The role of the bandwidth matrix in influencing kernel home range estimates for snakes using VHF telemetry data

Javan M. Bauder[A,F], *David R. Breininger*[B], *M. Rebecca Bolt*[C], *Michael L. Legare*[D], *Christopher L. Jenkins*[E] *and Kevin McGarigal*[A]

[A]Department of Environmental Conservation, University of Massachusetts, 160 Holdsworth Way, Amherst, MA 01003, USA.

[B]InoMedic Health Applications, NASA Ecological Programs, Mail Code IHA-300, Kennedy Space Center, FL 32899, USA.

[C]InoMedic Health Applications, NASA Ecological Programs, Mail Code IHA-200, Kennedy Space Center, FL 32899, USA.

[D]Merritt Island National Wildlife Refuge, PO Box 6504, Titusville, FL 32782, USA.

[E]The Orianne Society, 100 Phoenix Road, Athens, GA 30605, USA.

[F]Corresponding author. Email: javanvonherp@gmail.com

Abstract

Context. Despite the diversity of available home range estimators, no single method performs equally well in all circumstances. It is therefore important to understand how different estimators perform for data collected under diverse conditions. Kernel density estimation is a popular approach for home range estimation. While many studies have evaluated different kernel bandwidth selectors, few studies have compared different formulations of the bandwidth matrix using wildlife telemetry data. Additionally, few studies have compared the performance of kernel bandwidth selectors using VHF radio-telemetry data from small-bodied taxa.

Aims. In this study, we used eight different combinations of bandwidth selectors and matrices to evaluate their ability to meet several criteria that could be potentially used to select a home range estimator.

Methods. We used handheld VHF telemetry data from two species of snake displaying non-migratory and migratory movement patterns. We used subsampling to estimate each estimator's sensitivity to sampling duration and fix rate and compared home range size, the number of disjunct volume contours and the proportion of telemetry fixes not included in those contours among estimators.

Key Results. We found marked differences among bandwidth selectors with regards to our criteria but comparatively little difference among bandwidth matrices for a given bandwidth selector. Least-squares cross-validation bandwidths exhibited near-universal convergence failure whereas likelihood cross-validation bandwidths showed high sensitivity to sampling duration and fix rate. The reference, plug-in and smoothed cross-validation bandwidths were more robust to variation in sampling intensity, with the former consistently producing the largest estimates of home range size.

Conclusions. Our study illustrates the performance of multiple kernel bandwidth estimators for estimating home ranges with datasets typical of many small-bodied taxa. The reference and plug-in bandwidths with an unconstrained bandwidth matrix generally had the best performance. However, our study concurs with earlier studies indicating that no single home range estimator performs equally well in all circumstances.

Implications. Although we did not find strong differences between bandwidth matrices, we encourage the use of unconstrained matrices because of their greater flexibility in smoothing data not parallel to the coordinate axes. We also encourage researchers to select an estimator suited to their study objectives and the life history of their study organism.

Introduction

Estimations of animal home ranges provide essential information for many aspects of ecology and conservation. They are used to describe individual variation in space use (Börger *et al.* 2006*a*), individual responses to landscape and climatic factors (Kie *et al.* 2002; Morellet *et al.* 2013), resource availability and selection

(Johnson 1980; Marzluff *et al.* 2004) and inter- and intra-specific interactions (Robert *et al.* 2012; Benson and Patterson 2013). The number of techniques available for estimating animal home ranges has increased greatly over the years (Börger *et al.* 2008; Kie *et al.* 2010). Despite this diversity, no single technique is without drawbacks, leading Fieberg and Börger (2012) to suggest that there is no single best method for estimating animal home ranges. Instead, they propose that the choice of a technique should be driven mostly by the research question and by the method's appropriateness for addressing that question. Different estimators may vary in their robustness to sampling design (Girard *et al.* 2002; Börger *et al.* 2006*b*) and the spatial arrangement of the underlying data points (Blundell *et al.* 2001; Hemson *et al.* 2005; Gitzen *et al.* 2006; Downs *et al.* 2012). As a result, different estimators may vary in their adequacy to address specific study questions, depending on the underlying characteristics of the data. Although stating well formulated research questions and developing a suitable sampling design are of primary importance in ensuring accurate home range estimates (Otis and White 1999; Börger *et al.* 2006*b*; Fieberg and Börger 2012), understanding how home range estimators perform under diverse situations and in response to multiple criteria can help researchers select the most appropriate estimator for their research question.

Kernel density estimators (Silverman 1986; Worton 1989; Wand and Jones 1995) are currently among the most popular techniques for quantifying animal space use (Laver and Kelly 2008; Kie *et al.* 2010). The size of the kernel is controlled by the bandwidth or smoothing parameter, which in turn influences the size and shape of the resulting utilisation distribution and volume contours (e.g. 95% volume contour; Worton 1995; Seaman and Powell 1996). Multiple bandwidth selectors are available, many of which have been evaluated in the context of home range estimation (Seaman and Powell 1996; Gitzen and Millspaugh 2003; Horne and Garton 2006; Gitzen *et al.* 2006; Lichti and Swihart 2011). However, very few studies have examined the influence of the bandwidth matrix. For bivariate data, such as telemetry data, the bandwidth matrix is a 2×2 matrix (Wand and Jones 1993, 1995). This matrix can include a single parameter along the diagonal, which imposes an equal degree of smoothing in all directions (H1, Wand and Jones 1993) or two parameters along the diagonal to allow for different degrees of smoothing along the coordinate axes (H2). An unconstrained matrix (H3) features three parameters that allow smoothing in any orientation. It is possible to obtain different degrees of smoothing using a single-parameter value by standardising the data (e.g. scaling or sphering, Fukunaga 1972), estimating a single bandwidth value, and then back-transforming this value to produce different matrix values. This facilitates asymmetrical smoothing (e.g. C2 and C3, Wand and Jones 1993). However, such approaches do not estimate a true unconstrained matrix and are generally inadvisable (Silverman 1986; Wand and Jones 1993). Recent statistical advances have allowed researchers to directly estimate the multiple parameters of the diagonal and unconstrained bandwidth matrices (Wand and Jones 1993; Duong and Hazelton 2003, 2005*a*, 2005*b*). These studies indicate that unconstrained matrices often outperform diagonal or single-parameter matrices (both with and without pre-estimation transformation), particularly if the distribution of the data is not parallel to the coordinate axes. Many animal species exhibit linear

movement patterns, including migratory species or those constrained to linear habitat features such as rivers or forest edges (Blundell *et al.* 2001; Gardiner *et al.* 2013). In such situations, an unconstrained bandwidth matrix may provide a more accurate estimate of space use. However, most of wildlife space use studies do not report using different smoothing parameters for different axes (Laver and Kelly 2008). Gitzen and Millspaugh (2003) found that diagonal least-squares cross-validation bandwidth matrices – estimated using pre-estimation data transformations – did not strongly outperform single-parameter bandwidth matrices. They also did not estimate an unconstrained bandwidth matrix and used simulated data. The unconstrained bandwidth matrix for different bandwidth selectors with actual wildlife field data remains to be tested.

Most wildlife home range studies comparing different bandwidth selectors, as well as other home range estimators, have used simulated data (Seaman and Powell 1996; Gitzen and Millspaugh 2003; Horne and Garton 2006; Gitzen *et al.* 2006; Lichti and Swihart 2011). While simulated data provide many advantages, they may fail to capture the spatial patterns and distributions of real animal movement data (Hemson *et al.* 2005; Downs *et al.* 2012). In particular, many small-bodied taxa exhibit repeated use of multiple refugia, resulting in highly clustered or duplicate fixes (Beck and Jennings 2003; Row and Blouin-Demers 2006), features not often explicitly evaluated in simulation studies. Additionally, relatively few studies have evaluated home range estimators using data from smaller bodied taxa, particularly non-mammalian taxa (Wauters *et al.* 2007; Ward *et al.* 2013). Many studies of small-bodied taxa (e.g. small mammals, herpetofauna) rely on handheld very high frequency (VHF) telemetry to collect space use data. Logistical constraints often restrict the number of animals and/ or fixes that can be obtained with handheld VHF telemetry, resulting in relatively small numbers of fixes per individual (e. g. <100 fixes per individual). Finally, animal telemetry data are often autocorrelated (Swihart and Slade 1985*a*, 1985*b*; McNay *et al.* 1994), thereby violating an assumption of kernel density estimation (Silverman 1986; Wand and Jones 1995). While the relevance of autocorrelation to kernel home range estimation is debated among wildlife biologists (Swihart and Slade 1985*a*; De Solla *et al.* 1999; Otis and White 1999; Fieberg 2007), evaluating home range estimators with real animal movement data may provide a better understanding of estimator performance in the presence of biologically induced autocorrelation (Cushman *et al.* 2005). As such, studies are increasingly needed to evaluate the performance of different bandwidth selectors in estimating utilisation distributions and home range sizes with data collected under the aforementioned circumstances.

In this paper, we compared multiple bandwidth selectors and bandwidth matrices to estimate kernel home ranges using very high frequency (VHF) telemetry data from two species that exhibit repeated use of multiple refugia. For consistency with the term's general usage in the wildlife literature, we considered the home range to be the two-dimensional space contained within some volume contour (e.g. 95%) of the kernel density surface (Kie *et al.* 2010). We evaluated five criteria that researchers might use to select a home range estimator depending on their research questions: (1) sensitivity to fix rate; (2) sensitivity to sampling duration; (3) volume contour (i.e. home range) size; (4) ability of

the home range to produce a single contiguous volume contour (*sensu* Blundell *et al*. 2001); and (5) ability to contain all telemetry fixes within the aforementioned volume contour(s). We considered that an ideal home range estimator should be relatively robust to variations in sampling intensity, including both the fix rate and duration of sampling. Home range size could be used as a criterion, depending on the importance of including areas of unobserved use within the home range. Larger (i.e. over-smoothed) home ranges may account for location uncertainty or incomplete sampling, whereas smaller (i.e. under-smoothed) home ranges emphasise regions of confirmed use. Use of our final two criteria might follow similar guidelines. We evaluated these criteria at multiple volume contours that are commonly used to delineate home ranges. We predicted that unconstrained bandwidth matrices would produce smaller home ranges (indicating a tighter 'fit' around the data) and fewer disjunct volume contours containing a higher proportion of telemetry fixes than single-parameter bandwidth matrices. To more fully evaluate the utility of different bandwidth matrices, we used data from a non-migratory and migratory species and predicted that the differences between single-parameter and unconstrained matrices would be greater for the migratory species. Finally, we use Mantel correlograms to examine the degree of autocorrelation within our data.

