Article (refereed)

Knight, Carolyn M.; **Kenward, Robert E.**; **Gozlan, Rodolphe E**; **Hodder, Kathryn H.**; **Walls, Sean S.**; Lucas, Martyn C.. 2009 Home range estimation within complex restricted environments: importance of method selection in detecting seasonal change. *Wildlife Research*, 36 (3). 213-224. 10.1071/WR08032

HOME RANGE ESTIMATION WITHIN COMPLEX RESTRICTED ENVIRONMENTS: IMPORTANCE OF METHOD SELECTION IN DETECTING SEASONAL CHANGE

CAROLYN M. KNIGHT[1,2,4], ROBERT E. KENWARD[1,3], RODOLPHE E. GOZLAN[1], KATHRYN H. HODDER[1], MARTYN C. LUCAS[2]

[1] *Centre for Ecology and Hydrology, Winfrith Technology Centre, Dorchester, Dorset. DT2 8ZD. United Kingdom.*

[2] *University of Durham, School of Biological and Biomedical Sciences, Science Laboratories, South Road, Durham. DH1 3LE. United Kingdom.*

[3] *Anatrack Ltd, Furzebrook, Wareham, Dorset. BH20 5AX. United Kingdom.*

[4]Corresponding Author Current Address: C. M. Knight. Jacobs Aquatic, Fawley, Southampton. SO45 1TW. UK. Tel. 02380 893513; Fax 02380 243274;
Corresponding Email: Carolyn.Knight@Jacobs.com

Running Headline: Home range estimation in restricted environments.

Abstract. Estimating home ranges of animals from telemetry data can provide vital information on their spatial behavior, which can be applied by managers to a wide range of situations including reserve design, habitat management and interactions between native and non-native species. Methods used to estimate home ranges of animals in restricted environments (e.g. rivers) are liable to overestimate areas and underestimate travel distances by including unusable habitat (e.g. river bank). Currently few studies collecting telemetry data from species in restricted environments maximize the information that can be gathered by using the most appropriate home range estimation techniques. Location data from 23 radio-tagged northern pike (*Esox lucius*) were used to examine the efficiency of range and travel estimators, with and without correction for unusable habitat, for detecting seasonal changes in movements. Cluster analysis most clearly demonstrated changes in range area between seasons, also showing changes in patchiness, and was least affected by unusable-environment error. Kernel analysis showed seasonal variation in range area more clearly than peripheral polygons or ellipses. Range span had no significant seasonal variation. All range area estimators were smallest in autumn, when cores were least fragmented and inter-location movements smallest. Cluster analysis showed that core ranges were largest and most fragmented in summer, when inter-location distances were most variable, whereas excursion-sensitive methods (e.g. kernels) recorded the largest outlines in spring, when inter-location distances were largest. Our results provide a rationale for *a priori* selection of home range estimators in restricted environments. Contours containing 95% of the location density defined by kernel analyses better reflected excursive activity than ellipses or peripheral polygons, whereas cluster analyses better defined range cores in usable habitat and indicate range fragmentation.

Keywords: analytical tool, cluster polygons, complex environment, Esox lucius*, home range, kernel contours, river, seasonal movements, telemetry*.

INTRODUCTION

For many animal populations, systematic radio-tracking can provide data on spatial behavior and demography more rapidly and with less bias than more traditional methods such as visual observations or mark recapture (White and Garrott 1990). The advantages of such tracking are at their greatest for elusive species, including fish.

Quantitative analysis of home range size, shape and core structure has become fundamental to understanding the movements and behavior of animals (White and Garrott 1990, Fisher 2000, Crook et al. 2001, Broomhall et al. 2003, Fuller et al. 2005). The use of telemetry data to estimate home ranges is now common-place for studies of resource use (Aebischer et al. 1993, Goguen and Mathews 2001, De Gayner et al. 2005, Flamm et al. 2005), social interactions (Sliwa 2004, Sunde and Bolstad 2004, Pejchar et al. 2005), activity (Taylor and Skinner 2003), predation (Madsen and Shine 1996, Yoder et al. 2004, Bergman et al. 2006). Home ranges can be considered as the spatial expressions of the behaviors carried out by animals to survive and reproduce (Burt 1943) that may change between seasons or year on year. Thus as spatial and temporal representations of an animal’s requirements they are well suited to use investigating applied issues of animal ecology. Home range assessment has helped to answer a wide range of applied ecological questions relating to spatial behavior including reserve design (Wielgus 2002), conservation planning (Bethke et al. 1996, Locke 1996), habitat management analyses (Peach et al. 2004), assessing establishment of reintroductions (Bar-David et al. 2005), controlling brood parasitism by pest species (Gates and Evans 1998) and interactions of native with non-native species (Kenward and Hodder 1998).

