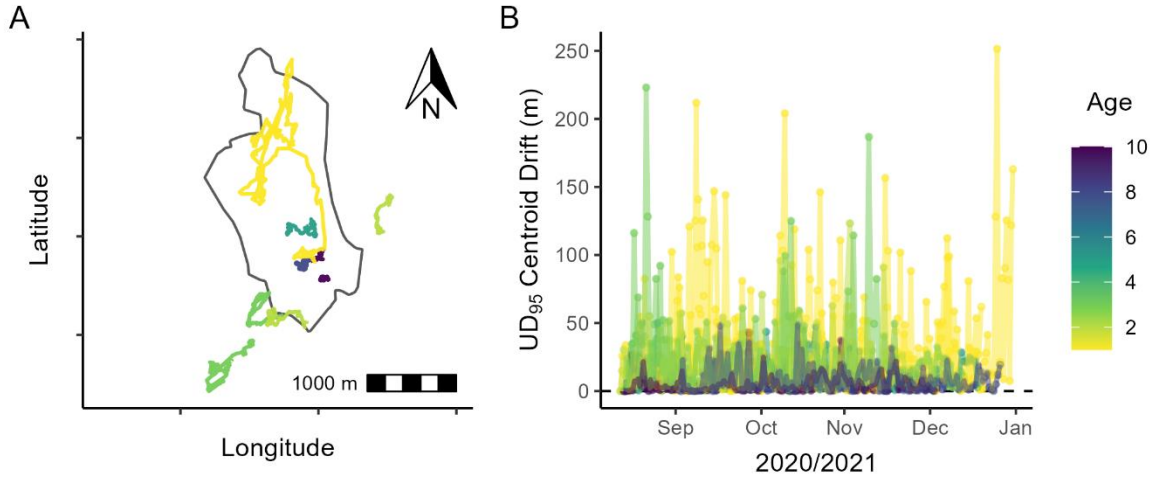

Figure 6: ***A****) Position of the* UD_{95} *centroid for each individual kākā throughout the study period, in relation to age (colour – legend to the right). The fence of Ōrokonui Ecosanctuary is shown in black. The scale bar is in 200m increments and is 1000m in total.* ***B****) Distance between* UD_{95} *centroids from one space use snapshot to the next. There appear to be no discernible temporal trends in space use drift.*

Discussion

In this study, we GPS-tracked kākā (*Nestor meridionalis*) from a reintroduced population to identify individual-level exposure to risk. We estimated their static and temporally dynamic space use and collected information on mortalities over an 18-month period. The home ranges of younger individuals (less than 3 years) were much larger than that of older individuals (up to 27 times as large), and the space use of juvenile kākā (1-year-old) were more temporally variable, with significant shifts of the UD_{95} centroid. We therefore suspect that the larger home ranges of individuals less than 3 years old and more exploratory behaviour of juveniles put these cohorts at higher risk than older individuals due to more time spent outside the reserve. These findings correlate with higher incidental mortality observations of younger individuals, of which the average known age was 1.8 years.

The temporal variability of dynamic space use in juvenile kākā predominately arose from positional changes of the UD_{95} centroid, which was due to the visitation of novel areas that were thereafter visited regularly, which suggests exploratory behaviour followed by exploitation. This pattern may indicate information gathering that may precede dispersal from their natal area (Andreassen, Stenseth, & Ims, 2002; Ronce, 2007), and would provide valuable evidence towards home range establishment, which has not been thoroughly tested empirically.

The age-related differences in home range area may be due to several factors. As shown in previous studies of wild kākā and other bird species, older individuals are typically more neophobic and more efficient foragers, which can limit the need for large home ranges relative to other individuals (Bond & Diamond, 2004; Loepelt, Shaw, & Burns, 2016; Clay et al., 2018; Sherratt & Morand-Ferron, 2018). The exploratory behaviour may be due to the more neophilic behaviours of the juveniles, and the two juveniles tracked were also the only two kākā throughout the study period to consistently visit suburban areas (Forrest, Recio and Seddon, in progress), which may indicate an adaptation to novel resources. The trial-and-error process that leads to foraging innovations and adaptation to novel resources will increase the kākā's exposure to novel risks but will be critical for the population's future success in this fragmented landscape.

