

# rKIN: Kernel-based method for estimating isotopic niche size and overlap

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Handling Editor: Andrew Jackson

## Abstract

1. The isotopic niche of consumers represents biologically relevant information on resource and habitat use. Several tools have been developed to quantify niche size and overlap. Nonetheless, methods adapted by spatial ecologists to quantify animal home ranges can be modified for use in stable isotope ecology when data are not normally distributed in bivariate space.
2. We offer a tool that draws on existing spatial metrics, such as minimum convex polygon (MCP) and standard ellipse area (SEA), and add novel metrics using kernel utilization density (KUD) estimators to measure isotopic niche size and overlap. We present examples using empirical and simulated data to demonstrate the performance of the package kernel isotopic niches in R (rKIN) under various scenarios.
3. Results of niche size from MCP, SEA and KUD were highly correlated but divergent among datasets. Overall, the KUD method produced the largest niche sizes and was more sensitive to the distribution of the isotopic data. Pairwise estimates of overlap were highly variable, likely because MCP and SEA inherently include or exclude unused areas in the resulting niche estimate. Four bandwidth methods (reference, normal scale, plug-in and biased cross-validation) produced comparable estimates of niche size and overlap at various sample sizes (10–40). Niche size and overlap were consistent across sample sizes >15.
4. Use of rKIN will allow isotope ecologists to quantify niche shifts, expansions or contractions, as well as assess the performance of several estimation methods. The package also can be applied to other data types (e.g. principal component analysis, multi-dimensional scaling) so long as axes and measurement units are identical and can be converted to Cartesian coordinates.

## KEYWORDS

kernel utilization density, niche overlap, stable isotope analysis, trophic niche

## 1 | INTRODUCTION

The use of stable isotope data to represent the dietary niches, as well as niche overlap, of animals has increased dramatically in recent years (Flaherty & Ben-David, 2010; Newsome, Martínez del Rio, Bearhop, & Phillips, 2007; Stewart, Bowyer, Kie, Dick, & Ben-David, 2003). Incorporating stable isotope ratios (typically of carbon [ $\delta^{13}\text{C}$ ] and nitrogen [ $\delta^{15}\text{N}$ ]) from diet into consumer tissues can be complicated and dependent on multiple ecological, behavioural and physiological processes (Ben-David & Flaherty, 2012; Martínez del Rio & Carleton, 2012). For example, assimilation of dietary nitrogen into proteinaceous tissues (blood cells, muscle, liver) can be regulated by the similarity in amino-acid composition of the food and the consumer (Ben-David, Newsome, & Whiteman, 2012; Robbins, Felicetti, & Florin, 2010) or growth rate of the animal (Carleton, Kelly, Anderson-Sprecher, & Martínez del Rio, 2008). Similarly, deuterium ( $\delta\text{D}$ ) in bird feathers depends on the relative assimilation of drinking and food-derived water (Wolf, Bowen, & Martínez del Rio, 2011).

Nonetheless, comparisons of the distribution of consumer isotopic signatures, where food and water resources are shared, can provide powerful insights into multiple ecological processes (Bearhop, Adams, Waldron, Fuller, & Macleod, 2004; Newsome et al., 2007). Although the isotopic niche mostly corresponds to a portion of the ecological niche of organisms, these variables represent patterns of resource and habitat use (Flaherty & Ben-David, 2010; Rader et al., 2017). Therefore, similar to more classical variables, isotopic data can be used to define niche hypervolumes and assess overlap in resource requirements (Hutchinson, 1957; Newsome et al., 2009; Newsome, Yeakel, Wheatley, & Tinker, 2012). For example, American and Pacific golden plovers *Pluvialis dominica* and *Pluvialis fulva*, respectively co-nesting on the Seward Peninsula in Alaska exhibited highly divergent sizes of isotopic niches ( $\delta\text{D}$ ,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ), with that of *P. fulva* nearly completely encompassed by *P. dominica* (Rocque, Ben-David, Barry, & Winker, 2006). Rader et al. (2017) reported a positive correlation between the breadth of elevational range (measured via  $\delta\text{D}$  and  $\delta^{18}\text{O}$ ) and diversity of diets and habitats (measured via  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) used by *Cinclodes* birds in South America. Using  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, Karlson, Gorokhova, and Elmgren (2015) determined that the non-native *Marenzelleria arctica* has occupied a previously vacant ecological niche in the Baltic Sea. More recently, Eckrich, Flaherty, and Ben-David (2018) demonstrated that a dietary shift (based on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) in dusky shrews *Sorex monticolus* in Southeast Alaska following a population crash of Keen's mice *Peromyscus keeni* resulted in the shrews exploiting resources previously used by their competitors.

Several approaches to infer isotopic niche size and overlap have been proposed. Bearhop et al. (2004) proposed that the variance of stable isotope values could be used as a measure of niche size and compared among groups of individuals, populations or species using simple *F* tests. This concept was expanded by Layman, Arrington, Montaña, and Post (2007), who suggested additional spatial metrics to quantify the niche of a group of organisms. These metrics included the convex hull area (TA: the smallest convex hull area [or

minimum convex polygon (MCP)] encompassed by the data points) and the mean nearest neighbour distance (MNND). Nonetheless, Hoeinghaus and Zeug (2008) argued that when comparing among sites with divergent resource availability, some metrics might be biased unless such variation was considered. As an alternative to MCP, which is sensitive to sample size and outliers, Jackson, Inger, Parnell, and Bearhop (2011) proposed use of the standard ellipse area (SEA) to define the isotopic niche. In the associated R package SIBER, Jackson et al. (2011) provide traditional and Bayesian approaches to calculate the size of the standard ellipse while accounting for sample size effects. The package also produces estimates of sampling error. Indeed, most current studies of dietary specialization, niche partitioning and competition among individuals, populations and species rely on MCP and SEA techniques to delineate isotopic niche estimates (Botta et al., 2017; Galetti, Rodarte, Neves, Moreira, & Costa-Pereira, 2016; Gallagher, Shiffman, Byrnes, Hammerschlag-Peyer, & Hammerschlag, 2017; Staudinger, McAlarney, McLellan, & Pabst, 2014; but see Sepulveda, Lowe, & Marra, 2012).

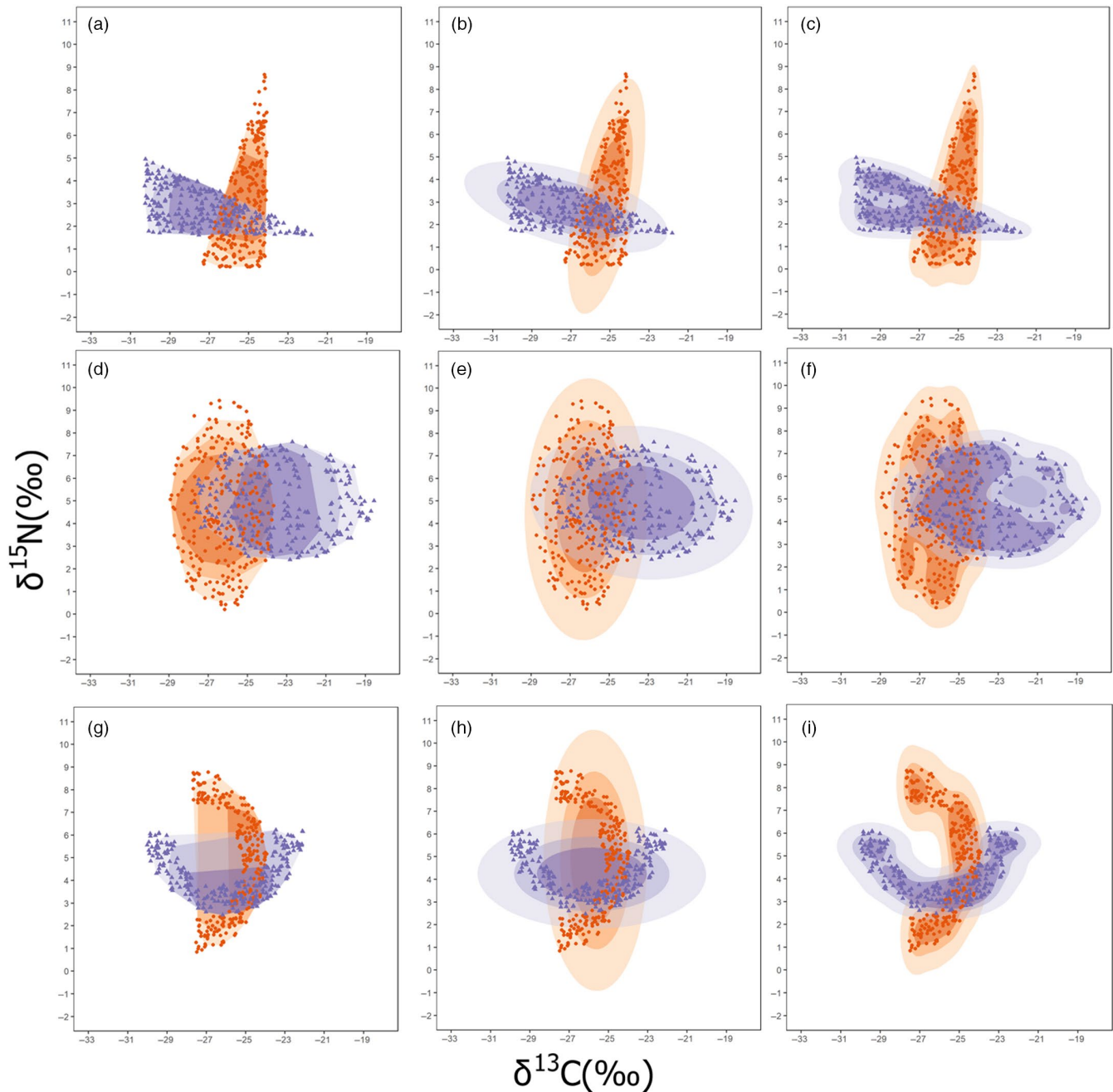
Development of the MCP and SEA isotopic niche tools mimics the past progression of advances in the estimation of animal home-range size (Worton, 1987). Therefore, modern statistical methods adapted by spatial ecologists to quantify animal home ranges could be modified for use in stable isotope ecology. Kernel-based methods are distinguished among non-mechanistic estimators because they are free of the influences of grid size and placement. These metrics are also less sensitive to extreme values, perform well with multimodal data and can provide estimates based on specified contours (Börger et al., 2006; Seaman et al., 1999). Kernel-based metrics require the identification of geographic coordinates from animal relocations. Similarly, such tools can be applied to any observations where data are equally spaced in all dimensions. Therefore, the application of kernel estimators to isotopic bivariate space, both measured as parts per thousand (‰), is evident.