There is a wide choice of possible methods for estimating home range. One group consists of ellipses or contours based on density distributions (Dalke and Sime 1938, Jennrich and Turner 1969, Worton 1989), which are derived from all the locations and hence tend to be influenced by outliers that represent the excursions of an individual. The second group creates polygons (Dalke and Sime 1938, Jennrich and Turner 1969, Worton 1989) that minimize linkage distances between pairs of locations. Polygon methods include an excursive-sensitive minimum convex polygon around the peripheral locations, but can also exclude the influence of outliers by peeling or with cluster analysis to define range cores. The various density and linkage methods differ in their ability to (i) estimate home range outlines that conform to the observed locations; (ii) derive statistics describing the range structure; and (iii) achieve stable estimates with few locations (Harris et al. 1990, Kenward 1992, Robertson et al. 1998).

Methods of estimating home range use were primarily designed for species that move freely throughout the landscape (Dalke and Sime 1938, Calhoun & Casby 1958, Dixon and Chapman 1980). However, many species are tightly associated with restricted and fragmented habitats such as woodland (Redpath 1995, Major and Gowing 2001) or confine their movements to largely linear pathways. Mammals, such as weasels (*Mustela nivalis*), inhabiting field edges in agricultural areas tend to remain confined to these linear corridors rather than venturing far into cultivated fields (MacDonald et al. 2004). Species such as river otter (*Lutra canadensis*) (Blundell et al. 2001), watervole (*Arvicola terrestris*) (Barreto and MacDonald 2000, Fedriani et al. 2002) and bald eagle (*Haliaeetus leucocephalus*) (Harmata and Montopoli 2001) often associate themselves with rivers and shorelines and many freshwater fish are limited to rivers. The use of standard home range methods in these cases may estimate outlines that include large areas of unusable habitat. This is particularly true where narrow corridors of usable habitat are highly convoluted, as occurs for braided river channels and meanders. The result is bias in size and home range structure statistics that indicate foraging movements.

Recently some investigators have attempted to develop new techniques to address this issue using simulated datasets (Burgman and Fox 2003, Matthiopoulos 2003, Getz and Wilmers 2004), however these techniques have not become widely available or used in ecological management. Few applied studies of species with linear patterns of movement maximize the information gained from the data by employing the most appropriate methods to quantify home ranges. Currently, while most work using linear home range estimation has focused on fish in rivers (Bridcut and Giller 1993, Baras 1997, Masters et al. 2002, Bahr and Shrimpton 2004), novel analysis has been applied mainly to river otters (Sauer et al. 1999, Blundell et al. 2001). Despite an increasing number of telemetry studies on river fish species and related management issues, such as interactions between natives and non-natives, most either make no estimates of home range or calculate very basic measures, likely missing much of the ecological or behavioral information (Vokoun 2003). With potentially rapid alteration in habitats and movements of animals through climate change, coupled with strict targets for management through legislation such as the Water Framework Directive (European Commisssion 2000), the need to make best use of hard-won data from radio tracking is now greater than ever.

In this study, we test the effectiveness in a restricted environment of commonly used and widely available home range analysis techniques, including the clipping of range outlines to include only the water usable by an aquatic species. Pike (*Esox lucius* Linnaeus), like many fish species, are known to alter their behavior seasonally (Cook and Bergersen 1988, Tipping 2001). We postulate that size and internal structure of home ranges of river-dwelling pike, would differ between seasons to reflect differences in behavior, and that these differences would be shown more effectively by some analysis methods than by others.

MATERIALS AND METHODS

Study area

The study was conducted on the lower River Frome, Dorset, UK. The river is largely unmodified, with a meandering main channel in its lower reaches, but also has a man-made millstream within the study site. Most fish locations were collected within a 2 km stretch of river (UK national grid references SY867863 to SY882870), although fish were also tracked outside this stretch.

Radio tagging and tracking

Data from 23 adult pike were used to test the range estimators. Radio tags (TW-5 tags, Biotrack Ltd., Wareham BH20 5AX, UK) were implanted into the body cavity of the pike (58 – 101 cm FL) as described in Beaumont et al. (2002). Fish locations were determined to within 1 m by triangulation from within 10 m on the river bank, using a Sika radio-receiver (Biotrack Ltd.) and a hand-held three-element Yagi antenna.

Data were collected between May 2000 and September 2003, during March, June, September and December to provide home range estimates for each season. Fish were located at dawn, midday and dusk every day over a 13 day period, resulting in standard home range data sets of 39 locations per fish in each season. The timing of dawn, midday and dusk locations was selected as a result of a pilot study that demonstrated the diel activity of pike to be at dawn and dusk (Masters et al. 2002; Hodder et al. in press). In addition, fish were routinely located two or three times per week during the entire study period in order to prevent loss of mobile individuals.