Despite clear trends in the age-related difference in home range area and patterns of dynamic space use, we acknowledge the sample size of ten individuals from a single study site may not represent the full breadth of behavioural variability present in this or in other populations. The duration of tracking also did not cover a full year and we may have missed seasonal variation outside of the tracking period. However, the coverage of sex and age groups provided valuable and convincing evidence towards age-related differences in spatial behaviour, and the relatively fine-scale tracking data was important to provide sufficient resolution to estimate temporally variable space use.

Although at least one other method has been developed to assess temporal space use variability with a sweeping window framework (Schlägel et al., 2019), how an animal's space use changes

throughout time and whether this aligns with certain groups has otherwise been given little attention in the literature. We hope to address this by providing an easily applicable and intuitive temporal space use variability estimation framework. Estimating both home ranges and space use variability allowed us to strengthen our understanding of the kākā's spatial behaviours, and in this framework the window width, increment size and statistical space use estimator can be adjusted to suit the data and questions being asked. Reducing the width of the temporal window that controls the number of locations that define the UD can reveal finer scale space use changes; but may make it more difficult to identify persistent space use changes as the stochasticity between snapshots will be greater. Decreasing the number of locations in the increment that the window is swept along by will provide more resolution to identify changes in space use, with the only expense being more computation time. Tracking the area and centroid of the utilisation distribution allows for space use patterns to be identified as the UDs expand, contract, and shift in position, which can allow a multitude of questions about site fidelity, space use patterns, dispersal and exploration to be posed (Börger, Dalziel, & Fryxell, 2008; Kranstauber, Smolla, & Safi, 2016; Kranstauber et al., 2020).

Differences in spatial behaviour could lead to increased risk for certain groups of taxa in conservation reserves, particularly when threats remain in the wider landscape beyond the reserve. In this study, the exposure to presumed risk did not vary substantially between groups throughout time, but this may not be the case if the kākā were tracked for longer, or for other taxa that may have more predictable seasonal behavioural changes. Species that increase their space use area or decrease their site fidelity to develop sufficient condition for breeding or hibernation, or to take advantage of ephemeral resources, may be exposed to greater risk as they venture beyond the boundaries of conservation reserves. Differences in home range sizes between individuals and groups of species has been well studied but understanding which groups or individuals of a species are at the highest risk may assist managements decisions, particularly for planning translocations or reintroductions.

Management Implications

Management of birds and other species of wide-ranging behaviour in conservation reserves should consider differences between groups of individuals that may lead to differential exposure to risk beyond areas of safety. In nearby fragmented landscapes that contain atypical features such as urban areas, infrastructure and exotic predatory species, reintroduced animal species will need to explore and adapt to survive, which could lead to innovations and a greater behavioural repertoire, improving their acquisition of resources and avoidance of threats. This study additionally highlights the importance of appropriate management of threats outside the conservation reserve, particularly for wide-ranging flighted species. We recommend quantifying both home ranges and space use variability to assess and understand the area requirements and space use patterns of individuals, and we provide code and data such that all the analyses and figures in this study can be reproduced.

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Availability of data and materials

The kākā GPS location dataset and all code is available in the GitHub repository [https://github.com/swforrest/kaka_HRandSUV.git]

Conflicts of interest

The authors declare they have no conflicts of interest.

Author contributions

SWF, MRR and PJS conceived the ideas and designed the methodology, SWF developed the idea of temporal space use variability, analysed the data and wrote the manuscript, MRR provided feedback on the data analysis, and all authors contributed critically to the drafts and gave final approval for publication.