Materials and methods

Data collection

Our primary dataset included VHF telemetry data collected from eastern indigo snakes (*Drymarchon couperi*) in peninsular Florida. Within our study area, indigo snakes are surface active year-round, have relatively large home range sizes (>700 ha, Breininger *et al*. 2011) and are capable of moving >1 km per day (J. Bauder, unpubl. data). Most individuals included in this study had substantial overlap between seasonal home ranges and did not seasonally migrate among different portions of their annual home range. We used data collected from two separate studies. The first study occurred on the southern 40 km of the Lake Wales Ridge in Highlands County (27°17′N, 81°21′W) from 2011–2013. The study area and sampling methodology were described in Bauder and Barnhart (2014). The second study occurred primarily at three locations in

central peninsular Florida, including Brevard (28°38′N, 80°42′W), Indian River (27°50′N, 80°35′W) and Polk counties (27°37′N, 81°19′W), Florida. Data were collected from 1998–2003 as described in Breininger *et al*. (2011). We hereafter refer to these two datasets as Highlands and Brevard.

We estimated annual and seasonal home ranges for our indigo snake data. We recognised two 6 month seasons (winter and summer) based on seasonal variation in movement patterns (J. Bauder, unpubl. data) and indigo snake reproductive biology (Stevenson *et al*. 2009; Hyslop *et al*. 2014). Seasonal home ranges were estimated for individuals monitored for complete seasons with at least five and three fixes per month for Highlands and Brevard, respectively (Table 1). We estimated annual home ranges using 12 month blocks of data consisting of two consecutive and complete (6 month) seasons, with at least four fixes and one fix per month for Highlands and Brevard, respectively (Table 1). To increase our sample size, we also estimated 11 month annual home ranges for the Highlands data using data from two consecutive 5 or 6 month seasons. Lastly, for one individual from Highlands and four individuals from Brevard, we had data for two full years and thus estimated two separate annual home ranges and four separate seasonal ranges.

To evaluate bandwidth selector and matrix performance for data from a migratory species, we used VHF telemetry data from western rattlesnakes (*Crotalus oreganus*) in southeast Idaho (43°40′ N, 112°46′ W). Our study populations overwintered in communal hibernacula and undertook linear migrations to summer foraging and breeding habitats during a 5–6 month activity season (Jenkins 2007). The study area and data collection methods are described in Jenkins (2007). Rattlesnakes were monitored throughout their activity season after spring emergence, but equipment failures or lost telemetry signals meant that not all individuals were monitored for their entire outbound or inbound migration. Total sampling duration also varied due to differing dates of spring emergence, which varied as much as 4 weeks in a single population. We therefore truncated each individual's data so that individuals with a complete outbound migration had data from their first capture at their hibernaculum through 30 July, and individuals with a complete inbound migration had data from 15 July until their return to the hibernaculum. In this way, all individuals included

Table 1. Sampling intensities and autocorrelation results for the very high frequency (VHF) telemetry datasets used in this paper
Duration of autocorrelation refers to interval between fixes (days) over which fixes are autocorrelated. Means and standard errors (s.e.) for rattlesnake number of fixes per month represent number of fixes per half-month blocks (see text for details)

			Number of fixes per month		Total number of fixes		Duration of autocorrelation (days)	
		N	Mean (s.e.)	Range	Mean (s.e.)	Range	Mean	Range
Annual	Indigo snake - Highlands	8[A]	10.61 (0.33)	4–18	122 (6.37)	89–148	5.6	3–11
	Indigo snake - Brevard	33	3.25 (0.07)	1–7	39 (1.50)	23–57	13.7[B]	10–31
Seasonal	Indigo snake - Highlands	21	10.21 (0.27)	4–18	61.29 (2.08)	45–84	8.1	4–18
	Indigo snake - Brevard	35	4.05 (0.07)	3–9	24.31 (0.66)	20–34	12.9[C]	10–24
	Rattlesnake	13	9.81 (0.39)	4–14	39.23 (2.10)	23–49	6.9	4–12

[A]Four individuals were monitored for 12 months and four for 11 months.

[B]Each individual's annual data were split into their two respective seasons for a total of 66 Mantel correlograms. 43 seasons were not autocorrelated at the minimum lag distance of 7 days.

[C]16 seasons were not autocorrelated at the minimum lag distance of 7 days.

in our analyses were monitored for approximately four 2 week blocks (48–60 days), had at least four fixes per block and included a full outbound or inbound migration (Table 1). Three individuals had data for a complete activity season so we randomly assigned each individual as outbound or inbound and truncated their data as above.

Bandwidth estimation

We compared five kernel bandwidth selectors that have either received widespread use in the wildlife literature or have recently emerged as alternatives to previously used selectors: (1) the reference or normal bandwidth; (2) least-squares cross-validation; (3) likelihood cross-validation; (4) plug-in; and (5) smoothed cross-validation. The reference (REF) and least-squares cross-validation (LSCV) methods have been used extensively in wildlife home range estimation (Laver and Kelly 2008) and many studies have evaluated their performance using simulated and field data (Seaman and Powell 1996; Gitzen and Millspaugh 2003; Hemson *et al.* 2005; Gitzen *et al.* 2006; Lichti and Swihart 2011). The remaining three selectors have received comparatively less use in the wildlife literature. Horne and Garton (2006) found likelihood cross-validation (LCV) to outperform LSCV, particularly at small sample sizes (< ~50 fixes), but no studies have yet evaluated LCV against other selectors or with field data. Plug-in bandwidths (PI) have received increasing attention in recent years both for their theoretical properties (Wand and Jones 1995; Duong and Hazelton 2003) and frequent outperformance of REF and LSCV in studies using simulated telemetry data (Gitzen *et al.* 2006; Lichti and Swihart 2011). An increasing number of wildlife telemetry studies use PI selectors (Kertson and Marzluff 2011; Ward *et al.* 2013), though they do not appear to have attained widespread use (Laver and Kelly 2008). Smoothed cross-validation (SCV; Hall *et al.* 1992) has perhaps received the least use in wildlife home range estimation to date (Coates *et al.* 2013). This method combines features of both plug-in and cross-validation selectors. It uses a pilot bandwidth to estimate the integrated squared bias component of mean integrated squared error rather than its asymptotic approximation and pre-smooth's pairwise differences of observations before cross-validation. These features provide SCV with a lower degree of variability and greater stability than other cross-validation selectors (Wand and Jones 1995; Duong and Hazelton 2005*a*).

We used the ks package (version 1.9.2, Duong 2007, 2014) in R (version 3.0.2; R Core Development Team 2013) to estimate unconstrained bandwidth matrices of the form H3 (*sensu* Wand and Jones 1993) for REF, LSCV, PI and SCV, using the default settings on their respective functions. The ks package directly estimates each parameter within the bandwidth matrix (Duong 2007). We did not consider single-parameter bandwidth matrices (H1) for PI or SCV because ks currently does not provide those estimates. For comparison with earlier studies, we estimated a single-parameter bandwidth matrix for REF following Worton (1989) and LSCV using the package adehabitatHR (version 0.4.11; Calenge 2006). We considered LSCV to have failed if the numerical optimisation function did not minimise the error function within the optimisation interval (0.1*REF–4*REF). The LCV is currently only estimated as a single-parameter bandwidth matrix. We therefore used the pre-sphere functions from ks to

standardise our data to have unit variance, then applied the LCV function (J. Horne, pers. comm.) to estimate a single parameter and back-transformed these values to obtain a 'full' bandwidth matrix (C2 and C3 *sensu* Wand and Jones 1993). However, our full bandwidth matrix for LCV is not a true unconstrained bandwidth matrix even though it allows the kernel to rotate on the coordinate plane. Despite poor statistical performance of bandwidth matrices estimated using these pre-estimation transformations (Wand and Jones 1993), we included it because we were more interested in how well each home range estimator met our criteria rather than how well we estimated the 'correct' utilisation distribution. Although diagonally constrained bandwidth matrices have received limited attention in wildlife home range estimation (Gitzen and Millspaugh 2003; Laver and Kelly 2008), we did not include them in our analyses because we felt that the coordinate axes rarely, if ever, would correspond to biologically meaningful orientations. We therefore included a total of eight bandwidth selector–matrix combinations, hereafter referred to as estimators.