One range was used from each fish per season. If data were collected from an individual in more than one year, the average range area for that season was used. In order to enable direct seasonal comparison of river channel habitat use ranges estimated during flooding were not included as these may have included floodplain habitat not available to fish in all seasons. In total, 16 records were available for spring, 12 for summer, 14 for autumn and 12 for winter (Table 1).

Home range and movement analyses

Four methods of area-based range analysis were used. All were methods readily available in commercial software (as reviewed by Larson (2001)) that are widely applied (Kernohan et al. 2001, Walls and Kenward 2001, Fuller et al. 2005) to give trade-offs between precision in conforming to peripheral and core locations (Table 2) and sample-size requirements (Robertson et al. 1998). All were estimated with RANGES 6F (Anatrack Ltd., Wareham. BH20 5AX, UK), with abbreviations and classification following Kenward *et al* (2001).

Density methods

Jennrich-Turner ellipses, estimated to include 95% of the density distribution (E_{95}), are least precise in conforming to locations, but can give stable estimates of total range area with 12-15 locations that have low spatio-temporal correlation (Kenward, 2001). Kernel contours containing 95% of the estimated density distribution (K_{95}) were estimated using least squares cross-validation with a fixed smoothing multiplier of 1 and a 40×40 matrix as a total area measure with more flexible conformation. A widely-used estimator of core size (Fuller et al. 2005) is the kernel contour K_{50}, containing 50% of density distribution (Table 2).

Link distance methods

As an estimate of total range size, a single convex polygon around 100% of the locations (X_{100}) provides greatest comparability with other publications (Harris et al. 1990), but its conformation to the range periphery requires large sample sizes to minimize sample-size-dependence. Similarly, core polygons derived by cluster analysis require large samples of locations for stability (Robertson et al. 1998). Cluster polygons were estimated around 85% of the locations in each range (Cx_{85}) as this excluded peripheral locations for 95% of the ranges (Kenward et al. 2001). In addition to area and number of cores, cluster analysis provides an index of range patchiness: the sum of areas of the separate cores as a fraction of the area of a single convex polygon around all the clusters decreases from 1, if locations are all in one nucleus, to a small fraction if nuclei are far apart (Harris et al. 1990).

Areas and distances in restricted environments

A problem with analyzing movements in restricted environments is that measurement of distances by straight lines may underestimate travel distances for example, in rivers, by cutting across curves, islands and junctions with tributaries. RANGES 6F avoids this problem by estimating inter-location distances along a river midline for travel estimates and the nearest-neighbor distances used in cluster analysis. Similar functions may be performed in widely used software such as ArcView. A more pervasive problem with analyses in rivers is that home range outlines often extend beyond the river banks (Fig. 1), so that inaccuracy (over-estimation of area) may mask biologically meaningful relationships. Cluster analysis minimizes this error (Hodder et al. in press) but cannot entirely eliminate it. Outlines for all six range area estimators were therefore clipped to a map of the river banks that was imported to RANGES 6F from ArcView GIS 3.2 (ESRI Inc, Redlands, California). An excursion-excluded range span was calculated as the summed midline lengths of 85% cluster cores. The clipped X_{100} measures maximum river area covered by excursions and is equivalent to maximum linear distance at constant river width.

Comparing estimators

Two approaches were used to compare the performance of different spatial estimators. ‘Discrimination testing’ compared the ability of different estimators (of area, span, patchiness and distance between consecutive locations) to detect variation between seasons. When testing for seasonal variation with six estimators of range area in the same data set, there was an enhanced probability of Type I error. Therefore a Bonferroni correction was applied. ‘Error testing’ compared, for each method, the extent of unusable environment (out-of-river) error, its coefficient of variance and its correlation with range span (as an independent estimate of range size). The index of out-of-river error was total range area divided by clipped area.

Seasonal variation in range areas, patchiness and distances between consecutive locations was investigated with a global test across all seasons, followed by pair-wise comparison of seasons. A Friedman test of overall seasonal variation in range size was used for seven fish that contributed a range in all four seasons, followed by Mann-Whitney U-tests of range size differences between pairs of seasons for all fish. Wilcoxon tests of estimators for each season paired across the same fish gave similar results, albeit at lower significance levels due to reduced sample sizes.

RESULTS

Friedman tests demonstrated overall differences in area between seasons only when calculated with Cx_{85} and Cx_{85} clipped ($P < 0.01$). However, range area was found also to differ significantly between pairs of seasons for K_{95} and K_{50} using Mann-Whitney U-tests (Fig. 2). All methods estimated the smallest ranges in autumn. For the kernel estimators, summer range areas were significantly larger ($P < 0.001$) than autumn range areas for both kernel and cluster estimators. These seasonal patterns remained the same after clipping. There were no significant seasonal differences in range span (Fig. 2g).