References

Aichele, A., Seddon, P., & van Heezik, Y. (2021). Intake of sugar water by kākā in Ōrokonui Eco-sanctuary. *N. Z. J. Ecol.* **45**, 3431.

Alston, J. M., Fleming, C. H., Noonan, M. J., Tucker, M. A., Silva, I., Folta, C., Akre, T. S. B., Ali, A. H., Belant, J. L., Beyer, D., Blaum, N., Böhning-Gaese, K., de Paula, R. C., Dekker, J., Drescher-Lehman, J., Farwig, N., Fichtel, C., Fischer, C., Ford, A. T., Janssen, R., Jeltsch, F., Kappeler, P. M., LaPoint, S. D., Catherine Markham, A., Patricia Medici, E., Morato, R. G., Nathan, R., Olson, K. A., Patterson, B. D., Petroelje, T. R., Ramalho, E. E., Rösner, S., Santos, L. G. O., Schabo, D. G., Selva, N., Sergiel, A., Spiegel, O., Ullmann, W., Zieba, F., Zwijacz-Kozica, T.,

Wittemyer, G., Fagan, W. F., Müller, T., & Calabrese, J. M. (2022, September 30). Clarifying space use concepts in ecology: range vs. occurrence distributions. *bioRxiv*.

Andreassen, H. P., Stenseth, N. C., & Ims, R. A. (2002). Dispersal behaviour and population dynamics of vertebrates. In R. Bullock James, E. Kenward Robert, & S. Hailis Rosie (Eds.), *Dispersal Ecology*. pp. 238–240. Blackwell Science.

Bartoń, K. (2020). MuMIn: Multi-Model Inference.

Beggs, & Wilson. (1987). Energetics of South Island kaka (Nestor meridionalis meridionalis) feeding on the larvae of kanuka longhorn beetles (Ochrocydus huttoni). *N. Z. J. Ecol.* **10**, 143–147.

Bogisch, M., Cree, A., & Monks, J. M. (2016). Short-term success of a translocation of Otago skinks (Oligosoma otagense) to Ōrokonui Ecosanctuary. *N. Z. J. Zool.* **43**, 211–220.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.* **161**, 1–28.

Bond, A., & Diamond, J. (2004). Social play in kaka (Nestor meridionalis) with comparisons to kea (Nestor notabilis). *Behaviour* **141**, 777–798.

Börger, L., Dalziel, B. D., & Fryxell, J. M. (2008). Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecol. Lett.* **11**, 637–650.

Bright, J., Langston, R., Bullman, R., Evans, R., Gardner, S., & Pearce-Higgins, J. (2008). Map of bird sensitivities to wind farms in Scotland: A tool to aid planning and conservation. *Biol. Conserv.* **141**, 2342–2356.

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav. Ecol. Sociobiol.* **65**, 23–35.

Burns, B., Innes, J., & Day, T. (2012). The Use and Potential of Pest-Proof Fencing for Ecosystem Restoration and Fauna Conservation in New Zealand. In M. J. Somers & M. Hayward (Eds.),

Fencing for Conservation: Restriction of Evolutionary Potential or a Riposte to Threatening Processes? pp. 65–90. New York, NY: Springer New York.

Clay, T. A., Pearmain, E. J., McGill, R. A. R., Manica, A., & Phillips, R. A. (2018). Age-related variation in non-breeding foraging behaviour and carry-over effects on fitness in an extremely long-lived bird. *Funct. Ecol.* **32**, 1832–1846.

Dall, S. R. X., Bell, A. M., Bolnick, D. I., & Ratnieks, F. L. W. (2012). An evolutionary ecology of individual differences. *Ecol. Lett.* **15**, 1189–1198.

Dunbar, R. I. M., & Shultz, S. (2007, September 7). Evolution in the social brain. *Science*. American Association for the Advancement of Science.

Dunn, P., & Smyth, G. (2014). Generalized Linear Models. p. 573. Springer New York.

Fieberg, J., & Kochanny, C. O. (2005). Quantifying home-range overlap: The importance of the utilization distribution. *J. Wildl. Manage.* **69**, 1346–1359.