Herein, we repurpose kernel utilization density (KUD) estimators into a set of isotopic niche metrics that complement those developed by Layman et al. (2007) and Jackson et al. (2011). We offer a tool that draws on existing spatial metrics, such as MCP and SEA, and propose additional novel metrics using KUD (Figure 1). This new method is presented in detail here and has been made available via the package kernel isotopic niches in R (rKIN; <https://github.com/salbeke/rKIN>). Finally, we compare our new KUD metrics to existing methods using both empirical (Eckrich et al., 2018; Flaherty, Noakes, & Ben-David, 2014) and simulated (Flaherty & Ben-David, 2010) data to investigate their requirements and performance in exploring niche size and overlap.

## 2 | MATERIALS AND METHODS

### 2.1 | Models of niche size

rKIN offers three options to estimate niche size: MCP, SEA and KUD. MCP is created by connecting the minimum number of points



**FIGURE 1** Niche size and overlap for three sets of simulated data using the estimation methods. The rows represent the different datasets (triangle, ellipse and crescent), while the columns represent the estimation methods (minimum convex polygon [MCP], standard ellipse area [SEA] and kernel utilization density [KUD]). The right triangle has the highest correspondence with MCP (a, d, g). The ellipse shows highest correspondence with SEA (b, e, h), and the crescent is best represented via KUD (c, f, i). The two polygons for each shape contain 250 randomly placed points and are oriented perpendicular to each other

in bivariate space that enclose the remaining data. The Euclidean distance of each observation to the centroid (mean  $x$  and  $y$ ) is estimated, and the quantile values for selected contours (e.g. 0.95 or 95%, 0.75 or 75%, 0.50 or 50%) are the estimate of niche size without accounting for uncertainty (Equation S1). This method is sensitive to the number of samples; polygon area usually increases with sample size (Jackson et al., 2011; Syväranta, Lensu, Marjomäki, Oksanen, & Jones, 2013). Outliers or other extreme data points can significantly

influence the MCP by including unused areas. Also, MCP does not account for the density of points (assuming uniform distribution) and therefore does not naturally identify core areas. Comparisons among populations, communities and species with different sample sizes may result in bias and are likely invalid.

The SEA is described by its centre (i.e. the means of  $x$  and  $y$ ) and the eigenvalues and eigenvectors of its covariance matrix (Jackson et al., 2011). The ellipse radii are calculated as the square root of the quantile

value for a selected confidence level from a  $\chi^2$  distribution with 2 degrees of freedom (Equation S2). The resulting ellipse is the SEA estimate of niche size. The niche shape is always elliptical and therefore may include unused or exclude used areas. SEA assumes that organisms forage randomly within their environment yielding isotopic data that are independently and normally distributed in multivariate space. Such an assumption is appropriate for some data (Inger et al., 2006), but many natural systems are prone to non-normality (Flaherty & Ben-David, 2010; Flaherty, Ben-David, & Smith, 2010). The SEA is not as sensitive to sample size as MCP, but is less precise with low sample sizes ( $n < 30$ ; Jackson et al., 2011; Syväranta et al., 2013). Nonetheless, given a sufficient number of samples, the SEA method offers a more robust estimation technique than MCP when sample sizes differ among groups.

The kernel density function is generated by summing two separate kernel functions ( $x$  and  $y$ ), placed over an observed data point (Venables & Ripley, 2002). The KUD is estimated across a regular network of equally spaced points, with the extent (min/max  $x$  and  $y$ ) of the grid larger than that of the observations (Equations S3 and S4). In rKIN, the default kernel is derived based on the assumption of a fixed normal reference bandwidth as described in Venables and Ripley (2002; eq. 5.5). The KUD estimate is then the minimum size that includes a given percentage of the estimated utilization distribution. KUD estimates rely on independence of data points but are largely free from distributional assumptions (see Supporting Information). Also, the KUD estimate is less sensitive to outliers while still considering extreme points as part of the overall distribution (Seaman et al., 1999). The animal home-range literature suggests that a minimum of 30 samples (but preferably  $\geq 50$ ) are necessary for accurate KUD better delineated the bivariate distribution of data estimates (Seaman et al., 1999), but see Silverman (1986) and our results for lower values.

## 2.2 | rKIN metrics

The first of the two rKIN metrics measures the extent of spacing within the bivariate isotopic space and represents niche size. The second reflects the position of species, populations or groups of individuals relative to each other and represents dietary overlap. The size of the niche as measured by MCP, SEA and KUD in bivariate space represents a measure area encompassed by the contours of a particular per cent of data (e.g. 50%, 75%, 95%). Overlap is defined as the size of the overlapping region between niche A and niche B divided by the total niche size of B (and vice versa). Within rKIN, overlap can be calculated for all pairwise comparisons using each of the niche estimators and at each contour level.

## 2.3 | Known shapes

To assess the performance of the three estimators in relation to the bivariate distribution of data, we created the following set of shapes: a right triangle (highest correspondence with MCP), an ellipse (highest correspondence with SEA) and a crescent (best represented via KUD;

Figure 1). For each shape, we created two polygons representing the niche boundaries of two hypothetical species, oriented perpendicular to each other. The target overlap of 0.20 was specific to each known shape at the 50% contour. We randomly placed 250  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  points within each polygon and estimated niche size using MCP, SEA and KUD at 50%, 75% and 95% contours. We then calculated the overlap of area for each pair of shapes for each group. We evaluated whether the difference in niche size and overlap estimates were consistent among the three methods using regression analyses.

## 2.4 | Simulated data

To test the sensitivity of each niche estimator in quantifying overlap, we generated random  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  data points for a single group (group 1), using the mean and standard deviation (SD) of empirical data for Keen's mice and dusky shrews published by Eckrich et al. (2018). Both species were sampled over the course of 3 years (2010–2012) in 21 grids on the northern part of Prince of Wales Island, Southeast Alaska. Isotopic data for individuals (derived from whole blood and muscle samples) were separated into two groups representing animals sampled during 2010–2011 (280 mice and 231 shrews) when mice densities were high, and in 2012 following a crash of the mouse population (21 mice and 64 shrew samples; Figure 2; Eckrich et al., 2018).

Using the distributional pattern of these data, we generated simulated data using a gamma distribution with the shape defined as:

$$\alpha = \left( \frac{\text{mean}}{\text{SD}} \right)^2, \quad (1)$$

and the scale defined as:

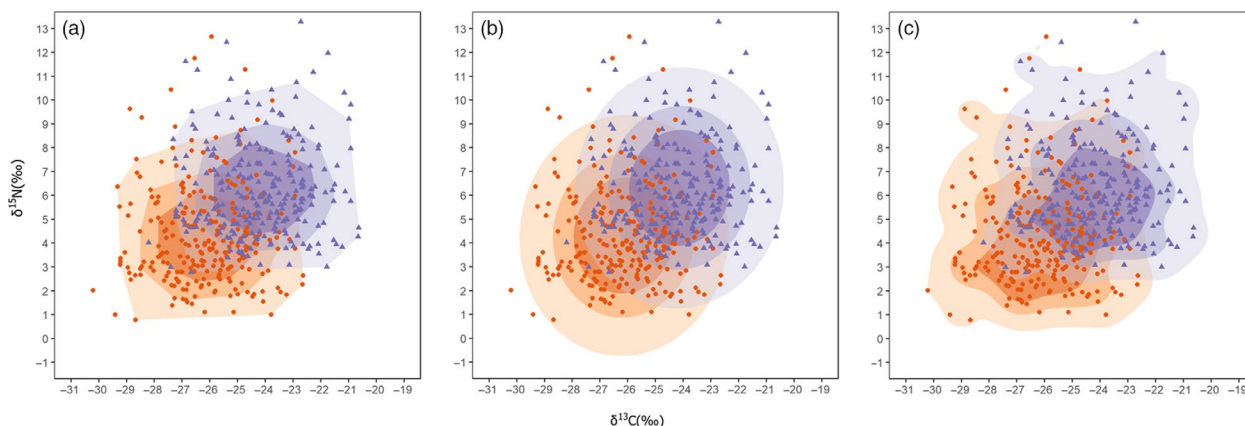
$$\beta = \left( \frac{\text{SD}^2}{\text{mean}} \right). \quad (2)$$

The gamma distribution allowed us to model extreme data points (a tail) while accounting for the continuous distribution of the isotopic data. We then generated a second group (group 2) of data by offsetting group 1 values on the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  axes by an additive static quantity. For shrews, we offset group 2 values by 0.5, 1 and 1.6‰ on the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  axes, and for mice by 1, 2 and 3.2‰. These values were chosen with 95% MCP contours to create an approximate niche overlap between the two groups of 0.75, 0.5 and 0.25, respectively (Figure 2). Each iteration of the simulation followed these steps: (a) generate 250 random  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values using a gamma distribution for group 1; (b) create group 2 and offset it relative to group 1 using one of the three static values; (c) estimate the niche size for both groups using MCP, SEA and KUD at 50%, 75% and 95% contours; and (d) calculate the amount of overlap between the two groups with each method. This process was repeated 10,000 times for each offset value and each species. The quantiles (2.5%, 50% and 97.5%) of niche overlap were calculated from the 10,000 iterations.