Excursion sensitive range estimators X_{100}, E_{95} and K_{95} gave larger range areas than core estimators Cx_{85} and K_{95}, by a factor of ten (Fig. 2). However, clipping increased comparability between range cores and excursion-sensitive methods.

Ellipses produced the highest proportion of out-of-river error within each range (Fig. 3a). However the two kernel estimators, particularly K_{50}, had the highest variability in out-of-river error created during range estimation (Fig. 3b). Clusters (Cx_{85}) gave lowest and least variable errors.

Range span provides an index for investigating the extent to which out-of-river error depends on range size, because the greater the span along a curvaceous river, the more meanders the outline is likely to encompass. The influence of range size on the amount of out-of-river error included into estimation of range size varied greatly between different estimators from 8% to 73% (Fig. 4). Error of core range estimators was less correlated with range span (maximum $R^2 = 44\%$) than for excursion sensitive kernels and polygons (maximum $R^2 = 73\%$) but not ellipses ($R^2 = 8\%$)

Overall distances traveled differed between seasons in a Friedman test ($P < 0.05$). Distances moved between locations in spring were significantly longer than in autumn and winter ($P < 0.01$). Distances were highly variable in summer, because some pike appeared to exhibit less excursive activity than others, and therefore only showed tendencies ($0.05 < P < 0.01$) to differ from spring and winter (Fig. 5).

Variation in home range patchiness indicated differences in core range structure between seasons (Fig. 6). Home ranges were significantly less patchy in autumn than summer ($P < 0.01$), when fish activity was less tightly focused in the core areas.

DISCUSSION

The area that is repeatedly traversed by an animal tends not to be used either in a uniform manner, or as defined by a normal distribution (White and Garrott 1990). Typically, there are one or more patches of intensive use surrounded by an area used for excursions (Kenward 1987, 2001) or for patrolling territorial boundaries (Kruuk 1978). An ability to identify the number of high-use cores, and their placement with regard to habitats and other animals, can reveal much more about foraging and sociality than can mere range size (Fuller et al. 2005) and is crucial to many management and conservation applications. Relative size and usage of peripheral areas can indicate the effort directed to exploratory behavior, mating and territoriality, as well as quantifying the habitats and neighbors available to an individual (Allouche et al. 1999).

In this study, cores defined by cluster analysis showed the strongest variation between seasons, the lowest and least variable inclusion of unusable habitat, the second lowest correlation with range span, and also showed seasonal variation in core fragmentation. The least variation due to estimation processes might be expected in cluster cores, because the exclusion of outliers eliminates a small number of locations with very variable placement due to behavior that may differ from core activities (Kenward et al. 2001). Areas of clusters are totally uninfluenced by excluded outliers. In contrast density estimators include effects of all locations in every calculation, although distance functions of harmonic mean estimators (Dixon and Chapman 1980) minimize this effect (Kenward et al. 2001) and peripheral polygons are defined by outliers. With least methodological variance, cluster areas should be best able to show biological variance, in this case due to seasonality. Moreover, their tight definition by polygons minimizes the expansion into unusable habitat that results from smoothing implicit in density estimation. A similar restriction to local nearest-neighbor linkages may give equally good performance from the convex-hull approach of (Getz and Wilmers 2004) if an algorithm becomes more generally available.

For estimating a home-range periphery, a K_{95} contour gave better detection of seasonal variation than either an E_{95} ellipse or a peripheral convex polygon (X_{100}). This resulted despite the peripheral polygon having least (and relatively invariable) out-of-river error, probably because only the kernel contours could define multinuclear range outlines. The moderate sensitivity to outliers of K_{95}, as opposed to the high sensitivity of E_{95} and total dependence of X_{100} may also have been advantageous.

The extent of unusable-environment error would be expected to depend both on the home range estimator and the behavior of each animal. Expansive estimators and far ranging individuals will tend to cause more unused area to be included in the home range calculation than those that occupy smaller areas. Ellipse estimates tended to be very large (Fig. 2), such that error was large and relatively invariable (Fig. 3), which apparently minimized scope for correlation with range span (Fig. 4). Yet in no cases was there a tendency for seasonal variation to be better defined by clipping of unusable habitat. This poor result from an intuitively attractive analysis approach was surprising. If confirmed for other species, this finding implies that unclipped estimates of range area might serve for fish in both linear and non-linear (e.g. lakes) habitats. Indeed, unclipped kernel and cluster analyses showed significant range expansion of home ranges when the river

Frome flooded adjacent fields (Hodder et al. in press). However, clipping might be more necessary for habitat analyses and when range overlaps are used to investigate sociality.

Seasonal differences in range size reflected variation partly in linear distances traveled and partly in the patchiness of range structure. Range span alone however, was not informative in terms of pike behavior. It did not show the significant differences in space use between seasons demonstrated by area based range analysis methods in this study or the spring peak and autumn dip in movement described in Cook and Bergersen's (1988) radio telemetry study in a Colorado reservoir. A high level of range span variation between individuals hindered detection of statistically significant seasonal trends, as it did for peripheral convex polygon areas, with which range span correlated strongly (Fig. 4). Differences in river width between seasons might also have contributed to area-based methods having greater statistical significance than range span in seasonal differences.