Subsampling routine

We used a bootstrap procedure to evaluate the sensitivity of each estimator to fix rate and sampling duration. Because each dataset varied in its sampling design, we analysed each one separately. We randomly selected 3–11 and 3–12 consecutive months from the 11 and 12 month annual Highlands data respectively, and then randomly selected 1, 2, 3, 4 or all fixes per month. Our design was identical for the seasonal data except that we randomly selected 3–6 consecutive months. For the rattlesnake data, we first randomly selected 1–4 2 week blocks and then randomly selected 1, 2, 3, 4 or all fixes per block. We did not have a sufficient number of fixes per month to examine fix rate in the Brevard data, so we randomly subsampled consecutive months as described above and used all fixes. We excluded combinations of sampling duration and fix rate with <5 fixes for the annual and rattlesnake data and <3 fixes for the seasonal data. We used 100 bootstrapped replicates per individual sampled with replacement and computed fixed kernel home range estimates at the 80%, 90%, 95% and 99% volume contours for each estimator. We selected these contours because they are the most commonly used to delineate home ranges. Replicates for bandwidth values that could not be estimated were excluded. For each replicate we calculated the relative bias in home range size as the size of the home range derived from the reduced duration and/or fix rate (hereafter referred to as the reduced distribution) divided by the size of the home range using all fixes from the entire duration (hereafter referred to as the full distribution). Our measure of bias, therefore, is a measure of the consistency of the estimator. Under this formulation, a value of one reflects no bias relative to the full home range. We used the Volume of Intersection index (VI; Seidel 1992; Millspaugh *et al.* 2004; Fieberg and Kochanny 2005) to compare the reduced and full utilisation distributions. We pooled data from across all replicates and all individuals within each treatment level and then calculated the mean and 95% quantiles of these pooled data.

Statistical analysis

To determine how home range size varied among estimators, we used linear mixed-effects models in the nlme package (version

3.1–111; Pinheiro *et al.* 2013). We combined indigo snake data from both sites, but performed separate analyses for annual and seasonal data and conducted separate analyses for each volume contour. We used log-transformed home range size as the dependent variable and estimator, sex and a sex-by-season interaction (indigo snake seasonal data only) as fixed effects. Although sampling duration was relatively constant across individuals within each analysis, we included an estimator-by-number-of-fixes interaction to control for variation in fix rate. We centred the number of fixes by dividing each value from the mean, so the estimate of the regression intercept could be interpreted as the predicted log home range size for the reference levels at the mean number of fixes. We evaluated the significance of our fixed effects using backwards stepwise selection with likelihood ratio tests. We included individual as a random effect for the annual and rattlesnake analyses and individual-season as a random effect in the seasonal analysis. We examined our data for heterogeneity of variances and included a varIdent variance structure with regards to estimator and a varPower or varExp variance structure with regards to number of fixes where appropriate (Zuur *et al.* 2009). We removed the LCV seasonal home range sizes from one outlying individual in the seasonal home range analysis to allow for model convergence. We report the median and range of number of disjunct volume contours formed with each estimator, and the median proportion of points outside of these contours(s) for each estimator, volume contour and dataset.

Autocorrelation analysis

We calculated Mantel correlograms using the package vegan (version 2.2–0; Oksanen *et al.* 2014) to determine the durations over which our telemetry fixes were autocorrelated (Cushman *et al.* 2005). We calculated a correlogram for each individual's season within the Highlands and Brevard seasonal data and the rattlesnake data. To minimise non-stationarity, we split the Highlands and Brevard annual data for each individual into their two respective seasons and then calculated a correlogram for each season. For each individual's season, we created two distance matrices: one representing Euclidean distance between all pairs of fixes and the second representing the 'distance' in time (days) between all pairs of fixes. We used lag distances of 1 day (starting with a 2 day distance bin) for the Highlands and rattlesnake data and 7 days (starting with a 7 day distance bin) for the Brevard data, which approximated the finest temporal sampling resolution of each dataset. We used 999 permutations to assess significance with the default adjustment for multiple comparisons and identified the last significant ($\alpha = 0.05$) lag distance before the first non-significant distance as the duration of autocorrelation. We report the mean and range of these durations across individual seasons for each dataset.

Results

LSCV convergence

We observed failed LSCV convergence for the majority of individuals, although this rate varied by dataset and bandwidth matrix. For the Highland data, LSCV failed for all individuals with each bandwidth matrix for both annual and seasonal home ranges. Least-squares cross-validation performed better with the Brevard data. The single-parameter bandwidth matrix failed for

72% and 60% of annual and seasonal home ranges respectively, but failed in all annual and seasonal home ranges for the unconstrained bandwidth matrix. Least-squares cross-validation failed for all individuals in the rattlesnake data as well. Because of these high failure rates, we did not include LSCV in subsequent analyses.

Fix rate and sampling duration

Results were consistent across indigo snake datasets and volume contours, so for brevity we limit our discussion to results from the Highlands annual (12 month) home ranges and the 95% volume contour (see Figs S1–S10 for 12 month Highlands annual results at the 80% volume contour and 11 month Highlands annual, Highlands seasonal, Brevard annual and Brevard seasonal at the 95% volume contours).

Home range size and VI were more sensitive to fix rate than sampling duration, although the magnitude of sensitivity to both fix rate and sampling duration varied substantially among estimators. Reducing fix rate generally led to greater increases in relative bias and decreases in precision than reducing sampling duration (Fig. 1). For example, the mean relative bias across estimators for the 12 months sampling duration increased from one for the baseline representing all fixes to 1.58 for a fix rate of one per month, whereas the mean relative bias for all fixes decreased from one for the baseline representing 12 months sampling duration to only 0.82 for a sampling duration of 3 months. Similarly, the precision decreased (i.e. range among replicates increased) from 0.45 to 4.97 as the fix rate decreased to one per month for the 12 month sampling duration, whereas the precision decreased from 0.19 to 1.86 as the sampling duration shortened to 3 months for the estimates based on all fixes. These trends were apparent for all estimators, but they were most pronounced for LCV estimators. Plug-in, REF and SCV estimators showed less sensitivity to both fix rate and sampling duration, with the REF estimator being the least sensitive. Overall, these trends were consistent for VI, as VI decreased more rapidly with decreasing fix rate than with decreasing sampling duration (Fig. 2). However, while relative bias and precision were similar for PI, REF and SCV estimators across fix rates and sampling durations, REF showed the least sensitivity and was the only estimator to have mean VI >0.90 at any sampling intensity (Fig. S4).

For any given sampling intensity, home range size and VI were more sensitive to bandwidth selector than matrix type. Relative bias and VI were very consistent between the single-parameter and full LCV bandwidth matrix but showed more variation with REF (Figs 1, 2). However, the difference in relative bias between the single-parameter and unconstrained bandwidth matrix for REF was 0.04 for 9 months with all fixes and 12 months with four fixes, and the difference in VI was 0.02 for 9 months with all fixes and 0.01 for 12 months with four fixes.

Results were consistent across volume contours for the rattlesnake dataset, so for brevity we limit our discussion to results from the 95% volume contour (see Figs S11, S12 for 80% volume contour results).

Similar to indigo snakes, decreasing fix rate at the longer sampling duration (2 months) resulted in positive relative bias in home range size, whereas at the shorter sampling durations
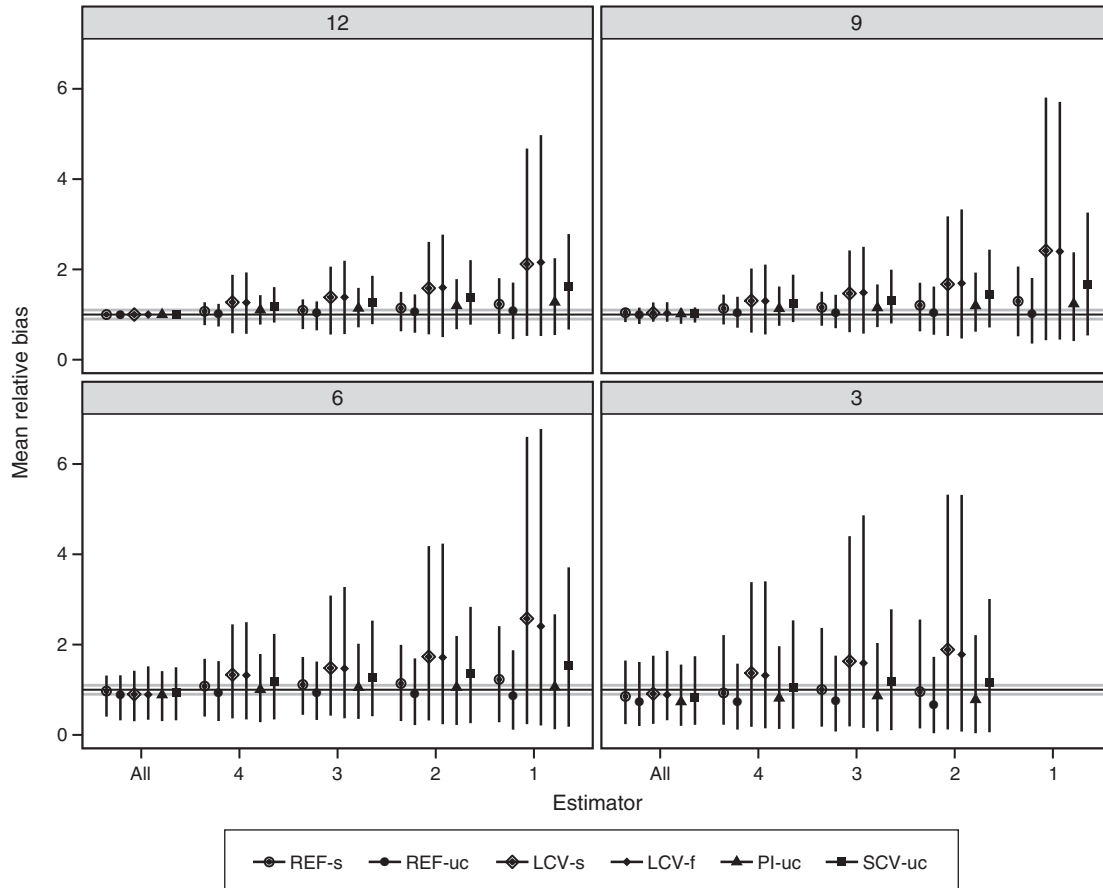
Fig. 1. Relative bias (mean and 95th quantile) of eastern indigo snake annual (Highlands 12 month) home range size (95% volume contour) by bandwidth at 3, 6, 9 and 12 month sampling durations with 1, 2, 3, 4 or all fixes per month. A value of one indicates no bias and the dark line indicates one, while the grey lines indicate 0.90 and 1.10. Estimator codes denote the bandwidth selector (REF = reference, LCV = likelihood cross-validation, PI = plug-in, SCV = smoothed cross-validation) and matrix type (s = single-parameter, uc = unconstrained, f = full).