Forrest, S. W., Recio, M. R., & Seddon, P. J. (2022). Moving wildlife tracking forward under forested conditions with the SWIFT GPS algorithm. *Animal Biotelemetry 2022 10:1* **10**, 1–11.

Hanski. (1998). Metapolulation dynamics. *Nature* **396**, 41–49.

Horne, J. S., Garton, E. O., Krone, S. M., & Lewis, J. S. (2007). Analyzing animal movements using Brownian bridges. *Ecology* **88**, 2354–2363.

Innes, J., Fitzgerald, N., Binny, R., Byrom, A., Pech, R., Watts, C., Gillies, C., Maitland, M., Campbell-Hunt, C., & Burns, B. (2019). New Zealand ecosanctuaries: types, attributes and outcomes. *J. R. Soc. N. Z.* **49**, 370–393.

Iwaniuk, A. N., Dean, K. M., & Nelson, J. E. (2005). Interspecific allometry of the brain and brain regions in parrots (psittaciformes): comparisons with other birds and primates. *Brain Behav. Evol.* **65**, 40–59.

Jarvie, S., University of Otago, Recio, M., Adolph, S., Seddon, P., & Cree, A. (2016). Resource selection by tuatara following translocation: a comparison of wild-caught and captive-reared juveniles. *NZ J Ecol* **40**, 334–341.

Johnson, J. B., & Omland, K. S. (2004). Model selection in ecology and evolution. *Trends in Ecology and Evolution*.

Karl, B. J., & Clout, M. N. (1987). An Improved Radio Transmitter Harness with a Weak Link to Prevent Snagging (Nuevo arnés para colocar radiotransmisores en aves). *J. Field Ornithol.* **58**, 73–77.

Kernohan, B. J., Gitzen, R. A., & Millspaugh, J. J. (2001). Analysis of animal space use and movements. In *Radio Tracking and Animal Populations*. pp. 125–166. Elsevier.

Kie, J. G., Matthiopoulos, J., Fieberg, J., Powell, R. A., Cagnacci, F., Mitchell, M. S., Gaillard, J.-M., & Moorcroft, P. R. (2010). The home-range concept: are traditional estimators still relevant with modern telemetry technology? *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365**, 2221–2231.

Kranstauber, B., Gall, G. E. C., Vink, T., Clutton-Brock, T., & Manser, M. B. (2020). Long-term movements and home-range changes: Rapid territory shifts in meerkats. *J. Anim. Ecol.* **89**, 772–783.

Kranstauber, B., Kays, R., Lapoint, S. D., Wikelski, M., & Safi, K. (2012). A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *J. Anim. Ecol.* **81**, 738–746.

Kranstauber, B., Smolla, M., & Safi, K. (2016). Similarity in spatial utilization distributions measured by the earth mover's distance. *Methods in Ecology and Evolution*.

Lesmerises, R., & St-Laurent, M.-H. (2017). Not accounting for interindividual variability can mask habitat selection patterns: a case study on black bears. *Oecologia* **185**, 415–425.

Loepelt, J., Shaw, R. C., & Burns, K. C. (2016). Can you teach an old parrot new tricks? Cognitive development in wild kaka (Nestor meridionalis). *Proc. Biol. Sci.* **283**.

Merrick, M. J., & Koprowski, J. L. (2017). Should we consider individual behavior differences in applied wildlife conservation studies? *Biol. Conserv.* **209**, 34–44.

Moorhouse. (1997). The diet of the North Island kaka (Nestor meridionalis septentrionalis) on Kapiti Island. *N. Z. J. Ecol.* **21**, 141–152.

Moorhouse, & Greene. (1995). Identification of Fledgling and Juvenile Kaka (Nestor meridionalis). *Notornis* **42**, 187–196.