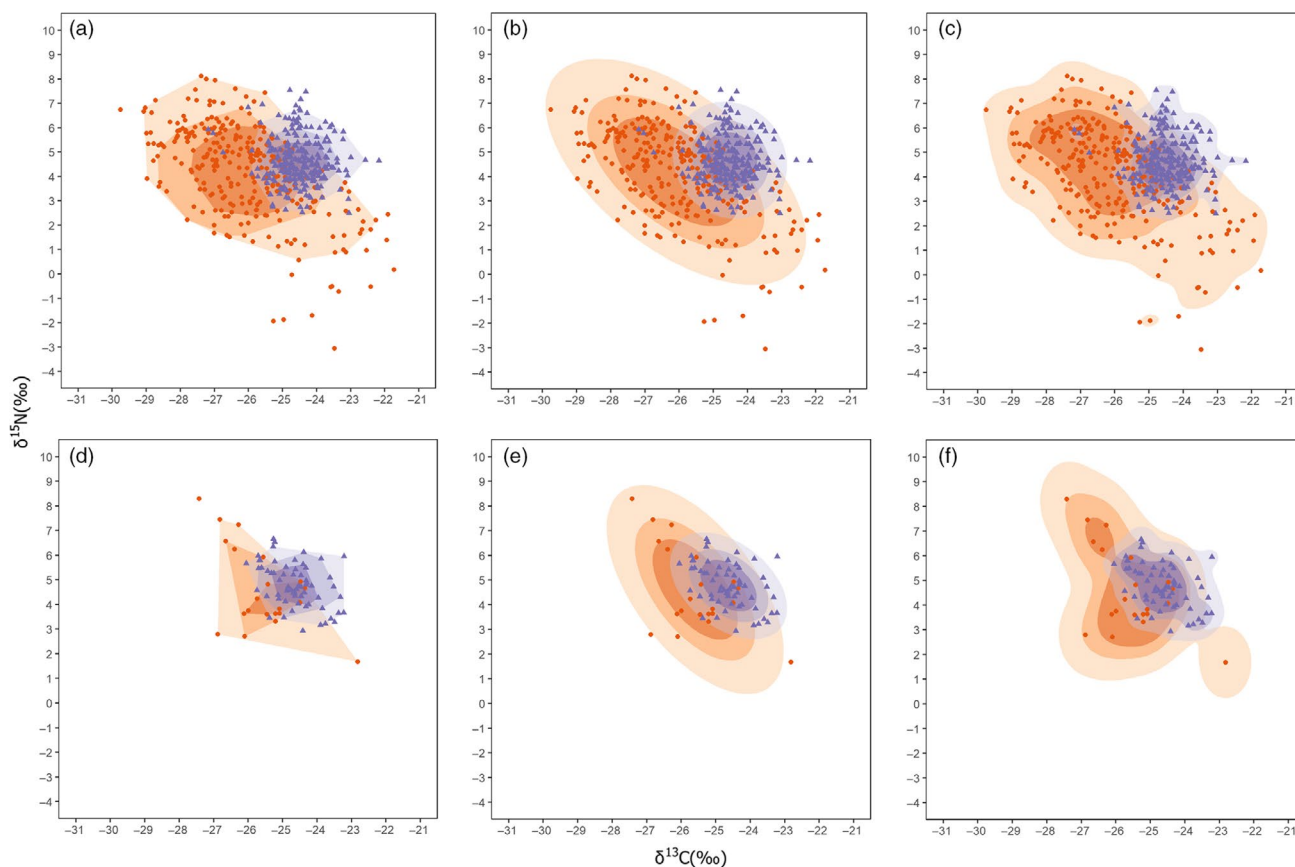
## 2.5 | Testing performance with case studies

We illustrate the performance of rKIN niche metrics using the empirical data collected from Keen's mice and dusky shrews from Southeast

Alaska (Figure 3; Eckrich et al., 2018) and two populations of least chipmunks *Tamias minimus* from the Laramie Range of Wyoming (Figure 4; Flaherty et al., 2014). Least chipmunks were live-trapped twice in 2013 in both forest and sagebrush habitats (spring: 25 forest

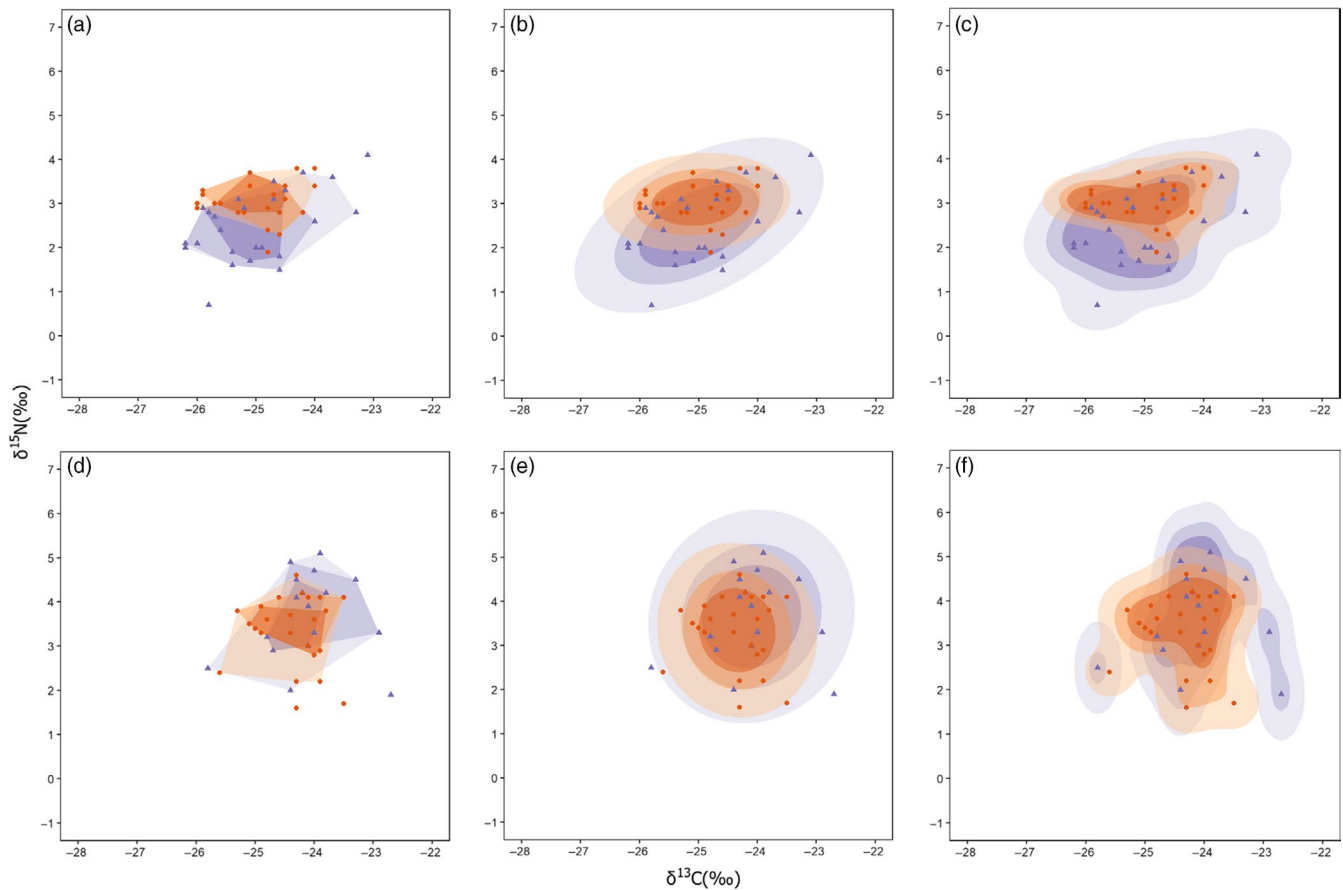


**FIGURE 2** An example of offsetting group 2 (purple) relative to group 1 (orange) for data simulated based on isotopic values from Keen's mice *Peromyscus keeni* and dusky shrews *Sorex monticolus* from Prince of Wales Island, Southeast Alaska, in 2010–2011 (Eckrich et al., 2018). In this analysis, 250 random  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were generated using a gamma distribution for group 1. A second group was then created and placed such that the overlap between them was 0.50 at the 95% minimum convex polygon (MCP) contour. This was repeated with offsets that created an overlap of 0.25 and 0.75. Niche size and overlap for all scenarios were calculated using MCP, standard ellipse area and KUD at 50%, 75% and 95% contours (Table 2)



**FIGURE 3** Isotopic niche data for Keen's mice (orange) and dusky shrews (purple) from Prince of Wales Island, Southeast Alaska, during 2010–2011 (top) and 2012 (bottom). Estimates were generated for each contour level (e.g. 50%, 75% and 95%) with each of three estimators: minimum convex polygon (a, d), standard ellipse area (b, e) and kernel utilization density (c, f)





**FIGURE 4** Isotopic niche data for least chipmunks *Tamias minimus* sampled in 2013 from forest (top) and sagebrush (bottom) habitats in spring (orange) and autumn (purple) in Wyoming. Size and overlap estimates were generated for 50%, 75% and 95% contour levels with MCP (a, d), standard ellipse area (b, e) and kernel utilization density (c, f)

and 17 sagebrush chipmunks, and autumn: 24 forest and 25 sagebrush). These represent a dataset that is nearly normally distributed (mice and shrews) and one that is not (chipmunks) and thus offer an assessment of the value of each method in estimating niche size and overlap. See Eckrich et al. (2018) and Flaherty et al. (2014) for details on sampling design, tissue collection and preparation, isotopic analyses and modelling.

## 2.6 | Sample size and bandwidth

Kernel utilization density estimates are sensitive to the selected bandwidth (or smoothing parameter; a value that determines the size and shape of the kernel) method and sample size (Gitzen, Millsaugh, & Kernohan, 2006; Horne & Garton, 2006; Kie, 2013). To assess effects of sample size and bandwidth on the performance of the KUD estimator in rKIN, we randomly selected 10, 20, 30 and 40 data points from 50 points per group from a simulated dataset published by Flaherty and Ben-David (2010). The simulated isotopic data represent the behaviour of 150 American Kestrels *Falco sparverius* foraging on five types of macroinvertebrates in three habitat types (old-growth, young-growth and clear-cut stands) in Southeast Alaska. Flaherty and Ben-David (2010) modelled four

foraging scenarios of which we selected the dietary and habitat specialist case ( $D_s H_s$ , Model 3). We use this example because it represents results of known foraging decisions by the simulated Kestrels of three groups and provides sufficiently large sample size from which to subsample (the comparisons of niche size and overlap for the full dataset using MCP, SEA and KUD are presented in the Supporting Information).

We tested the effects of six different bandwidth estimators available in two R packages (Duong, 2018; Venables & Ripley, 2002): the reference bandwidth (ref) found in MASS, and the normal scale (hns), plug-in (hpi), smoothed cross-validation (hscv), least-squares cross-validation (hls cv) and biased cross-validation (hbcv) bandwidths available in ks. The reference (ref) method is calculated based on the assumption that each kernel is normally distributed in bivariate space (Gitzen et al., 2006). The normal scale parameter (hns) is derived from the ref estimator through multiplication by a fixed scalar selected prior to analysis (Gitzen et al., 2006). In contrast, the plug-in (hpi) estimator relies on an iterative process in which initial (pilot) values are arbitrarily selected and then modified based on the distribution of data until an optimal bandwidth is calculated (Gitzen et al., 2006). Both smoothed cross-validation (hscv) and the least-squares cross-validation (hls cv) methods are based on the difference between the true and estimated distribution of the

data and are calculated by minimizing the integrated square error between them, although the hscv method employs an iterative process similar to hpi (Bauder et al., 2015). Finally, the hbcv is based on a biased-random-bridge algorithm (Duong, 2018). This method accounts for sequential acquisition of data (e.g. animal movement trajectories). Thus, this method is less applicable to estimates of niche size and overlap from stable isotope data, although this approach may be useful when investigating sequential changes in niche size and overlap over time.

For each sample size and bandwidth combination per habitat and the three contours (216 scenarios), we calculated the niche size and overlap and repeated the analyses 10 times to produce a mean and 95% confidence intervals (CI). We used these metrics to compare among the various scenarios and included several options for user-selected bandwidths in rKIN. Finally, to derive an empirical recommendation for minimum sample size required for KUD analyses, we subsampled the same kestrel dataset with 12, 15 and 17 points. We calculated niche size and overlap and determined the sample size at which these metrics and associated confidence intervals did not change.