(0.5–1.5 months) the relative bias was generally negative (Fig. 3). Likewise, reducing fix rate generally led to greater relative bias and reduced precision compared with reducing sampling duration, although the results were less clear than with the indigo snake data, and the trends were again most pronounced for LCV estimators (Fig. 3). As with the vast majority of indigo snake data, no estimator had mean VI >0.90, although REF always had the highest VI (Fig. 4). Lastly, as with the indigo snake data, for most sampling intensities, home range size and VI were more sensitive to bandwidth selector than matrix type (Figs 3, 4).

Home range size

For indigo snakes, home range size differed by estimator, number of fixes and sex for both annual and seasonal home ranges (Table 2). These patterns were consistent across volume contours (see Table S1 and Fig. S13 for 80% volume contour results), so we discuss results from the 95% volume contours for brevity. Neither season nor its interactive effect with sex was significant ($P \geq 0.1448$). Annual and seasonal home range estimates were 4.3 times larger for males than females. The reference bandwidth produced the largest estimates while LCV

produced the smallest (Fig. 5). The effect of number of fixes on home range size varied among estimators and between annual and seasonal home ranges. The effect was more pronounced among bandwidth selectors than matrix types with a 1.0–1.7 fold difference in annual home range size and 1.0–2.0 fold difference in seasonal home range size across estimators over the range of fixes we obtained (Fig. 5). With increasing number of fixes, home range size consistently increased for REF and decreased for LCV, whereas trends differed between annual and seasonal home range size for PI and SCV. Plug-in and SCV showed the least sensitivity to fix rate for annual and seasonal home range size, respectively. Unconstrained matrices produced smaller home range sizes than single-parameter matrices for REF (Fig. 6) while there was virtually no difference in home range size between the single-parameter and full matrices for LCV.

Rattlesnake home range size also differed significantly by estimator ($P < 0.0001$) but the effect of sex was marginal ($P = 0.0756$) and the conclusions equivocal, so we excluded sex from further analyses. Results were again consistent across volume contours, so we only discuss results from the 95% volume contours (see Table S2 and Fig. S14 for 80% volume contour results). As with the indigo snake home ranges, REF generally produced the
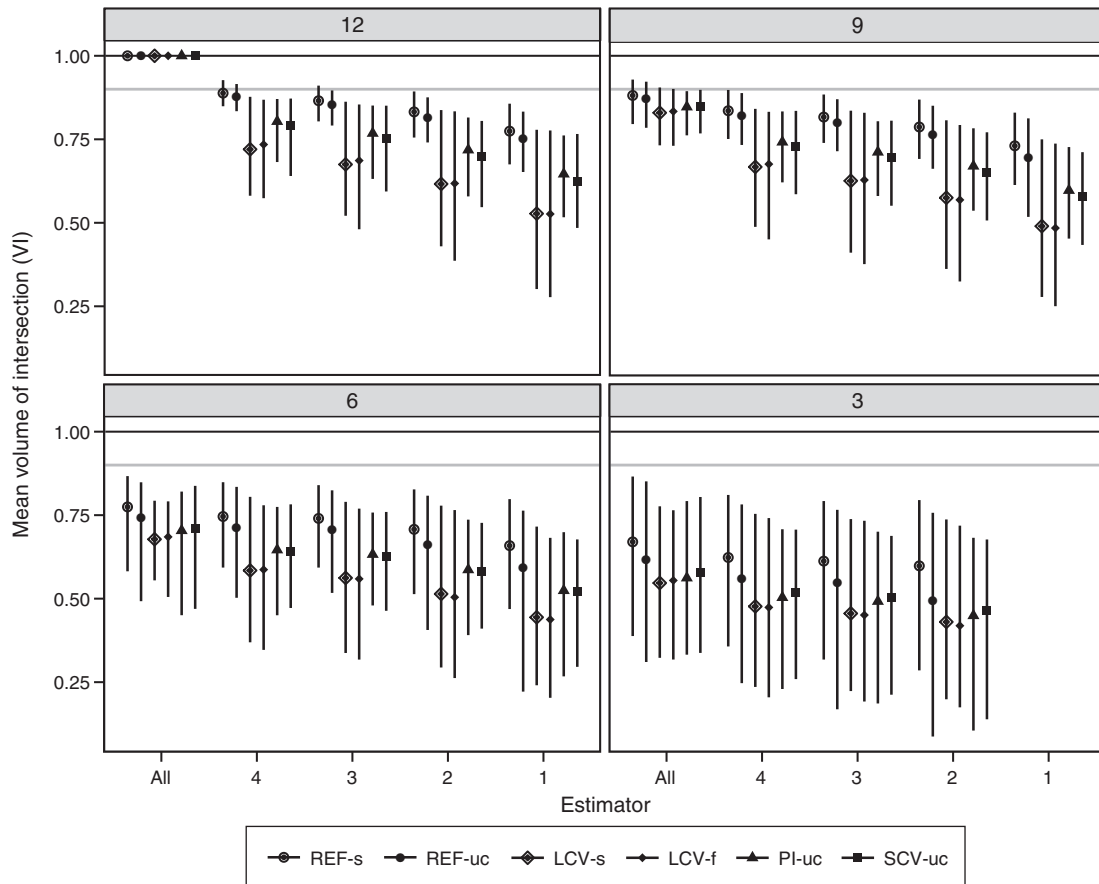
Fig. 2. Volume of intersection (mean and 95th quantile) of eastern indigo snake annual (Highlands 12 month) home ranges (95% volume contour) by bandwidth at 3, 6, 9 and 12 month sampling durations with 1, 2, 3, 4 or all fixes per month. A value of one indicates identical utilisation distributions and the dark line indicates one, while the grey line indicates 0.90. Estimator codes denote the bandwidth selector (REF = reference, LCV = likelihood cross-validation, PI = plug-in, SCV = smoothed cross-validation) and matrix type (s = single-parameter, uc = unconstrained, f = full).

largest home range estimates (Fig. 6). Most estimators were relatively insensitive to sampling intensity, except for the single-parameter REF and both LCV estimators, which varied 4.2–12.2 fold across our range of observed sampling intensities (Fig. 7; Table 3). The effect of sampling intensity was also more pronounced between single-parameter and unconstrained or full matrix types for rattlesnake home ranges than for indigo snake home ranges (Fig. 7). In addition, in contrast to the indigo snakes, with increasing number of fixes home range size generally decreased or stayed roughly the same.

Number of disjunct volume contours

For indigo snakes, trends in the mean number of disjunct volume contours for annual and seasonal home ranges were similar, so we only discuss results from the annual data (see Fig. S15 for seasonal home range results). The mean number of disjunct volume contours generally decreased with increasing contour size, although the effect was most pronounced for LCV (Fig. 8). Only the single-parameter REF (at the 99% and 90% volume contours for the Brevard annual and the 99% volume contour for the Brevard seasonal data) produced a single contiguous volume contour for every individual. The largest differences in the

number of disjunct volume contours were among bandwidth selectors and between datasets, with relatively little difference among matrix types. The Highlands data generally produced more disjunct volume contours than the Brevard data for all estimators except REF. Within the Highlands data, LCV produced substantially more disjunct volume contours than all other bandwidth matrices at all volume contour sizes. The REF estimators produced the fewest disjunct volume contours across all datasets at all volume contour sizes, and thus were the least sensitive estimators based on this criterion; PI and SCV were intermediate in this regard.