Therefore, although range span has traditionally been the most common analysis technique of animals in restricted habitats (Powell 2000), linear distance measures of movement should be complemented by estimates of home range. For pike in the River Frome, this showed that all range area estimators were smallest in autumn (Fig. 2), at which time cores were least fragmented (Fig. 6) and inter-location movements smallest (Fig. 5). Cluster analysis showed that core ranges were largest and most fragmented in summer, when inter-location distances were at their most variable. However, the largest peripheral range areas, with statistically significant differences from autumn for the most moderately excursion-sensitive methods (K_{95}) were in spring, when inter-location distances were at their largest.

Application

In a review of how twelve estimators of home range area scored subjectively in seven performance criteria, Kernohan et al. (2001) rated kernels first and clusters second. Our objective comparison of four methods in a complex restricted environment concurs with this result for estimating peripheral outlines, but we rate cluster polygons as the more appropriate for estimating range cores because of their greater ability to eliminate influence of outlying locations and their generation of structure statistics. A multifaceted approach with more than one technique enables the most thorough interrogation of the data and also helps to overcome some of the drawbacks inherent in the different methods of home range analysis. Continued estimation of range span will provide an index that remains comparable with previous studies in restricted environments, such as rivers and hedgerows.

Maximizing data interrogation and comparability of results between studies should aid the application of findings to management situations For example, improved study and analysis of space-use interactions between native and non-native fish species in river systems could contribute usefully to understanding mechanisms of observed declines in native species (e.g. Marchetti et al. 2004). Furthermore, improved data interrogation and comparability of space-use statistics in restricted habitats would enhance their utility for meta-analyses that can give broad ecological insights. Current progress in the analysis of telemetry data (Börger et al. 2006), should permit even greater exploitation of available information and provision of resources for managers. Management may also require predictive modeling, for which it is important to minimize sources of error and bias.

ACKNOWLEDGEMENTS

We thank the many fieldworkers for their hard work tracking pike, in particular J. Masters, A. Pinder, W. Beaumont and L. Scott and also S. Walls for comments on the manuscript. C. M. Knight was in receipt of a Natural Environment Research Council (NERC) studentship. The data collection was supported by a Centre for Ecology and Hydrology Integrated Fund project and a NERC LOCAR grant.

LITERATURE CITED

Aebischer, N.J., P.A. Robertson, and R.E. Kenward. (1993) Compositional analysis of habitat use from animal radio-tracking data. Ecology, **74**, 1313-1325.

Allouche, S., A. Thevenet, and P. Gaudin. (1999) Habitat use by chub (*Leuciscus cephalus* L. 1766) in a large river, the French Upper Rhone, as determined by radiotelemetry. Archiv fur Hydrobiologie, **145**, 219-236.

Bahr, M.A., and J.M. Shrimpton. (2004) Spatial and quantitative patterns of movement in large bull trout (*Salvelinus confluentus*) from a watershed in north-western British Columbia, Canada, are due to habitat selection and not differences in life history. Ecology of Freshwater Fish, **13**, 294-304.

Bar-David, S., D. Saltz, and T. Davan. (2005) Predicting the spatial dynamics of a reintroduced population: The Persian fallow dear. Ecological Applications, **15**, 1833-1846.

Baras, E. (1997) Environmental determinants of residence area selection by *Barbus barbus* in the River Ourthe. Aquatic Living Resources, **10**, 195-206.

Barreto, G.R., and D.W. MacDonald. (2000) The decline and local extinction of a population of water voles, *Arvicola terrestris*, in southern England. International Journal of Mammalian Biology, **65**, 110-120.

Beaumont, W.R.C., B. Cresswell, K.H. Hodder, J.E.G. Masters, and J.S. Welton. (2002) A simple activity monitoring radio tag for fish. Hydrobiologia, **483**, 219-224.

Bergman, E. J., R. A. Garrott, S. Creel, J. J. Borkowski, R. Jaffe, and E. G. R. Watson. (2006) Assessment of prey vulnerability through analysis of wolf movements and kill sites. Ecological Applications, **16**, 273-284.

Bethke, R., M. Taylor, S. Amstrup, and F. Messier. (1996) Population delineation of polar bears using satellite collar data. Ecological Applications, **6**, 311-317.

Blundell, G.M., J.A.K. Maier, and E.M. Debevec. (2001) Linear home ranges: Effects of smoothing, sample size and autocorrelation on kernel estimates. Ecological Monographs, **71**, 469-489.