### 3 | RESULTS

#### 3.1 | Known shapes

As expected, size estimates for the three shapes were lowest with their corresponding method, except for the ellipse with SEA at 95% contour and the MCP with the crescent (Figure 1; Table 1). The SEA estimator yielded larger sizes in all but the 50% triangle. Overlap estimates varied with contour level, shape and method, but were consistently higher with both MCP and SEA for the crescent shape (Figure 1; Table 1). In this shape, both methods included unused areas inflating overlap estimates.

#### 3.2 | Simulated data

Little correspondence existed between simulated and calculated niche overlap values at 50% and 75% contours for all three estimators (Table 2). Also, the quantile range of 10,000 simulations relative to the mean was generally larger at lower contours (Table 2), likely because we simulated the overlap based on the 95% level and because of the random placement of points in each iteration.

Niche overlap estimates derived from SEA and KUD (Figure 5) were consistently higher for both randomly generated datasets (16.1% and 29.4% for the shrews-based data and 31.2% and 36.9% for the mice-based data) than those stemming from MCP (Table 2). As a result, KUD overlap estimates for the shrews-based dataset were on average 1.48 times higher from MCP than those generated by SEA. These estimates were similar (mean 1.00) in the mice-based dataset (Table 2).

#### 3.3 | Case studies

Results from the three methods were highly correlated but divergent for all datasets (Figures 5 and 6). Highest among-methods correspondence occurred at the 50% contour. Overall, the KUD method produced estimates of niche size that were 0%–17% larger than those derived from SEA, because the former encompasses areas associated with points that fall outside the bivariate normal space (Figures 3 and 4). On several occasions, SEA estimates were larger (e.g. sagebrush chipmunks in spring; Figure 6; Figure S1). This outcome likely occurs when the distribution of isotopic data is irregular and disjointed, and unused areas are encompassed within the ellipse. MCP estimates for the same contour level were consistently lower than KUD and SEA. Although all methods described the differences and temporal changes in niche size, KUD was more sensitive to the bivariate distribution of points. This

**TABLE 1** Comparison of estimates of isotopic niche overlap from minimum convex polygon (MCP), standard ellipse area (SEA) and kernel utilization density (KUD) for 250 random  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values generated in three shapes: triangle, ellipse and crescent

Shape	Method	Group 1 size			Group 2 size			Overlap		
		50%	75%	95%	50%	75%	95%	50%	75%	95%
Triangle	MCP	7.2	10.8	13.2	7.0	10.4	13.5	<b>0.21</b>	0.25	0.27
	SEA	6.2	12.5	27.0	6.4	12.9	27.9	0.22	0.31	0.35
	KUD	7.8	13.6	23.7	8.2	13.8	23.6	0.15	0.24	0.30
Ellipse	MCP	18.2	26.6	33.2	16.6	26.9	33.9	0.29	0.40	0.42
	SEA	13.2	26.5	57.2	14.1	28.1	60.8	<b>0.20</b>	0.39	0.55
	KUD	18.6	30.5	49.1	19.0	34.0	50.1	0.40	0.43	0.48
Crescent	MCP	7.4	17.8	21.2	7.3	17.3	21.0	0.40	0.61	0.56
	SEA	11.0	21.9	47.4	10.2	20.4	44.1	0.49	0.50	0.50
	KUD	9.4	17.3	31.1	8.9	16.2	29.6	<b>0.20</b>	0.23	0.33

*Note:* The two groups were displaced by the same value and angle to overlap at 0.2 at the 50% contour (bolded values). Niche size and overlap were calculated using MCP, SEA and KUD at 50%, 75% and 95% contours. Because each set of two groups is identical, only one value of overlap is reported. See Figure 1 for shape placements.

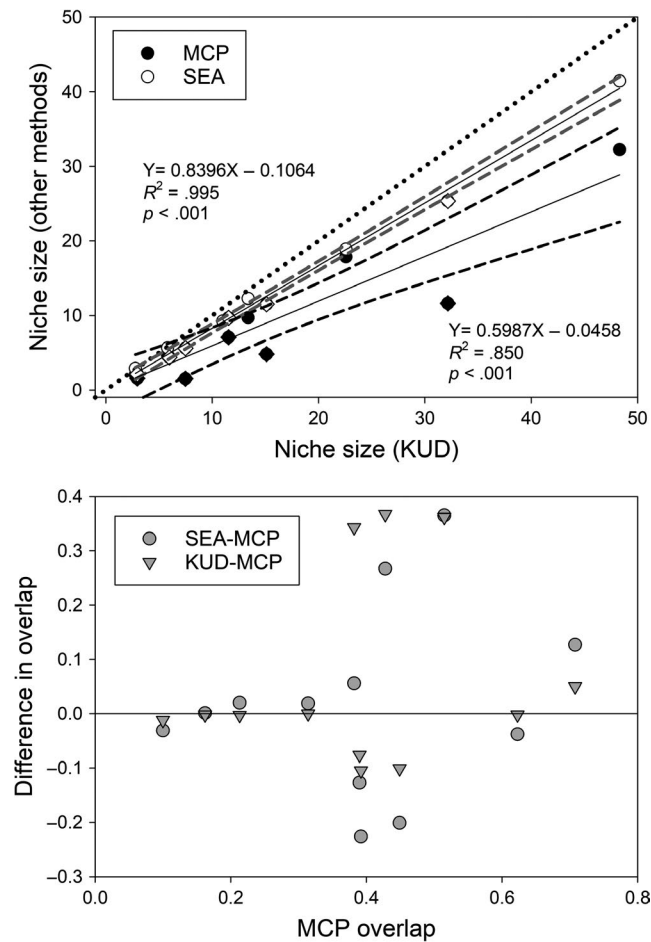
**TABLE 2** Comparison of estimates of isotopic niche overlap from MCP, SEA and KUD for 250 random  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values generated using a gamma distribution and based on empirical data of shrews *Sorex monticolus* and mice *Peromyscus keeni*

Contour	Target overlap	MCP		SEA		KUD		SEA-MCP	Proportion increase	KUD-MCP	Proportion increase	Ratio KUD/SEA
		Observed overlap	Quantile range	Observed overlap	Quantile range	Observed overlap	Quantile range					
Shrews												
50	0.25	0.000	0.000	0.000	0.000	0.000	0.004					
50	0.50	0.108	0.126	0.135	0.110	0.160	0.189	0.027	0.25	0.052	0.48	1.93
50	0.75	0.505	0.099	0.527	0.078	0.535	0.134	0.022	0.04	0.030	0.06	1.36
75	0.25	0.039	0.085	0.060	0.095	0.087	0.125	0.021	0.54	0.048	1.23	2.29
75	0.50	0.324	0.108	0.349	0.103	0.370	0.124	0.025	0.08	0.046	0.14	1.84
75	0.75	0.645	0.065	0.661	0.058	0.667	0.075	0.016	0.02	0.022	0.03	1.38
95	0.25	0.243	0.133	0.299	0.106	0.313	0.116	0.056	0.23	0.070	0.29	1.25
95	0.50	0.501	0.103	0.544	0.077	0.549	0.088	0.043	0.09	0.048	0.10	1.12
95	0.75	0.742	0.057	0.768	0.041	0.760	0.055	0.026	0.04	0.018	0.02	0.69
						Mean		0.030	0.161	0.042	0.294	1.48
Mice												
50	0.25	0.000	0.000	0.000	0.000	0.000	0.018					
50	0.50	0.125	0.128	0.179	0.118	0.190	0.189	0.054	0.43	0.065	0.52	1.20
50	0.75	0.518	0.095	0.557	0.078	0.554	0.125	0.039	0.08	0.036	0.07	0.92
75	0.25	0.045	0.089	0.101	0.110	0.118	0.133	0.056	1.24	0.073	1.62	1.30
75	0.50	0.331	0.107	0.389	0.103	0.396	0.123	0.058	0.18	0.065	0.20	1.12
75	0.75	0.649	0.063	0.683	0.058	0.680	0.073	0.034	0.05	0.031	0.05	0.91
95	0.25	0.255	0.130	0.340	0.107	0.344	0.117	0.085	0.33	0.089	0.35	1.05
95	0.50	0.507	0.100	0.574	0.076	0.567	0.085	0.067	0.13	0.060	0.12	0.90
95	0.75	0.746	0.056	0.783	0.040	0.767	0.061	0.037	0.05	0.021	0.03	0.57
						Mean		0.054	0.312	0.055	0.369	1.00

Note: The two identical groups were displaced by set values to overlap at 0.25, 0.50 and 0.75. Niche size and overlap were calculated at 50%, 75% and 95% contours. Niche size data are not presented because the two groups were identical. Only one value of overlap is reported. The difference between overlap estimates of SEA and MCP (SEA-MCP) and KUD and MCP (KUD-MCP) is presented, as well as the proportion of increase these values represent. In bold are the targeted overlap estimates. See Figure 2 for an example of displacement.

Abbreviations: KUD, kernel utilization density; MCP, minimum convex polygon; SEA, standard ellipse area.



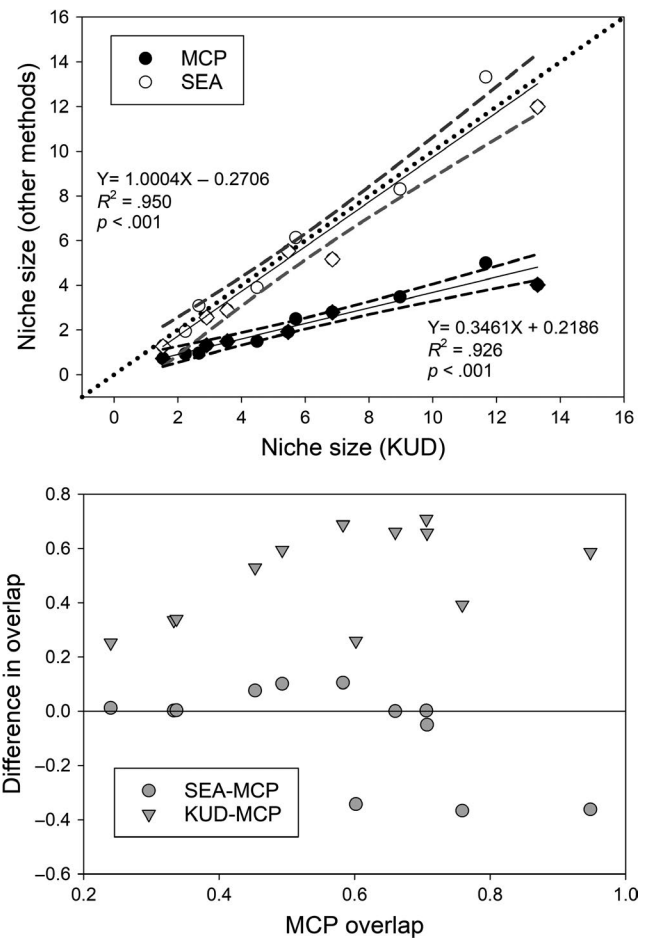


**FIGURE 5** Estimates of isotopic niche size ( $\pm 95\%$  confidence intervals [CI]) from minimum convex polygon (MCP; closed symbols) and standard ellipse area (SEA; open symbols) in relation to values from kernel utilization density (KUD; top) for mice and shrews. Dashed line represents the 1:1 ratio. At bottom are differences in niche overlap values between SEA (closed symbols) and KUD (open symbols) and MCP. The solid line represents no difference. Overlap sample sizes are double those of niche size because they represent the proportion of overlap for each pair (e.g. mice vs. shrews and shrews vs. mice; see Table S1)

result was especially clear for the sagebrush-chipmunks dataset (Figures 4 and 6).