The mean number of disjunct volume contours produced for rattlesnake home ranges also decreased with increasing volume contour size, and was similarly more pronounced for LCV than other estimators (Fig. 9). The mean number of disjunct volume contours also varied by estimator and REF always produced the fewest disjunct volume contours. As with indigo snakes, only the single-parameter REF at the 99% volume contour produced a single contiguous volume contours for every individual. Likelihood cross-validation always produced the greatest number of disjunct volume contours, while PI and SCV were intermediate in this regard.
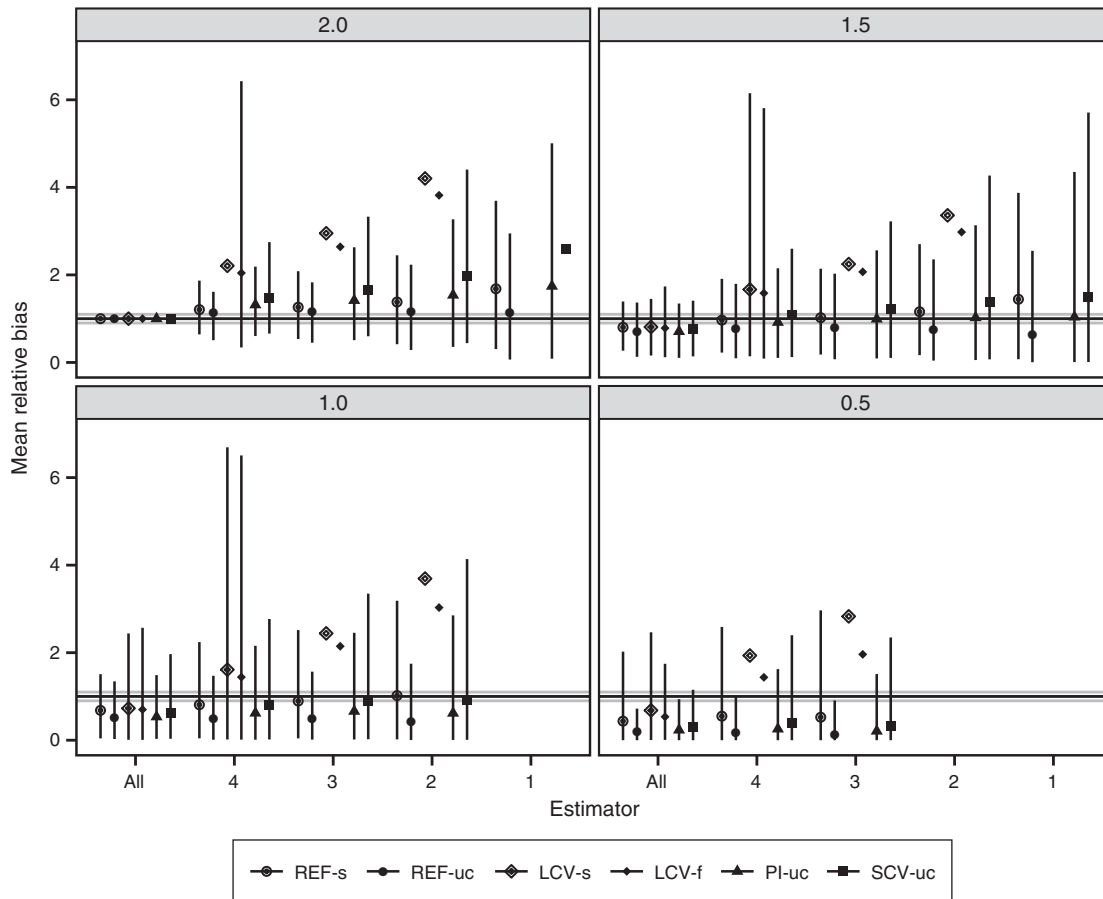
Fig. 3.   Relative bias (mean and 95th quantile) of western rattlesnake seasonal (2 month) home range size (95% volume contour) by estimator at 0.5, 1.0, 1.5 and 2.0 month sampling durations sampling durations with 1, 2, 3, 4 or all fixes per block. A value of one indicates no bias and the dark line indicates one, while the grey lines indicate 0.90 and 1.10. Estimator codes denote the bandwidth selector (REF = reference, LCV = likelihood cross-validation, PI = plug-in, SCV = smoothed cross-validation) and matrix type (s = single-parameter, uc = unconstrained, f = full). Mean bias for all LCV estimators was >7 for 1.5 and 2.0 month sampling durations with 1 fix per month. Points without error bars have 95th quantiles that exceeded the scale of the *y*-axis.

Proportion of fixes not included within the volume contour(s)

The 99% volume contour included all telemetry fixes across all estimators and datasets except the full LCV for the rattlesnake data. At the 95% volume contour, only the single-parameter and unconstrained REF, the unconstrained SCV for the indigo snake Highlands annual data and the full LCV for the rattlesnake data did not include all fixes; all telemetry fixes were included in the 95% volume contour for all other estimators and datasets. For the former cases, the percentage of points outside the 95% volume contours ranged from 0–2% for the single-parameter and unconstrained REF, 0–1% for the unconstrained SCV and 0–28% for the full LCV. Within the indigo snake data, the 90% volume contour only included all telemetry fixes for the single-parameter LCV and unconstrained PI for the Brevard seasonal data. Within the rattlesnake data, the 90% volume contour only included all telemetry fixes for the single-parameter LCV and unconstrained PI and SCV. The highest percentage of points not included in the volume contours for any individual across all datasets did not exceed 4% and 16% for the 90% and 80% volume contours for the

indigo snake data respectively, or 28% for the 90% and 80% volume contours for the rattlesnake data (Table S3).

Autocorrelation analysis

Telemetry fixes in the Highlands data were autocorrelated up to a mean of ~7 days apart, which corresponds to approximately four fixes per month (Table 1). In contrast, 43 of the 66 (65%) 6 month seasons comprising the 33 Brevard annual home ranges were not autocorrelated at the 7 day lag distance. Similarly, 16 of the 35 (46%) Brevard seasonal home ranges were not autocorrelated at the 7 day lag distance. Among seasons showing significant autocorrelation within the Brevard datasets, mean duration to autocorrelation was ~13 days (Table 1). Telemetry fixes from the rattlesnake data showed an intermediate degree of autocorrelation (Table 1).

Discussion

Although other studies have evaluated the performance of different kernel bandwidths, several aspects of our study allow it to make a unique contribution to estimating wildlife home
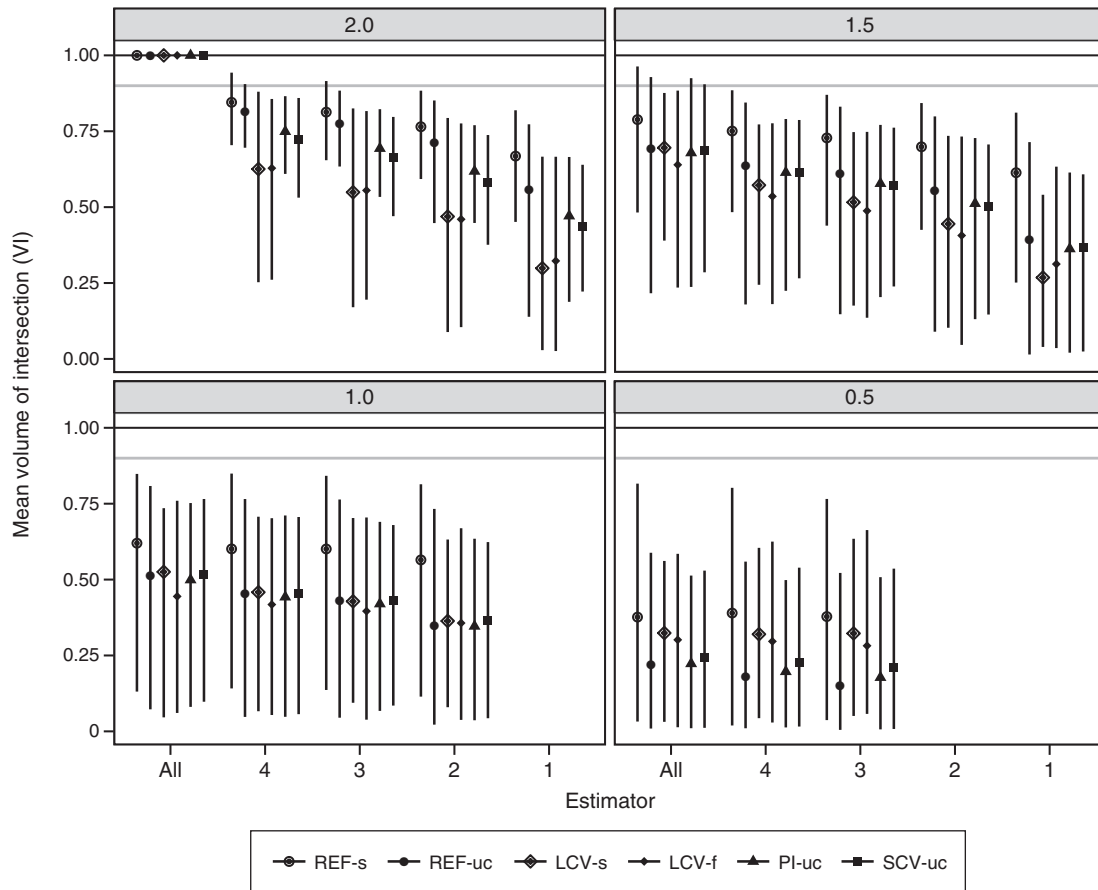
Fig. 4. Volume of intersection (mean and 95th quantile) of western rattlesnake seasonal (2 month) home ranges (95% volume contour) by estimator at 0.5, 1.0, 1.5 and 2.0 month sampling durations sampling durations with 1, 2, 3, 4 or all fixes per block. A value of one indicates identical utilisation distributions and the dark line indicates one, while the grey line indicates 0.90. Estimator codes denote the bandwidth selector (REF = reference, LCV = likelihood cross-validation, PI = plug-in, SCV = smoothed cross-validation) and matrix type (s = single-parameter, uc = unconstrained, f = full).

Table 2. Beta estimates, standard errors (s.e.) and *P* values for fixed effects in the linear mixed-effects models for eastern indigo snake annual and seasonal home range size at the 95% volume contour

Estimator codes denote the bandwidth selector (REF = reference, LCV = likelihood cross-validation, PI = plug-in, SCV = smoothed cross-validation) and matrix type (s = single-parameter, uc = unconstrained, f = full). The reference levels were the single-parameter REF and females and the response variable (home range size) was log-transformed