Börger, L., N. Franconi, F. Ferretti, F. Meschi, G. De Michele, A. Gantz, and T. Coulson. (2006) An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. The American Naturalist, **168** , 471-485.

Bridcut, E.E., and P.S. Giller. (1993) Movement and site fidelity in young brown trout *Salmo trutta* populations in a southern Irish stream. Journal of Fish Biology, **43**, 889-899.

Broomhall, L.S., M.G.L. Mills, and J.T. du Toit. (2003) Home range and habitat use by cheetahs (*Acinonyx jubatus*) in the Kruger National Park. Journal of the Zoological Society of London, **261**, 116-128.

Burgman, M. A. and J. C. Fox. (2003) Bias in species range estimates from minimum convex polygons: implications for conservation and options for improved planning. Animal Conservation, **6**, 19-28

Burt, W.H. (1943) Territoriality and home range concepts as applied to mammals. Journal of Mammology, **24**, 346-352.

Calhoun, J.B., and J.U. Casby. (1958) Calculation of home range and density of small mammals. In Public Health Monograph 55. United States Public Health Service.

Cook, M.F., and E.P. Bergersen. (1988) Movements, habitat selection, and activity periods of northern pike in Eleven Mile Reservoir, Colorado. Transactions of the American Fisheries Society, **117**, 495-502.

Crook, D.A., A.I. Robertson, A.J. King, and P. Humphries. (2001) The influence of spatial scale and habitat arrangement on diel patterns of habitat use by two lowland river fishes. Oecologia, **129**, 525-533.

Dalke, P.D., and P.R. Sime. (1938) Home and seasonal ranges of eastern cottontail in Connecticut. Transcripts of the North American Wildlife Conference, **3**, 659-669.

De Gayner, E. J, M., G. Kramer, J. G. Doerr, and M. J. Robertsen. (2005) Windstorm disturbance effects of forest structure and black bear dens in southeast Alaska. Ecological Applications, **15**, 1306-1316

Dixon, K.R., and J.A. Chapman. (1980) Harmonic mean measure of animal activity areas. Ecology, **61**, 1040-1044.

European Commission (2000) Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy In Official Journal of the European Community, pp. 1-72.

Fedriani, J.M., M. Delibes, P. Ferreras, and J. Roman. (2002) Local and landscape habitat determinants of water vole distribution in a patchy Mediterranean environment. Ecoscience, **9**, 12-19.

Fisher, D.O. (2000) Effect of vegetation structure, food and shelter on the home range and habitat use of an endangered wallaby. Journal of Applied Ecology, **37**, 660-671.

Flamm, R. O., B. L. Weigle, I. E. Wright, M. Ross, and S. Aglietti. (2005) Estimation of manatee (*Trichechus manatus latirostris*) places and movement corridors using telemetry data. Ecological Applications, **15**, 1415-1426.

Fuller, M.R., K.E. Church, J.J. Millspaugh, and R.E. Kenward. (2005). Wildlife Telemetry. In Manual of Wildlife Management Techniques. (ed C.L. Braun), pp. 377-417. The Wildlife Society, Maryland.

Gates, J. E., and D. R. Evans. (1998) Cowbirds breeding in the central Appalachians: Spatial and temporal patterns and habitat selection. Ecological Applications, **8**, 27-40.

Getz, W.M., and C.C. Wilmers. (2004) A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. Ecography, **27**, 489-505.

Goguen, C. B., and N. E. Mathews. (2001) Brown-headed cowbird behavior and movements in relation to livestock grazing. Ecological Applications, **11**, 1533-1544.

Harmata, A.R., and G.R. Montopoli. (2001) Analysis of bald eagle spatial use of linear habitat. Journal of Raptor Research, **35**, 207-213.

Harris, S., W.J. Cresswell, P.G. Forde, W.J. Trewhella, T. Woollard, and S. Wray. (1990) Home-range analysis using radio-tracking data - a review of problems and techniques particularly as applied to the study of mammals. Mammal Review, **20**, 97-123.

Hodder, K.H., R.E. Kenward, S.S. Walls, and R.T. Clarke. (1998) Estimating core ranges: A comparison of techniques using the common buzzard (*Buteo buteo*). Journal of Raptor Research, **32**, 82-89.

Hodder, K.H., J.E.G. Masters, W.R.C. Beaumont, R.E. Gozlan, A.C. Pinder, C.M. Knight, and R.E. Kenward. (in press) Techniques for evaluating the spatial behaviour of river-fish. Hydrobiologia.

Jennrich, R.J., and F.B. Turner. (1969) Measurement of non-circular home range. Journal of Theoretical Biology, **22**, 227-237.

Kenward, R.E. (1987) Wildlife radio tagging: Equipment, field techniques and data analysis Academic Press, London.