In contrast with the consistent trends in niche size, pairwise estimates of overlap from KUD and SEA were highly variable among datasets (Figures 5 and 6; Figure S2). Similarly, overlap estimates from MCP were usually, but not consistently, lower than those estimated by KUD and SEA (Table 2). This result may be an artefact of underestimation of niche size by MCP.

Overlap estimates for the different pairwise comparisons varied. For example, while shrew isotopic niches only partially overlapped with the isotopic niche of mice (shrews–mice), their niche was nearly completely encompassed by that of their competitors (mice–shrews; Figure 3 and Table S1). Such instances were more prevalent with KUD estimators than the other two methods (Figures 3 and 4; Figure S1).

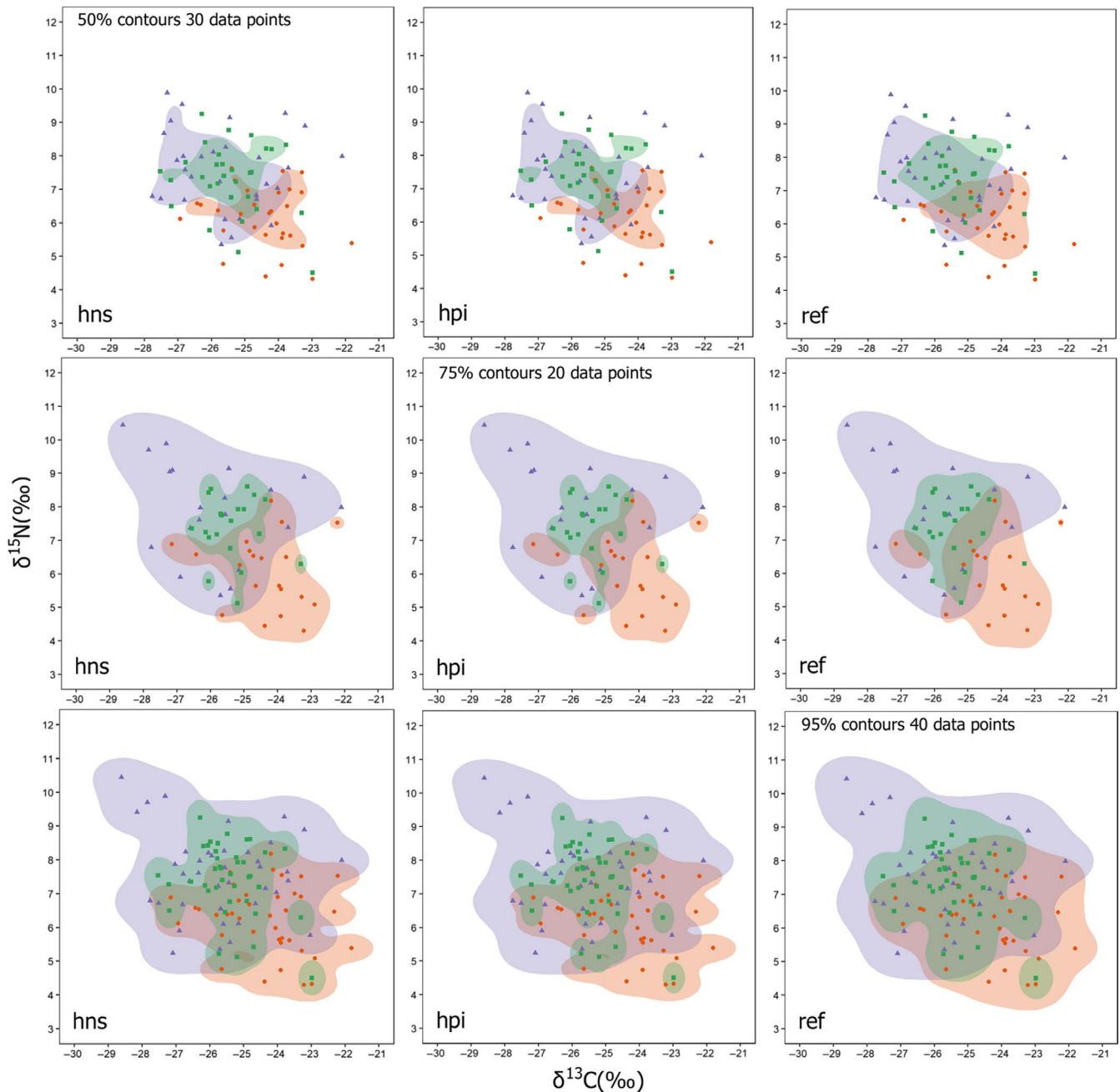


**FIGURE 6** Estimates of isotopic niche size ( $\pm 95\%$  CI) from minimum convex polygon (MCP; closed symbols) and standard ellipse area (SEA; open symbols) in relation to values from kernel utilization density (KUD; top) for least chipmunks in 2013 in Wyoming. Dashed line represents the 1:1 ratio. At bottom are differences in niche overlap values between SEA (closed symbols) and KUD (open symbols) and MCP. The solid line represents no difference

### 3.4 | Sample size and bandwidth

Two of six bandwidth methods (hscv and hlscv) resulted in an inflated niche size when 10 Kestrel data points were randomly selected from the original 50 per group (Figure 7). The other four methods (hns, hbcv, hpi and ref) yielded relatively consistent values regardless of dataset, sample size or contour level. Nonetheless, the ref method had the lowest overall average deviation in size estimates with increasing sample size (average  $-0.13$  and range,  $-0.86$  to  $0.68$ ) compared with the other three estimators (hbcv: average  $-2.80$  and range  $1.41$ – $5.17$ ; hns:  $2.18$ ,  $1.10$ – $3.82$ ; hpi:  $2.13$ ,  $1.01$ – $3.68$ ; Table S3). Concurrently, the ref method often yielded larger estimates of niche size, potentially because it produced fewer disjointed contours than the other methods (Figures 7 and 8).

Although overlap estimates of isotopic niches of simulated Kestrels data varied by habitat, no distinct differences among

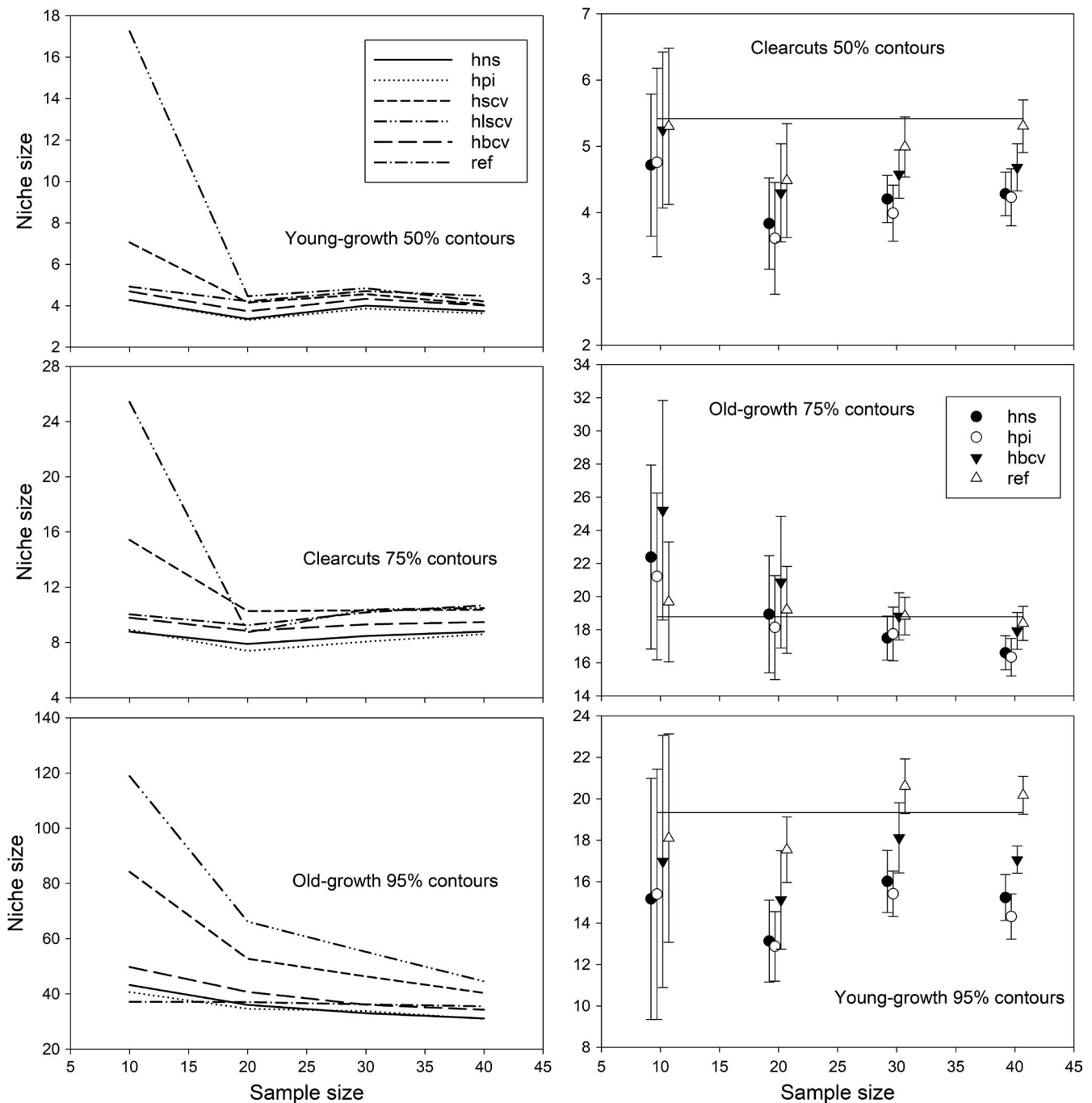


**FIGURE 7** Isotopic niche data for simulated American Kestrels *Falco sparverius* representing foraging behaviour in old-growth, young-growth and clear-cut stands in Southeast Alaska using data from the dietary and habitat specialist model ( $D_sH_s$ , Model 3) published by Flaherty and Ben-David (2010). From the original dataset (see Figure S1), 10, 20, 30 and 40 data points were randomly drawn 10 times. Niche size was estimated using six different bandwidth methods in kernel utilization density. Top panel depicts representative results from the 50% contours with 30 samples, middle panel 75% contours with 20 samples and bottom panel 95% contour with 40 samples. Data for the intermediary hbcv method are not shown

sample sizes occurred when considering the ref bandwidth method for all three contours (Figure 9). Differences in overlap estimates among other bandwidth methods (hbcv, hpi, hns) relative to ref at increasing sample sizes ranged from an average of  $-0.03$  in 50% contours (range  $-0.08$ – $0.11$ ),  $-0.04$  in the 75% contours (range  $-0.11$ – $0.13$ ), to  $0.00$  in the 95% contours (range  $-0.06$ – $0.06$ ). Nonetheless, these differences in overlap estimates were within the 95% confidence intervals ( $0.02$ – $0.16$ ) of

point estimates (10 replicates; Table S4). This result indicates that overlap estimates among bandwidth methods and sample sizes are similar.