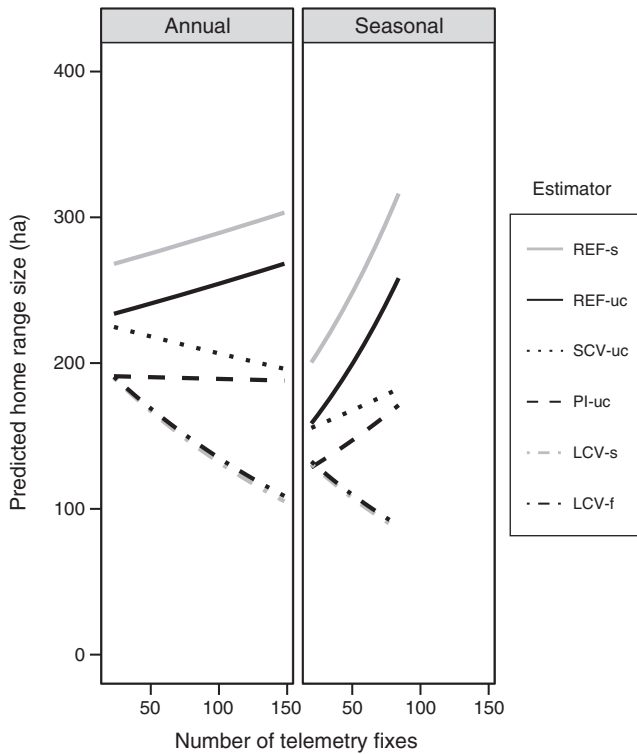|	Annual home range			Seasonal home range		
	Beta	s.e.	*P* value	Beta	s.e.	*P* value
(Intercept)	4.1644	0.1580	0.0000	4.1708	0.1492	0.0000
REF-uc	−0.1330	0.0359	0.0003	−0.2253	0.0434	0.0000
LCV-s	−0.5288	0.0672	0.0000	−0.6734	0.0437	0.0000
LCV-f	−0.5171	0.0648	0.0000	−0.6563	0.0437	0.0000
DPI-uc	−0.3747	0.0309	0.0000	−0.4924	0.0434	0.0000
SCV-uc	−0.2429	0.0316	0.0000	−0.3373	0.0434	0.0000
Number of fixes	0.0010	0.0034	0.7752	0.0071	0.0057	0.2154
Sex (males)	1.4585	0.2341	0.0000	1.2585	0.2080	0.0000
REF-uc × fixes	0.0001	0.0008	0.8926	0.0005	0.0024	0.8369
LCV-s × fixes	−0.0057	0.0015	0.0002	−0.0137	0.0024	0.0000
LCV-f × fixes	−0.0055	0.0015	0.0003	−0.0134	0.0024	0.0000
DPI-uc × fixes	−0.0011	0.0007	0.1160	−0.0027	0.0024	0.2715
SCV-uc × fixes	−0.0021	0.0007	0.0043	−0.0046	0.0024	0.0552

Fig. 5. Predicted eastern indigo snake annual and seasonal home range sizes (ha at the 95% volume contour) as a function of estimator and number of telemetry fixes. Only the predicted sizes for males are shown. Estimator codes denote the bandwidth selector (REF = reference, LCV = likelihood cross-validation, PI = plug-in, SCV = smoothed cross-validation) and matrix type (s = single-parameter, uc = unconstrained, f = full).

ranges. First, our study was the first, to our knowledge, to compare unconstrained bandwidth matrices against different forms of constrained bandwidth matrices. We not only compared different bandwidth matrices but did so with data from a migratory and non-migratory species, therefore evaluating scenarios where the advantages of using an unconstrained bandwidth matrix may vary. However, we acknowledge that the low fix rates present in our rattlesnake data limited our ability to make comparisons between these two movement patterns. Second, while other studies have evaluated REF, LSCV and, to a lesser extent, PI bandwidths, our study also included LCV and SCV, which have received comparatively less attention in studies evaluating home range estimators (Horne and Garton 2006). Finally, our study used field data collected with handheld VHF telemetry over different sampling durations in two species that regularly exhibit repeated use of multiple refugia. Although use of field data itself is not unique in studies comparing different home range estimators (Hemson *et al.* 2005; Börger *et al.* 2006*b*; Wauters *et al.* 2007; Pellerin *et al.* 2008), previous studies primarily compared REF and LSCV and predominately used higher fix rates made possible with GPS telemetry. Additionally, these studies primarily used data from large mammals, which may limit the applicability of the results to small-bodied taxa (Wauters *et al.* 2007). While higher fix rates allow for greater flexibility in evaluating different sampling designs, the sample sizes and intensities used in our study are typical

of many studies employing handheld VHF telemetry. It is therefore important to understand how different bandwidth selectors and bandwidth matrices perform in studies with limited numbers of telemetry fixes and/or sampling duration. This helps to inform the choice of a home range estimator that will best address a researcher's objectives.

Our rates of failure for LSCV were much higher than previously reported. Gitzen *et al.* (2006) reported LSCV failures of 13% for simulations representing broad home ranges with a single patch of highly concentrated use. Hemson *et al.* (2005) reported LSCV failures of 61% with subsampled GPS telemetry datasets with over 100 fixes. Counter-intuitively, both of these studies found that failure rates increased with increasing sample size. Other studies have reported even lower LSCV failure rates using field (Wauters *et al.* 2007) and simulated data (Gitzen and Millspaugh 2003). The higher failure rates in our study were likely due in large part to multiple sets of identical fixes in each individual. Such movement patterns may be common across multiple taxa, particularly herpetofauna (Beck and Jennings 2003; Row and Blouin-Demers 2006). Simulated data may fail to adequately represent such movement patterns, thereby highlighting the importance of using field data to evaluate home range estimators. Removing duplicate fixes may alleviate this problem (Wauters *et al.* 2007; Hyslop *et al.* 2014), although doing so removes relevant biological information about the intensity of space use. Adding a small amount of random variation to identical coordinates may help reduce LSCV failure rates, but this will not eliminate the clustered nature of the fixes. Ensuring that LSCV finds a solution does not eliminate the inherent variability of this approach (Silverman 1986; Sain *et al.* 1994; Wand and Jones 1995; Hemson *et al.* 2005). Many wildlife home range studies do not discuss LSCV failure or the lack thereof. Additionally, some studies reporting poor performances (relative to other home range estimators) of kernel home range estimators used LSCV (Row and Blouin-Demers 2006; Downs *et al.* 2012). The default options of many contemporary home range software products vary from reporting the reference bandwidth to the smallest bandwidth value in the score function. Uncritically accepting LSCV bandwidth values could lead to erroneous conclusions, making it important that researchers assess their data for the presence of LSCV failure.

Our indigo snake data showed greater sensitivity to fix rate than sampling duration and still produced relatively unbiased home range estimates with data from as little as 75% of the total sampling duration. We suspect that the greater sensitivity to fix rate exists because, even though fixes were subsampled evenly from throughout the home range, lower fix rates resulted in smaller sample sizes than all fixes within a shorter sampling duration. The full 12 month Highlands annual data had a mean 122 fixes per individual. Using 4 fixes per month resulted in 48 fixes, while using all fixes from 9 months resulted in a mean of 94 fixes. The greater bias for our subsampled rattlesnake home ranges may be due in part to the smaller number of fixes per individual. Seaman *et al.* (1999) suggested that $\geq$50 fixes were preferable for kernel home range estimation, but recent studies have suggested that <20 fixes can still produce accurate estimates (Saïd *et al.* 2005; Börger *et al.* 2006*b*). Indigo snakes in our study generally traversed most or all of their home range (annual or seasonal) throughout our sampling duration, which means that
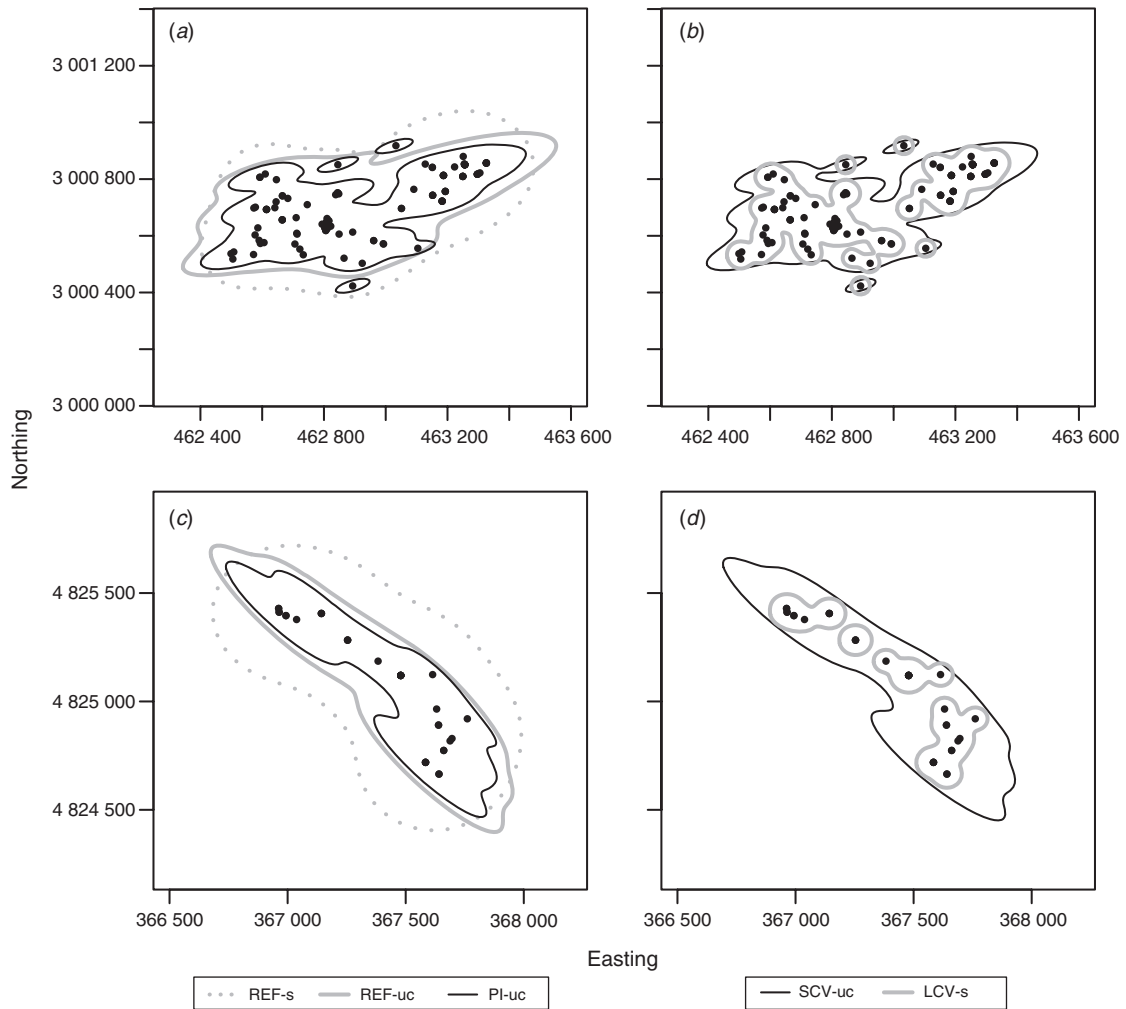
Fig. 6. Kernel home range estimates (95% volume contour) for one female eastern indigo snake (Highlands 12 month annual home range, *a* and *b*) and one male western rattlesnake (*c* and *d*) illustrating the differences in home range size between different estimators. Telemetry fixes are denoted by the black points. Bandwidths illustrated are the reference (REF), likelihood cross-validation (LCV), plug-in (PI) and smoothed cross-validation (SCV) while matrices include single-parameter (s) and unconstrained (uc).