Moorhouse, R. J., Sibley, M. J., Lloyd, B. D., & Greene, T. C. (2008). Sexual dimorphism in the North Island Kaka Nestor meridionalis septentrionalis: selection for enhanced male provisioning ability? *Ibis* **141**, 644–651.

Muralidhar, A., Moore, F. L., Easton, L. J., Jamieson, I. G., Seddon, P. J., & van Heezik, Y. (2019). Know your enemy? Conservation management causes loss of antipredator behaviour to novel predators in New Zealand robins. *Anim. Behav.* **149**, 135–142.

O'Donnell, C. F. J., & Rasch, G. (1991). Conservation of kaka in New Zealand : a review of status, threats, priorities for research and implications for management. Wellington: Department of Conservation.

Phillips, R. A., Lewis, S., González-Solís, J., & Daunt, F. (2017). Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. *Mar. Ecol. Prog. Ser.* **578**, 117–150.

Reader, S. M., & Laland, K. N. (2002). Social intelligence, innovation, and enhanced brain size in primates. *Proc. Natl. Acad. Sci. U. S. A.* **99**, 4436–4441.

Recio, M. R., Payne, K., & Seddon, P. J. (2016). Emblematic forest dwellers reintroduced into cities: resource selection by translocated juvenile kaka. *Curr. Zool.* **62**, 15–22.

Ronce, O. (2007). How does it feel to be like a Rolling Stone? Ten questions about dispersal evolution. *Annu. Rev. Ecol. Evol. Syst.* **38**, 231–253.

Schlägel, U. E., Signer, J., Herde, A., Eden, S., Jeltsch, F., Eccard, J. A., & Dammhahn, M. (2019). Estimating interactions between individuals from concurrent animal movements. *Methods in Ecology and Evolution* **10**, 1234–1245.

Sherratt, T. N., & Morand-Ferron, J. (2018). The adaptive significance of age-dependent changes in the tendency of individuals to explore. *Anim. Behav.* **138**, 59–67.

Shimada, T., Jones, R., Limpus, C., & Hamann, M. (2012). Improving data retention and home range estimates by data-driven screening. *Mar. Ecol. Prog. Ser.* **457**, 171–180.

Shimada, T., Limpus, C., Jones, R., Hazel, J., Groom, R., & Hamann, M. (2016). Sea turtles return home after intentional displacement from coastal foraging areas. *Mar. Biol.* **163**, 8.

Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P., & Lefebvre, L. (2005). Big brains, enhanced cognition, and response of birds to novel environments. *Proc. Natl. Acad. Sci. U. S. A.* **102**, 5460–5465.

Stark, D. J., Vaughan, I. P., Ramirez Saldivar, D. A., Nathan, S. K. S. S., & Goossens, B. (2017). Evaluating methods for estimating home ranges using GPS collars: A comparison using proboscis monkeys (Nasalis larvatus). *PLoS One* **12**, e0174891.

Stuber, E. F., Carlson, B. S., & Jesmer, B. R. (2022). Spatial personalities: a meta-analysis of consistent individual differences in spatial behavior. *Behav. Ecol.* **33**, 477–486.

Tanentzap, A. J., & Lloyd, K. M. (2017). Fencing in nature? Predator exclusion restores habitat for native fauna and leads biodiversity to spill over into the wider landscape. *Biol. Conserv.* **214**, 119–126.

Van Winkle, W. (1975). Comparison of Several Probabilistic Home-Range Models. *J. Wildl. Manage.* **39**, 118–123.

Weinstein, B. G., Double, M., Gales, N., Johnston, D. W., & Friedlaender, A. S. (2017). Identifying overlap between humpback whale foraging grounds and the Antarctic krill fishery. *Biol. Conserv.* **210**, 184–191.

Wilson, P. R., Karl, B. J., Toft, R. J., Beggs, J. R., & Taylor, R. H. (1998). The role of introduced predators and competitors in the decline of Kaka (Nestor meridionalis) populations in New Zealand. *Biol. Conserv.* **83**, 175–185.ŌrokonuiŌrokonui