Our regression analyses demonstrated that a minimum of 15 samples may be sufficient to obtain unbiased estimates of niche size and overlap with KUD and the reference bandwidth. There was no relation between number of samples and niche size at the 50%, 75% and 95% contours (Figure 10). Similarly, overlap values

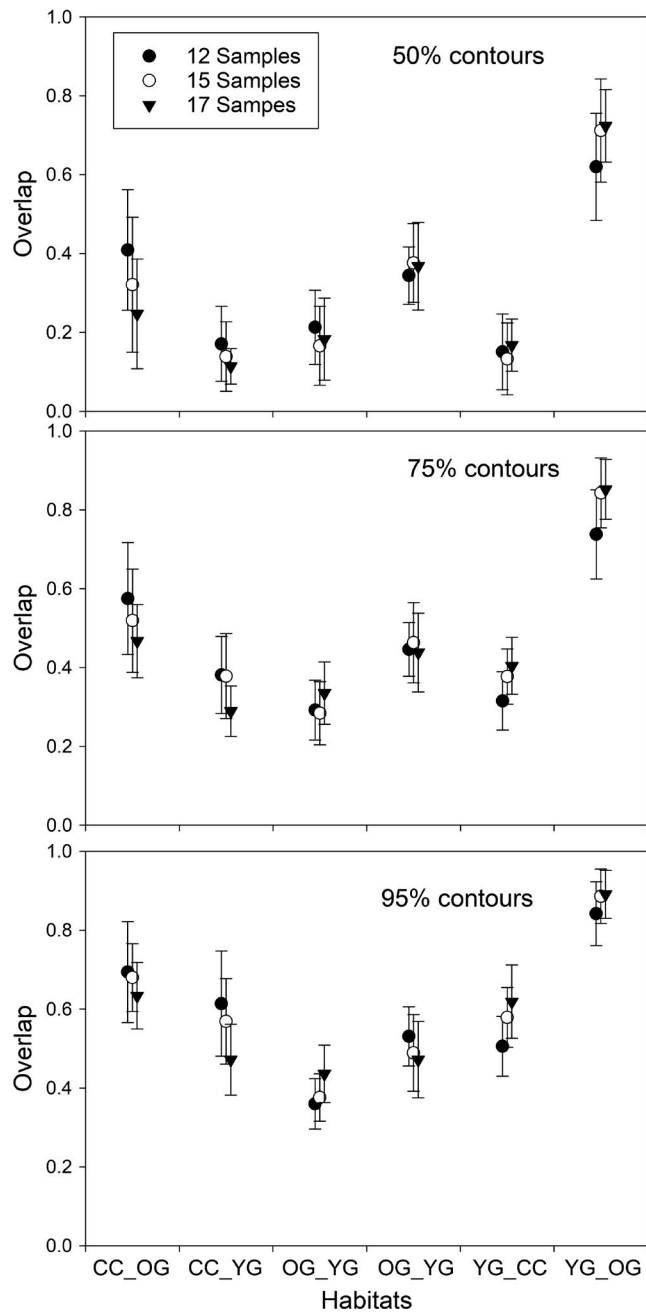


**FIGURE 8** Mean estimates of isotopic niche size for 10, 20, 30 and 40 data points randomly drawn from the simulated American Kestrels Model 3 dataset (see Figures S1 and S2 and Table S2) with six different bandwidth estimation methods (left). The three panels exemplify results from 72 of 216 scenarios. The right panels depict similar estimates ( $\pm 95\%$  CI) for the four consistent methods (48 of 144 scenarios). The horizontal line is the niche size of the full 50 points dataset (see Figure S1)

were consistent across sample sizes in the 50% contour. In the 75% and 95% contours, overlap increased from 10 to 15 samples but remained consistent above that number (Figure 10). In all contour levels and estimates, except overlap at 95%, confidence intervals declined but followed a decay function (Figure 10). This outcome indicates that the probability of obtaining an unbiased estimate of niche size and overlap does not change with a random draw of 15 samples or more.

## 4 | DISCUSSION

Our analyses indicate that KUD methods perform better than MCP and SEA in estimating isotope niche size when data are distributed in irregular patterns in bivariate space. This attribute leads to more accurate estimates of niche overlap based on known shapes and empirical data. Indeed, despite the consistent larger niche sizes, we observed no pattern in the estimates of overlap derived from KUD relative to the other two



**FIGURE 9** Mean estimates ( $\pm 95\%$  CI from 10 replications) of isotopic niche overlap for 10, 20, 30 and 40 data points randomly drawn from the simulated American Kestrels Model 3 dataset with the ref bandwidth estimation method

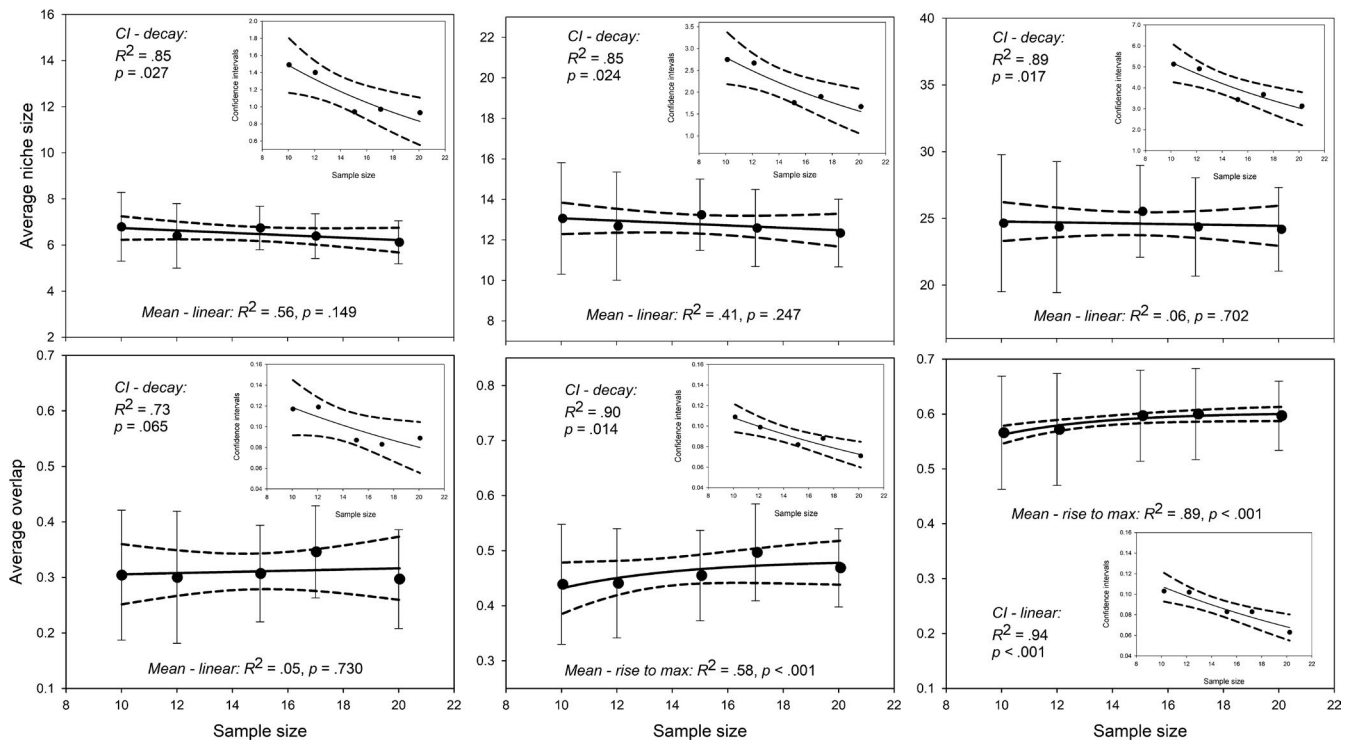
methods. In some cases, estimates of KUD overlap were smaller than those produced by MCP. In addition, we demonstrate that a minimum of 15 data points randomly drawn from a population, a common sample size in stable isotope studies, is sufficient to produce an unbiased estimate of niche size and overlap. Because random sampling can result in exclusion of data points that may be critical for understanding individual foraging strategies (Araújo, Bolnick, Machado, Giaretta, & Reis, 2007; Bearhop et al., 2004), our consistent results with as low as 15 samples are reassuring. The ability to incorporate individual-level variation yields a more complete assessment of the niche occupied by populations or species

(Bolnick, Yang, Fordyce, Davis, & Svanbäck, 2002). Although we endorse the use of KUD with the reference bandwidth, rKIN offers the user the ability to simultaneously compare results from all three methods and any number of contours, as well as the ability to select among different bandwidth methods. Thus, the user can achieve a better understanding of effects of data distributions on estimates of isotopic niche size and overlap.

Our application of KUD to describe the isotopic niche is not based on Bayesian principles (see Jackson et al., 2011), which offer more robust probabilistic measure of uncertainty of size and overlap. Nonetheless, this metric is largely free of assumptions of underlying statistical distributions. Therefore, this method can be applied to any natural system where data distribution is unknown or does not meet specific distributional assumptions (Seaman et al., 1999). Our analyses demonstrated that the KUD method nearly always leads to larger niche size estimates. Nonetheless, KUD more precisely delineates the distribution of data and niche space, especially when cryptic behavioural strategies (related to age, sex or social status; Araújo et al., 2007) may occur within the population. This is demonstrated well in Figures 1 and 4 where only the KUD method properly delineated the unique pattern of resource use in sagebrush chipmunks and the crescent shape.