subsampled data were more likely to approximate the full home range. In contrast, parts of our rattlesnake home ranges were only used during migration, making our home range estimates more sensitive to both fix rate and sampling duration. This also explains the negative relative bias at reduced sampling durations for rattlesnakes compared with a generally positive relative bias at reduced fix rates for indigo snakes. These results suggest that home range estimates for species exhibiting strong seasonal variation in space use may be more sensitive to sampling regime than species exhibiting uniform space use throughout the study period. Although the absolute value of the relative bias was greater for subsampled rattlesnake home ranges, the trends in bandwidth selector and matrix sensitivity to sampling intensity were also consistent across volume contours. This consistency across higher volume contours runs counter to previous studies reporting more variable estimates at higher volume contours (Seaman *et al.* 1999; Börger *et al.* 2006*b*).

Alternatively, the increase in relative bias with decreasing fix rate may reflect the fact that our Highlands and rattlesnake data

were autocorrelated at durations of shorter length than our subsampled fix rates. Some authors have reported that increasing autocorrelation may lead to smaller kernel home range estimates (Swihart and Slade 1985*a*; De Solla *et al.* 1999). However, the fact that eastern indigo snakes are capable of moving >1 km per day and that most of our fixes were ≥2 days apart suggests that many of our fixes were biologically independent (Lair 1987). Moreover, several studies have reported that autocorrelated fixes result in more accurate home range estimates than statistically independent fixes do (Reynolds and Laundre 1990), or have minimal effects on home range estimates (Andersen and Rongstad 1989; Gese *et al.* 1990; Blundell *et al.* 2001) or the accuracy or precision of those estimates (Swihart and Slade 1997; De Solla *et al.* 1999). Additionally, many researchers suggest increasing the number of fixes within an *a priori* specified and biologically meaningful time period in order to more accurately characterise an individual's pattern of space use within that period (De Solla *et al.* 1999; Otis and White 1999; Fieberg 2007). Finally, autocorrelation in telemetry data reflects
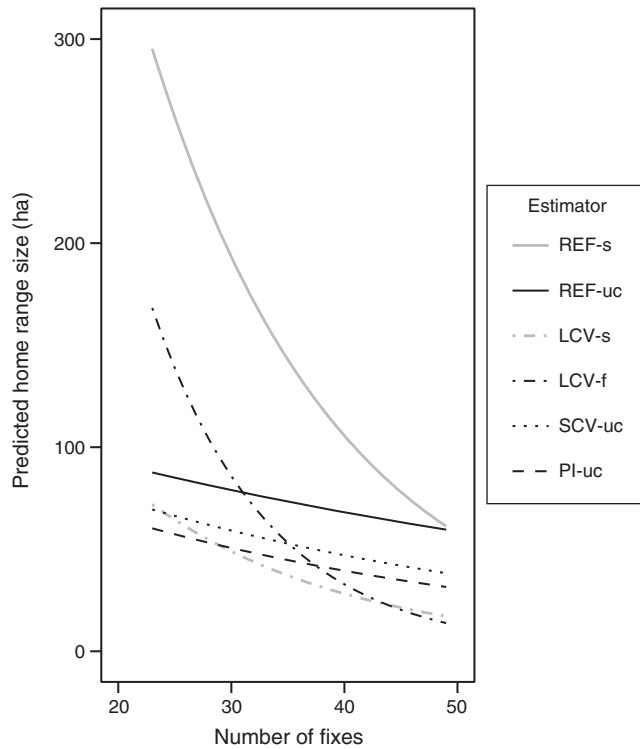
Fig. 7. Predicted western rattlesnake home range sizes (ha at the 95% volume contour) as a function of estimator and number of telemetry fixes. Estimator codes denote the bandwidth selector (REF = reference, LCV = likelihood cross-validation, PI = plug-in, SCV = smoothed cross-validation) and matrix type (s = single-parameter, uc = unconstrained, f = full).

Table 3. Beta estimates, standard errors (s.e.) and *P* values for fixed effects in the linear mixed-effects model for rattlesnake home range size at the 95% volume contour

Estimator codes denote the bandwidth selector (REF = reference, LCV = likelihood cross-validation, PI = plug-in, SCV = smoothed cross-validation) and matrix type (s = single-parameter, uc = unconstrained, f = full). The reference level was the single-parameter REF and the response variable (home range size) was log-transformed

	Beta	s.e.	*P* value
(Intercept)	4.7061	0.2861	0.0000
REF-uc	−0.4735	0.1050	0.0000
LCV-s	−1.3246	0.1873	0.0000
LCV-f	−1.1412	0.2331	0.0000
DPI-uc	−1.0117	0.0973	0.0000
SCV-uc	−0.8375	0.0967	0.0000
Number of fixes	−0.0605	0.0394	0.1529
REF-uc × fixes	0.0457	0.0145	0.0026
LCV-s × fixes	0.0054	0.0258	0.8366
LCV-f × fixes	−0.0357	0.0322	0.2722
DPI-uc × fixes	0.0356	0.0134	0.0105
SCV-uc × fixes	0.0375	0.0133	0.0068

biologically meaningful patterns of movement and space use (Cushman *et al.* 2005). Thus, while the issue of autocorrelation on home range estimation is equivocal, our principal objective was to compare the performance of different home range estimators

for any given fix rate, in which case any bias in home range estimates should not substantially affect the comparison across estimators.

We concur with previous researchers in stressing the importance of defining a biologically relevant sampling period and standardising the entire sampling regime within that period (Otis and White 1999; Börger *et al.* 2006*b*; Fieberg 2007). We also recognise that there are other techniques for modelling animal space use or movement pathways that are well suited for autocorrelated movement data, such as Brownian bridge models (Horne *et al.* 2007), time-geographic density estimation (Downs *et al.* 2011), elliptical time-density models (Wall *et al.* 2014) and autocorrelated kernel density estimators (Fleming *et al.* 2015). However, these techniques have generally been implemented with high frequency GPS telemetry data collected at fine (e.g. 15 min) intervals, which are better able to represent the actual movement pathway than handheld VHF telemetry. It is unclear how these techniques perform with the lower resolution data typically collected with handheld VHF telemetry data.

At high sampling intensities (i.e. ≥4 fixes per month or ≥75% of total sampling duration), all bandwidth selectors and matrices produced relatively unbiased and precise estimates of indigo snake annual home range size. These trends were also consistent for our other indigo snake datasets. However, precision was generally lower in the seasonal and Brevard annual datasets; we suspect this was due to lower absolute sample sizes because data were collected during shorter sampling durations (seasonal datasets) and at lower fix rates (Brevard datasets). Bandwidth selectors and matrices only varied in their performance at lower sampling intensities, particularly low fix rates. However, matrix type was relatively robust to sampling intensity while most of the variation in performance occurred among bandwidth selectors. Likelihood cross-validation exhibited the greatest sensitivity to sampling intensity, producing the most biased and least precise estimates at reduced sampling intensities. Smoothed cross-validation was second to LCV in increased bias and lost precision, albeit only at moderate to low sampling intensities, while REF and PI were most robust to low sampling intensities. Although relative bias was greater for rattlesnake home ranges at all sampling intensities, the relative performance of different bandwidth selectors and matrices was similar to those of the indigo snake data.

As expected, we found wide variation in the estimates of home range size among estimators, but the differences among different matrices for a given bandwidth selector were generally smaller than the differences among bandwidth selectors. There was virtually no difference among matrix types for LCV, with the exception of the full LCV for rattlesnake data. However, this was not a true unconstrained bandwidth matrix because we only estimated a single parameter using pre-transformed data. Such data transformations are generally ill-advised (Wand and Jones 1993) and did not appear to result in markedly different home range estimates with LCV. The single-parameter matrix for REF consistently produced larger home range estimates than the unconstrained matrix and the proportional increase in predicted home range size was greater for the rattlesnake data (0.61) than for the indigo snake annual and seasonal data (0.14 and 0.25, respectively). We would expect a greater effect of
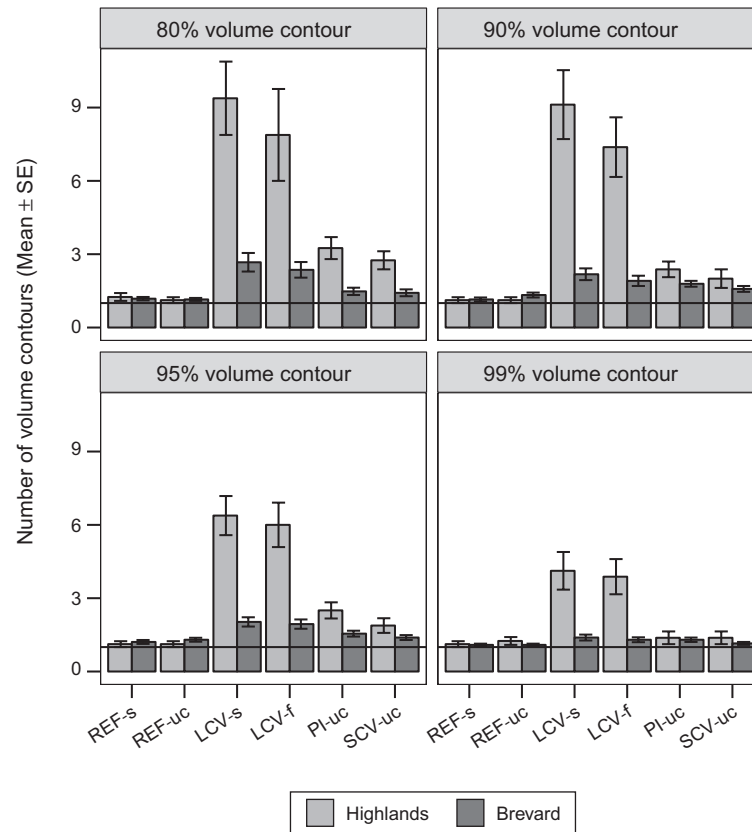
Fig. 8. Mean number of volume contours (±1 s.e.) for eastern indigo snake annual home ranges at the 80%, 90%, 95% and 99% volume contours for each estimator. The black horizontal line indicates one. Estimator codes denote the bandwidth selector (REF = reference, LCV = likelihood cross-validation, PI = plug-in, SCV = smoothed cross-validation) and matrix type (s = single-parameter, uc = unconstrained, f = full).