Kenward, R.E. (1992). Quantity versus quality: programming for collection and analysis of radio tag data. In Wildlife telemetry - Remote Monitoring and Tracking of Animals (eds I.G. Preide & S.M. Swift), pp. 231-246. Ellis Horwood, Chichester, UK.

Kenward, R.E. (2001) A manual for wildlife radio tagging Academic Press.

Kenward, R.E., R.T. Clarke, K.H. Hodder, and S.S. Walls. (2001) Density and linkage estimators of home range: nearest-neighbor clustering defines multinuclear cores. Ecology, **82**, 1905-1920.

Kenward, R.E., and K.H. Hodder. (1998) Red squirrels (*Sciurus vulgaris*) released in conifer woodland: the effects of source habitat, predation and interactions with grey squirrels (*Sciurus carolinensis*). Journal of the Zoological Society of London, **244**, 23-32.

Kernohan, B.J., R.A. Gitzen, and J.J. Millspaugh. (2001). Analysis of animal space use and movements. In Radio Tracking and Animal Populations (eds J.J. Millspaugh & J.M. Marzluff). Academic Press.

Kruuk, H. (1978) Spatial organisation and territorial behaviour of the European badger *Meles meles*. Journal of Zoology, **184**, 1-19.

Larson, M.A. (2001). A catalogue of software to analyze radiotelemetry data. In Radio Tracking and Animal Populations (eds J.J. Millspaugh & J.M. Marzluff), pp. 398-421. Academic Press, San Diego, USA.

Locke, H. (1996) Yellowstone to Yukon. Wildlife Conservation, **99**, 24-32.

MacDonald, D.W., T.E. Tew, and I.A. Todd. (2004) The ecology of weasels (*Mustela nivalis*) on mixed farmland in southern England. Biologia, **59**, 235-241.

Madsen, T., and R. Shine. (1996) Seasonal migration of predators and prey - a study of pythons and rats in tropical Australia. Ecology, **77**, 149-156.

Major, R.E., and G. Gowing. (2001) Survival of red-capped robins (*Petroica goodenovii*) in woodland remnants of central western New South Wales, Australia. Wildlife Research, **28**, 565-571.

Marchetti, M.P., Moyle, P.B., and R. Levine. (2004) Alien fishes in California watersheds: characteristics of successful and failed invaders. Ecological Applications, **14**, 587-596.

Markus, N., and L. Hall. (2004) Foraging behavior of the black flying-fox (*Pteropus alecto*) in the urban landscape of Brisbane, Queensland. Wildlife Research, **31**, 345-355.

Masters, J.E.G., J.S.Welton, W.R.C. Beaumont, K.H. Hodder, A.C. Pinder, R.E. Gozlan, and M. Ladle. (2002) Habitat utilisation by pike *Esox lucius* L. during winter floods in a southern English chalk river. Hydrobiologia, **483**, 185-191.

Matthiopoulos, J. (2003) Model-supervised kernel smoothing for the estimation of spatial usage. Oikos, **102**, 367-377

Peach, W.J., M. Denny, P.A. Cotton, I.F. Hill, D. Gruar, D. Barritt, A. Impey, and J. Mallord. (2004) Habitat selection by song thrushes in stable and declining farmland populations. Journal of Applied Ecology, **41**, 275-293.

Pejchar, L., K. D. Holl, and J. L. Lockwood. (2005) Hawaiian honeycreeper home range size varies with habitat: Implications for native Acacia koa forestry. Ecological Applications, **15**, 1053-1061.

Powell, R.A. (2000). Animal home ranges and territories and home range estimators. In Research Techniques in Animal Ecology: Controversies and Consequences (ed T.K. Fuller), pp. 65-110. Columbia University Press, New York.

Redpath, S.M. (1995) Habitat fragmentation and the individual: tawny owls *Strix aluco* in woodland patches. Journal of Animal Ecology, **64**, 652-661.

Robertson, P.A., N.J. Aebisher, R.E. Kenward, I.K. Hanski, and N.P. Williams. (1998) Simulation and jack-knifing assessment of home-range indices based on underlying trajectories. Journal of Applied Ecology, **35**, 928-940.

Sauer, T.M., M. Ben-David, and D.T. Bowyer. (1999) A new application of the adaptive-kernal method: Estimating linear home ranges of river otters, *Lutra canadensis*. Canadian Field-Naturalist, **113**, 419-424.

Schad, S., E. Revilla, T. Wiegand, F. Knauer, P. Kaczensky, U. Breitenmoser, L. Bufka, J. Cerveny, P. Koubek, T. Huber, C. Stanisa, and L. Terepl. (2002) Assessing the suitability of central European landscapes for the reintroduction of Eurasian lynx. Journal of Applied Ecology, **39**, 189-203.

Sliwa, A. (2004) Home range size and social organisation of black-footed cats (*Felis nigripes*). Mammalian Biology, **69**, 96-107.