One of the greatest strengths of rKIN is in presenting a framework for quantifying the isotopic niche overlap of several species or populations, or the same group of animals through time. The package allows assessment of the directionality of changes by providing the proportion of overlapping niche space for each pairwise comparison separately. Consequently, our package is more informative than simple estimates of symmetrical overlap or a single estimate representing both groups (such as 'volume index'; Clapp & Beck, 2015). By comparing the degree of overlap between species or through time, evidence of niche shifts, expansions or contractions can be investigated. Intersection of group isotopic signatures in bivariate space is crucial to understanding species coexistence as overlap in dietary axes can indicate the degree to which species may compete for the same food items (Bodey, Ward, Phillips, McGill, & Bearhop, 2014; Eckrich et al., 2018). Thus, coupled with quantitative estimates of niche size and position, rKIN provides a more complete description of the niche and an understanding of how it may change across space and time.

Stable isotope signatures of individual animals result from interactions of multiple ecological, behavioural and physiological processes (Ben-David & Flaherty, 2012; Martínez del Río & Carleton, 2012). This complexity can limit our ability to interpret stable isotope results including the various niche metrics. For example, differences in resource availability and the isotopic signatures of basal sources among communities influence the positions of consumers in bivariate space (Flaherty & Ben-David, 2010; Layman et al., 2007). This pattern is clear from the simulated Kestrel datasets (see Supporting Information). In these simulations, each Kestrel foraged on a single prey item with a unique isotopic signature in each of three habitats (Model 3; Flaherty & Ben-David, 2010). Thus, without knowledge on the Kestrel behaviour, interpretation of niche overlap would be erroneous. In this instance, the overlap in isotopic signatures of Kestrels was derived from overlapping values of prey not as a result of prey



**FIGURE 10** Relation between the number of randomly selected samples (10, 12, 15, 17 and 20) and niche size ( $\pm 95\%$  CI; top) and overlap ( $\pm 95\%$  confidence intervals from 10 replications; bottom) for simulated American Kestrels Model 3 dataset (see Figures S1 and S2; Table S2) at 50% (left), 75% (middle) and 95% (right) contours. Insets describe the relation between sample size and the spread of confidence intervals for each case

selection. In most isotopic studies, the foraging behaviour of individuals is unknown and inferred from the isotopic data themselves (Botta et al., 2017; Galetti et al., 2016; Gallagher et al., 2017; Sepulveda et al., 2012; Staudinger et al., 2014). Even when corrected for resource or basal (end-member) signatures (via mixing models; Newsome et al., 2007; Newsome et al., 2012; Post, 2002), niche estimates are difficult to compare among study systems. Consumption rates, assimilation of nutrients and nutrient distribution among tissues lead to uncertainty in diet composition and trophic enrichment factors and, thus, the isotopic signature of the consumers (Ben-David & Flaherty, 2012; DeNiro & Epstein, 1981). Nonetheless, Layman et al. (2007) suggested that the overall patterns generated by a species or community-wide approach may be less biased and that every factor influencing the isotopic ratio of an individual is not necessary to interpret size and overlap of niches. Interpretation of niche metrics, however, will benefit from any additional, non-isotopic data such as habitat use, elevational gradient (Rader et al., 2017) or density (Eckrich et al., 2018) that can be concurrently collected.

When applied to animal relocation data, KUD performed best with sample sizes of  $n > 30$  (Seaman et al., 1999). Similarly, Syväranta et al. (2013) reported that when applied to empirical isotopic data, SEA estimates were more precise with sample sizes of  $n > 30$ . Our analyses showed that increasing sample size beyond 15 had little effect on niche size and overlap. While we expected confidence intervals to tighten with increasing number of data points, the analyses suggested this did not occur in five of six scenarios. Among our case studies, the spring dataset

for sagebrush chipmunks and the mice in 2012 datasets were between 15 and 20 observations. Indeed, with this lower sample size, KUD better delineated the bivariate distribution of data than SEA (Figure 4).

Our results demonstrate that with ref, hns, hpi and hbcv bandwidth methods, estimates of niche size and overlap were consistent with only 10 data points, although the confidence intervals were larger than at higher sample sizes. The kde2d function in the MASS package in R (Venables & Ripley, 2002), which is called by rKIN, calculates area and overlap with just 5 relocation data points. Given our observations, this sample size may be too small for delineating isotopic niche and overlap. We recommend sample sizes  $\geq 15$ . Also, based on our results, we set the rKIN default bandwidth method to the ref because it was the least biased and variable in estimating niche size. Various studies assessing effects of sample size and bandwidth on home-range estimates from animal relocation data (empirical and simulated) report widely different results when considering size but limited effect on overlap (Horne & Garton, 2006; Kie, 2013). For example, Gitzen et al. (2006) reported that the ref estimator performed poorly relative to hpi or hlscv in all instances except when the distribution had a singular peak of activity. In contrast, Bauder et al. (2015) reported that ref and hpi provided comparable estimates, which were more robust than those produced by the hlscv. Nevertheless, few studies evaluated the consistency of size estimates with  $< 20$  data points (Bauder et al., 2015; Gitzen et al., 2006; Kie, 2013). Given our results and because of the inconsistent results in the home-range literature, we offer the rKIN user the



option of estimating niche size and overlap with all four methods and suggest that their applicability to specific datasets be evaluated.

We anticipate that in the future, quantitative descriptors of similarities or differences among individuals or populations will be in demand in a variety of ecological sub-disciplines. More broadly, the framework outlined here can be applied to any bivariate data (e.g. principal component analysis and multi-dimensional scaling) so long as axes and measurement units are identical; a critical aspect of conversion to Cartesian coordinates. We believe it will be useful to expand these metrics to higher dimensions (e.g.  $n > 2$  isotopes) so that they may be applied to more complex ecological questions (Blonder, Lamanna, Violle, & Enquist, 2014; Swanson et al., 2014), and allow the incorporation of multiple elements such as hydrogen, oxygen and sulphur. In ecology, quantitative tools that analyse non-normal, complicated data from the individual to community level are increasing in demand as technological methods are advanced. We believe that rKIN answers this need by providing a flexible framework that is free of statistical assumptions and allows for a more thorough understanding of the relationships among individuals and communities. As a consequence, we envision that the tools we provide here will serve a broad user-base of researchers interested in answering a variety of complex ecological questions.

## ACKNOWLEDGEMENTS

We thank M. Murphy, R. Liu, J. Goheen and D. Legg for providing helpful comments on early versions of the manuscript. We also thank C. Martínez del Río and M. Tabak for discussions on isotopic niches. Funding for this project was provided by the United States Forest Service Tongass National Forest, the National Fish and Wildlife Foundation, the University of Wyoming Biodiversity Institute and the University of Wyoming Department of Zoology and Physiology.

## AUTHORS' CONTRIBUTIONS

C.A.E., E.A.F., R.T.B. and M.B.-D conceived the ideas; C.A.E., E.A.F. and M.B.-D collected the data; S.E.A. wrote the code and created the rKIN package; C.A.E., S.E.A., E.A.F. and M.B.-D analysed the data; C.A.E. and M.B.-D led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Data included in this manuscript are available at the University of Wyoming Data Archive at the following: <https://doi.org/10.15786/20.500.11919/4878> (Eckrich, Albeke, Flaherty, Bowyer, & Ben-David, 2019)

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## REFERENCES

- Araújo, M. S., Bolnick, D. I., Machado, G., Giaretta, A. A., & Reis, S. F. (2007). Using  $\delta^{13}\text{C}$  stable isotopes to quantify individual-level diet variation. *Oecologia*, 152(4), 643–654. <https://doi.org/10.1007/s00442-007-0687-1>
- Bauder, J. M., Breininger, D. R., Bolt, M. R., Legare, M. L., Jenkins, C. L., & McGarigal, K. (2015). The role of the bandwidth matrix in influencing kernel home range estimates for snakes using VHF telemetry data. *Wildlife Research*, 42(5), 437–453. <https://doi.org/10.1071/WR14233>
- Bearhop, S., Adams, C. E., Waldron, S., Fuller, R. A., & Macleod, H. (2004). Determining trophic niche width: A novel approach using stable isotope analysis. *Journal of Animal Ecology*, 73(5), 1007–1012. <https://doi.org/10.1111/j.0021-8790.2004.00861.x>
- Ben-David, M., & Flaherty, E. A. (2012). Stable isotopes in mammalian research: A beginner's guide. *Journal of Mammalogy*, 93(2), 312–328. <https://doi.org/10.1644/11-MAMM-S-166.1>
- Ben-David, M., Newsome, S. D., & Whiteman, J. P. (2012). Lipid and amino acid composition influence incorporation and discrimination of  $^{13}\text{C}$  and  $^{15}\text{N}$  in mink. *Journal of Mammalogy*, 93(2), 399–412. <https://doi.org/10.1644/11-MAMM-S-168.1>
- Blonder, B., Lamanna, C., Violle, C., & Enquist, B. J. (2014). The  $n$ -dimensional hypervolume. *Global Ecology and Biogeography*, 23(5), 595–609. <https://doi.org/10.1111/geb.12146>
- Bodey, T. W., Ward, E. J., Phillips, R. A., McGill, R. A. R., & Bearhop, S. (2014). Species versus guild level differentiation revealed across the annual cycle by isotopic niche examination. *Journal of Animal Ecology*, 83(2), 470–478. <https://doi.org/10.1111/1365-2656.12156>
- Bolnick, D. I., Yang, L. H., Fordyce, J. A., Davis, J. M., & Svanbäck, R. (2002). Measuring individual-level resource specialization. *Ecology*, 83(10), 2936–2941. [https://doi.org/10.1890/0012-9658\(2002\)083\[2936:MILRS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2936:MILRS]2.0.CO;2)
- Börger, L., Franconi, N., De michele, G., Gantz, A., Meschi, F., Manica, A., ... Coulson, T. (2006). Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology*, 75(6), 1393–1405. <https://doi.org/10.1111/j.1365-2656.2006.01164.x>
- Botta, S., Secchi, E. R., Rogers, T. L., Prado, J. H., de Lima, R. C., Carlini, P., & Negrete, J. (2017). Isotopic niche overlap and partition among three Antarctic seals from the Western Antarctic Peninsula. *Deep Sea Research Part II: Tropical Studies in Oceanography*, 149, 240–249.
- Carleton, S. A., Kelly, L., Anderson-Sprecher, R., & Martínez del Río, C. (2008). Should we use one-, or multi-compartment models to describe  $^{13}\text{C}$  incorporation into animal tissues? *Rapid Communications in Mass Spectrometry*, 22(19), 3008–3014. <https://doi.org/10.1002/rcm.3691>
- Clapp, J. G., & Beck, J. L. (2015). Evaluating distributional shifts in home range estimates. *Ecology and Evolution*, 5(18), 3869–3878. <https://doi.org/10.1002/ece3.1655>
- DeNiro, M. J., & Epstein, S. (1981). Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta*, 45(3), 341–351. [https://doi.org/10.1016/0016-7037\(81\)90244-1](https://doi.org/10.1016/0016-7037(81)90244-1)
- Duong, T. (2018). ks: Kernel density estimation for bivariate data. Retrieved from <http://citeseerx.ist.psu.edu/viewdoc/summary?doi=10.1.1.190.8966>
- Eckrich, C. A., Albeke, S. E., Flaherty, E. A., Bowyer, R. T., & Ben-David, M. (2019). Data from: rKIN: Kernel-based method for estimating isotopic niche size and overlap. *University of Wyoming Data Archive*, <https://doi.org/10.15786/20.500.11919/4878>
- Eckrich, C. A., Flaherty, E. A., & Ben-David, M. (2018). Functional and numerical responses of shrews to competition vary with mouse density. *PLoS ONE*, 13(1), e0189471. <https://doi.org/10.1371/journal.pone.0189471>
- Flaherty, E. A., & Ben-David, M. (2010). Overlap and partitioning of the ecological and isotopic niches. *Oikos*, 119(9), 1409–1416. <https://doi.org/10.1111/j.1600-0706.2010.18259.x>
- Flaherty, E. A., Ben-David, M., & Smith, W. P. (2010). Diet and food availability: Implications for foraging and dispersal of Prince of Wales northern flying squirrels across managed landscapes. *Journal of Mammalogy*, 91(1), 79–91.
- Flaherty, E. A., Noakes, A. G., & Ben-David, M. (2014). Saphenous venipuncture for field collection of blood from least chipmunks.