bandwidth matrix on home range size for data from animals with predominately linear movements because of nonsymmetrical orientation of the data distribution (Wand and Jones 1993; Duong and Hazelton 2003, 2005*a*). However, we suggest caution when comparing the home range size results between our study species because of large differences in how the data were collected and the low number of fixes in the rattlesnake data. We encourage additional research to evaluate the performance of unconstrained bandwidth matrices in estimating wildlife home ranges from multiple data distributions.

In contrast to matrix type, we observed large differences in home range size due to bandwidth selector. The reference bandwidth produced the largest home range estimates in all the datasets we examined, which made it the most likely to produce a single contiguous volume contour. These results are consistent with the well-known tendency for REF to over-smooth wildlife telemetry data (Worton 1995; Seaman and Powell 1996; Seaman *et al*. 1999; Kie *et al*. 2010), which may reflect the presence and/or degree of autocorrelation in such data. In contrast, LCV exhibited the lowest degree of smoothing among our bandwidth selectors and produced the smallest home range estimates that invariably consisted of multiple disjunct volume contours. The highly clustered nature of our data may have caused LCV to under-smooth our data relative to the other estimators we examined.

Home ranges comprised of multiple disjunct volume contours may be undesirable for many species because areas of transit among disjunct volume contours are areas of known use, yet are excluded from the estimated home range. However, such estimates may still be useful to wildlife researchers and managers, depending on their specific objectives. For example, estimates with disjunct volume contours may be appropriate for birds, for which the travel routes among patches are arguably not areas of use (e.g. Barg *et al*. 2005), or to emphasise discrete resource patches (Gitzen *et al*. 2006). Plug-in and SCV produced intermediate-sized home range estimates.

The presence of a significant estimator-by-number-of-fixes interaction may suggest we had failed to collect sufficient data to obtain stable home range estimates (Harris *et al*. 1990). However, our subsampling analyses showed that indigo snake annual and seasonal home range size did stabilise as the number of fixes increased. We suspect that the generally positive relationship between number of fixes and indigo snake home range size primarily reflected differences in sampling intensity between the Brevard and Highlands datasets, with greater sample sizes in the latter producing relatively larger home ranges despite the greater degree of autocorrelation within the Highlands data. High sampling intensities in the latter (89–148 fixes) may have allowed us to obtain a more accurate representation of space
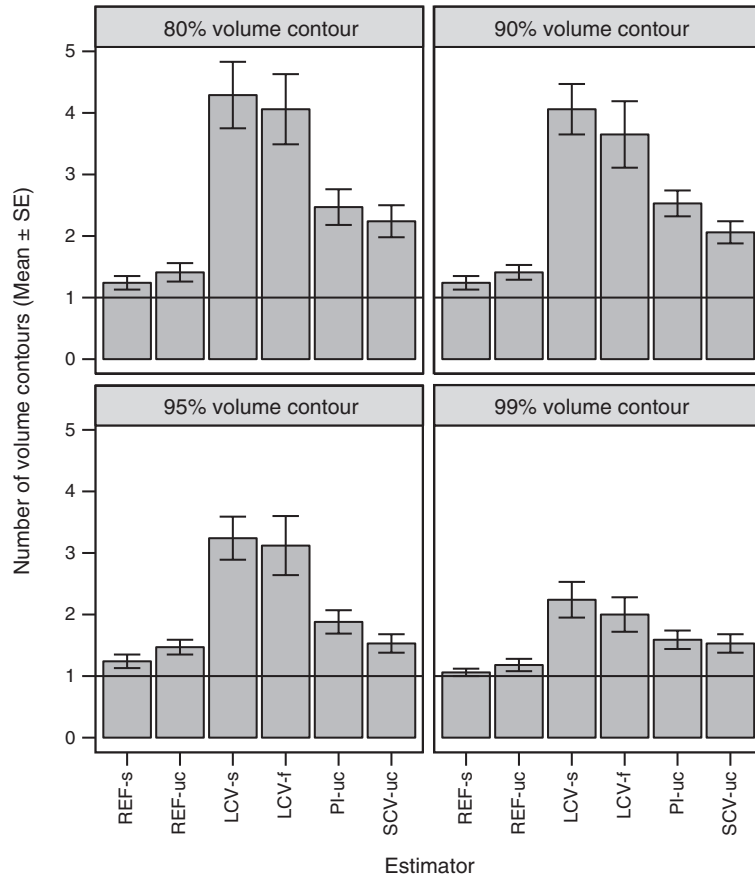
Fig. 9. Mean number of volume contours (±1 s.e.) for western rattlesnake home ranges at the 80%, 90%, 95% and 99% volume contours for each estimator. The black horizontal line indicates one. Estimator codes denote the bandwidth selector (REF = reference, LCV = likelihood cross-validation, PI = plug-in, SCV = smoothed cross-validation) and matrix type (s = single-parameter, uc = unconstrained, f = full).

Table 4.   Summary of the relative performance of each kernel home range estimator in response to our five criteria
Bandwidth codes are as follows: REF = reference; LCV = likelihood cross-validation; PI = plug-in; SCV = smoothed cross-validation. Home range size refers to the size of the area within a pre-specified volume contour, number of volume contours refers to the number of contiguous areas produced by the volume contour(s) and proportion of points excluded refers to the proportion of telemetry fixes within the aforementioned area(s)

	Sensitivity to fix rate	Sensitivity to sampling duration	Home range size	Number of volume contours	Proportion of points excluded
REF-single parameter	Moderate	Moderate	Largest	Mostly single; robust	Very few excluded
REF-unconstrained	Moderate-low	Moderate	Large	Mostly single; robust	Very few excluded
LCV-single parameter	High	High	Smallest	Highly variable, often many	None
LCV-full	High	High	Smallest	Highly variable, often many	None
PI-unconstrained	Moderate-low	Moderate	Moderate-small	Typically one-few depending on volume contour	None
SCV-unconstrained	Moderate	Moderate	Moderate	Typically one-few depending on volume contour	Very few excluded

use, which may have included forays outside of intensively used areas (Ward *et al*. 2013). In contrast, our subsampling and home range size analyses both indicate that rattlesnake home range size decreased with increasing number of fixes over a certain duration. This may be the result of a failure to adequately represent the migration pathway and/or the result of a greater number of autocorrelated fixes. Many studies have shown that kernel home range estimates generally decrease in size with increasing number

of fixes within a stable area, and studies comparing hand-collected VHF telemetry with GPS telemetry have found the former to overestimate home range size (Seaman *et al*. 1999; Girard *et al*. 2002; Pellerin *et al*. 2008). Ward *et al*. (2013) found that a fix rate once every 5 days overestimated ratsnake (*Pantherophis* spp.) home ranges greater than 2-fold compared with daily fix rates. Our results again emphasise the importance of standardising telemetry sampling schedules for estimating wildlife home ranges.

We reiterate the importance of carefully considering an estimator's suitability given the study objectives and life history of the study organism. The recent proliferation of home range estimators highlights the importance of interdisciplinary approaches to wildlife management, to ensure that biologically relevant objectives are defined and matched with the most appropriate estimators. Our study can provide guidelines to help researchers select a home range estimator that accomplishes this goal. Each of the estimators we considered differed in their response to our five criteria (Table 4). Despite its widespread use, we found that LSCV was unsuitable for our data. Our results suggest that the choice of bandwidth selector is more important than the matrix type. However, we encourage the use of an unconstrained matrix because of the greater flexibility it provides. With our data, LCV generally had the poorest performance particularly with respect to sampling intensity. Differences among the remaining three estimators generally reflected their relative degree of smoothing although SCV was slightly more sensitive to sampling intensity than REF and PI. The reference bandwidth was most likely to produce a single contiguous volume contour, though this came at the cost of greater smoothing. The unconstrained matrix greatly reduced the degree of smoothing, relative to the single-parameter matrix. We therefore recommend the unconstrained PI or REF for kernel home range estimation, depending on the importance of excluding or including areas of unobserved use within the home range. For example, REF may be desirable when the home range is used to define resource availability (e.g. Johnson's (1980) level III selection) because it may be more likely to include areas used by an individual but undetected (e.g. because of low sampling frequency). Alternatively, PI may be desirable when the researcher wishes to place emphasis on areas of observed use. We encourage additional research on the use of unconstrained bandwidth matrices on telemetry data from wildlife taxa with other life histories and movement patterns than those examined here, particularly with data collected using GPS telemetry. Future research should also compare the effects of bandwidth matrix type on the inner volume contours as these are commonly used to delineate core areas (Powell 2000).

Acknowledgements

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