- Wildlife Society Bulletin*, 38(2), 428–432. <https://doi.org/10.1002/wsb.385>
- Galetti, M., Rodarte, R. R., Neves, C. L., Moreira, M., & Costa-Pereira, R. (2016). Trophic niche differentiation in rodents and marsupials revealed by stable isotopes. *PLoS ONE*, 11(4), e0152494. <https://doi.org/10.1371/journal.pone.0152494>
- Gallagher, A. J., Shiffman, D. S., Byrnes, E. E., Hammerschlag-Peyer, C. M., & Hammerschlag, N. (2017). Patterns of resource use and isotopic niche overlap among three species of sharks occurring within a protected subtropical estuary. *Aquatic Ecology*, 51(3), 435–448. <https://doi.org/10.1007/s10452-017-9627-2>
- Gitzen, R. A., Millsaugh, J. J., & Kernohan, B. J. (2006). Bandwidth selection for fixed-kernel analysis of animal utilization distributions. *The Journal of Wildlife Management*, 70(5), 1334–1344. [https://doi.org/10.2193/0022-541X\(2006\)70\[1334:BSFFAO\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2006)70[1334:BSFFAO]2.0.CO;2)
- Hoeinghaus, D. J., & Zeug, S. C. (2008). Can stable isotope ratios provide for community-wide measures of trophic structure? *Comment. Ecology*, 89(8), 2353–2357. <https://doi.org/10.1890/07-1143.1>
- Horne, J. S., & Garton, E. O. (2006). Likelihood cross-validation versus least squares cross-validation for choosing the smoothing parameter in kernel home-range analysis. *The Journal of Wildlife Management*, 70(3), 641–648. [https://doi.org/10.2193/0022-541X\(2006\)70\[641:LCVLS\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2006)70[641:LCVLS]2.0.CO;2)
- Hutchinson, G. E. (1957). Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology*, 22, 415–427. <https://doi.org/10.1101/SQB.1957.022.01.039>
- Inger, R., Ruxton, G. D., Newton, J., Colhoun, K., Robinson, J. A., Jackson, A. L., & Bearhop, S. (2006). Temporal and intrapopulation variation in prey choice of wintering geese determined by stable isotope analysis. *Journal of Animal Ecology*, 75(5), 1190–1200. <https://doi.org/10.2307/3838412>
- Jackson, A. L., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER—stable isotope Bayesian ellipses in R. *Journal of Animal Ecology*, 80(3), 595–602. <https://doi.org/10.1111/j.1365-2656.2011.01806.x>
- Karlson, A. M. L., Gorokhova, E., & Elmgren, R. (2015). Do deposit-feeders compete? Isotopic niche analysis of an invasion in a species-poor system. *Scientific Reports*, 5, <https://doi.org/10.1038/srep09715>
- Kie, J. G. (2013). A rule-based ad hoc method for selecting a bandwidth in kernel home-range analyses. *Animal Biotelemetry*, 1, 13. <https://doi.org/10.1186/2050-3385-1-13>
- Layman, C. A., Arrington, D. A., Montaña, C. G., & Post, D. M. (2007). Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology*, 88(1), 42–48. [https://doi.org/10.1890/0012-9658\(2007\)88\[42:CSIRPF\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2)
- Martínez del Río, C., & Carleton, S. A. (2012). How fast and how faithful: The dynamics of isotopic incorporation into animal tissues. *Journal of Mammalogy*, 93(2), 353–359. <https://doi.org/10.1644/11-MAMM-S-165.1>
- Newsome, S. D., Martínez del Río, C. M., Bearhop, S., & Phillips, D. L. (2007). A niche for isotopic ecology. *Frontiers in Ecology and the Environment*, 5(8), 429–436. [https://doi.org/10.1890/1540-9295\(2007\)5\[429:ANFIE\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2007)5[429:ANFIE]2.0.CO;2)
- Newsome, S. D., Tinker, M. T., Monson, D. H., Oftedal, O. T., Ralls, K., Staedler, M. M., ... Estes, J. A. (2009). Using stable isotopes to investigate individual diet specialization in California sea otters (*Enhydra lutris nereis*). *Ecology*, 90(4), 961–974. <https://doi.org/10.1890/07-1812.1>
- Newsome, S. D., Yeakel, J. D., Wheatley, P. V., & Tinker, M. T. (2012). Tools for quantifying isotopic niche space and dietary variation at the individual and population level. *Journal of Mammalogy*, 93(2), 329–341. <https://doi.org/10.1644/11-MAMM-S-187.1>
- Post, D. M. (2002). Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology*, 83(3), 703–718. [https://doi.org/10.1890/0012-9658\(2002\)083\[0703:USITET\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2)
- Rader, J. A., Newsome, S. D., Sabat, P., Chessier, R. T., Dillon, M. E., & Martínez del Río, C. (2017). Isotopic niches support the resource breadth hypothesis. *Journal of Animal Ecology*, 86(2), 405–413. <https://doi.org/10.1111/1365-2656.12629>
- Robbins, C. T., Felicetti, L. A., & Florin, S. T. (2010). The impact of protein quality on stable nitrogen isotope ratio discrimination and assimilated diet estimation. *Oecologia*, 162(3), 571–579. <https://doi.org/10.1007/s00442-009-1485-8>
- Rocque, D. A., Ben-David, M., Barry, R. P., & Winker, K. (2006). Assigning birds to wintering and breeding grounds using stable isotopes: Lessons from two feather generations among three intercontinental migrants. *Journal of Ornithology*, 147(2), 395–404. <https://doi.org/10.1007/s10336-006-0068-2>
- Seaman, D. E., Millsaugh, J. J., Kernohan, B. J., Brundige, G. C., Raedeke, K. J., & Gitzen, R. A. (1999). Effects of sample size on kernel home range estimates. *The Journal of Wildlife Management*, 63(2), 739–747. <https://doi.org/10.2307/3802664>
- Sepulveda, A. J., Lowe, W. H., & Marra, P. P. (2012). Using stable isotopes to test for trophic niche partitioning: A case study with stream salamanders and fish. *Freshwater Biology*, 57(7), 1399–1409. <https://doi.org/10.1111/j.1365-2427.2012.02800.x>
- Silverman, B. W. (1986). *Density estimation for statistics and data analysis* (Vol. 26). Boca Raton, FL: CRC Press. Retrieved from <https://books.google.com/books?hl=en&lr=&xml:id=e-xsrjsL7WkC&oi=fnd&pg=PR9&dq=silverman&ots=iwPmot4BZu&sig=ONBphS3Gvq2WYzP65pgHZj-NRGo>
- Staudinger, M. D., McAlarney, R. J., McLellan, W. A., & Pabst, A. (2014). Foraging ecology and niche overlap in pygmy (*Kogia breviceps*) and dwarf (*Kogia sima*) sperm whales from waters of the U.S. mid-Atlantic coast. *Marine Mammal Science*, 30, 626–655.
- Stewart, K. M., Bowyer, R. T., Kie, J. G., Dick, B. L., & Ben-David, M. (2003). Niche partitioning among mule deer, elk, and cattle: Do stable isotopes reflect dietary niche? *Écoscience*, 10(3), 297–302. <https://doi.org/10.1080/11956860.2003.11682777>
- Swanson, H. K., Lysy, M., Power, M., Stasko, A. D., Johnson, J. D., & Reist, J. D. (2014). A new probabilistic method for quantifying n-dimensional ecological niches and niche overlap. *Ecology*, 96(2), 318–324. <https://doi.org/10.1890/14-0235.1>
- Syväranta, J., Lensu, A., Marjomäki, T. J., Oksanen, S., & Jones, R. I. (2013). An empirical evaluation of the utility of convex hull and standard ellipse areas for assessing population niche widths from stable isotope data. *PLoS ONE*, 8(2), e56094. <https://doi.org/10.1371/journal.pone.0056094>
- Venables, W. N., & Ripley, B. D. (2002). Non-linear and smooth regression. In *Modern applied statistics with S* (pp. 211–250). New York, NY: Springer. [https://doi.org/10.1007/978-0-387-21706-2\\_8](https://doi.org/10.1007/978-0-387-21706-2_8)
- Wolf, N., Bowen, G. J., & Martínez del Río, C. (2011). The influence of drinking water on the  $\delta D$  and  $\delta^{18}O$  values of house sparrow plasma, blood and feathers. *Journal of Experimental Biology*, 214(1), 98–103. <https://doi.org/10.1242/jeb.050211>
- Worton, B. J. (1987). A review of models of home range for animal movement. *Ecological Modelling*, 38(3), 277–298. [https://doi.org/10.1016/0304-3800\(87\)90101-3](https://doi.org/10.1016/0304-3800(87)90101-3)

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Eckrich CA, Albeke SE, Flaherty EA, Bowyer RT, Ben-David M. rKIN: Kernel-based method for estimating isotopic niche size and overlap. *J Anim Ecol*. 2020;89:757–771. <https://doi.org/10.1111/1365-2656.13159>