Sunde, P., and M.S. Bolstad. (2004) A telemetry study of the social organization of a tawny owl (*Strix aluco*) population. Journal of Zoology, **263**, 65-76.

Taylor, W.A., and J.D. Skinner. (2003) Activity patterns, home ranges and burrow use of aardvarks (*Orycteropus afer*) in the Karoo. Journal of the Zoological Society of London, **261**, 291-297.

Tipping, J. M. (2001) Movement of tiger muskellunge in Mayfield Reservoir, Washington. North American Journal of Fisheries Management, **21**, 683-687.

Vokoun, J.C. (2003) Kernel density estimates of linear home ranges for stream fishes: Advantages and data requirements. North American Journal of Fisheries Management, **23**, 1020-1029.

Walls, S.S., and R.E. Kenward. (2001) Spatial consequences of relatedness and age in buzzards. Animal Behaviour, **61**, 1069-1078.

White, G.C., and R.A. Garrott. (1990) Analysis of wildlife radio-tracking data. Academic Press, New York, USA.

Wielgus, R. B. (2002) Minimum viable population and reserve sizes for naturally regulated grizzly bears in British Columbia. Biological Conservation, **106**, 381-388.

Woodroffe, R., C. Donnelly, D.R. Cox, F.J. Bourne, C.L. Cheeseman, R.J. Delahay, G. Gettinby, J.P. McInerney, and W.I. Morrison. (2006) Effects of culling on badger *Meles meles* spatial organization: implications for the control of bovine tuberculosis. Journal of Applied Ecology, **43**, 1-10.

Worton, B.J. (1989) Kernel methods for estimating the utilization distribution in home-range studies. Ecology, **70**, 164-168.

Yoder, J.M., E.A. Marschall, and D.A. Swanson. (2004) The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. Behavioural Ecology, **15**, 469-476.

Table 1. Summary of home range tracks for each individual fish used for estimation of home range area.

Table 2. Summary of home range estimation techniques and their advantages and disadvantages for use in restricted environments.

	Fish ID Code																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Spring		▮		▮	▮			▮	▮	▮	▮	▮	▮	▮	▮	▮	▮			▮	▮		▮
Summer	▮		▮	▮	▮	▮			▮		▮	▮			▮	▮	▮					▮	
Autumn				▮	▮		▮	▮	▮		▮	▮	▮		▮	▮	▮	▮	▮	▮			
Winter					▮			▮	▮		▮	▮	▮		▮	▮	▮	▮		▮	▮		

Table 1

Home range Technique	Sample size considerations	Periphery/core representation	% locations included	Short name	Original reference
Density methods					
Ellipses	Size can be stable with as few as 12-15 locations (well separated in time).	Outline conforms poorly to locations and is sensitive to outlying locations.	95%	E_{95}	(Worton 1989)
Kernels	Size can be stable with as few as 15-20 locations.	Contours conform to multinuclear data but not to abrupt change in location density and are affected by outlying locations.	95% 50%	K_{95} K_{50}	(Dalke and Sime 1938)
Link distance methods					
Minimum convex polygon	Sample-size-dependent but often stable with 30+ locations.	Single polygon conforms only to peripheral locations.	100%	X_{100}	(Kenward 1987)
Clusters (core influenced)	Requires 30+ locations for stability.	Polygons fit core location patches and provide internal structure statistics.	85%	C_{X85}	(Kenward et al. 2001)

Table 2

FIG. 1. Example of out-of-river error from locations of the same fish fitted with (a) 85% clusters and (b) 95% kernels (solid line) and 50% kernels (dotted line).

FIG. 2. Mean home range area (with standard deviation bars) estimated with non-clipped methods (black) and clipping (grey) for three excursion-sensitive range estimation techniques; (a) 100% polygons, (b) 95% ellipses and (c) 95% kernels, followed by two coring methods; (d) 85% clusters and (e) 50% kernels with (f) excursion-excluded range span. Letters, indicate Bonferroni corrected significant differences between the seasons labeled; Spring – P, Summer – S, Autumn – A and Winter – W. Note different scales for the top, middle and bottom plots.

FIG. 3. (a) Index of out-of-river error, as the proportion of the clipped range area in the total unclipped range area, and (b) its coefficient of variation.

FIG. 4. Regression of error index on range span for (a) 100% polygons, (b) 95% ellipses, (c) 95% kernels, (d) 50% kernels and (e) 85% clusters.

FIG. 5. Boxes show median, 25th and 75th percentiles, with whiskers at 10th and 90th percentiles (and outliers as dots) for mean midline distances between consecutive locations ($\log_{10}$ transformed). . Upper case letters indicate differences significant at the 1% level, with lower case letters for the 5% level.

FIG. 6. Home range patchiness of 85% clusters. Low scores indicate the patchiest ranges. Upper case letters indicate differences significant at the 1% level, with lower case for the 5% level.

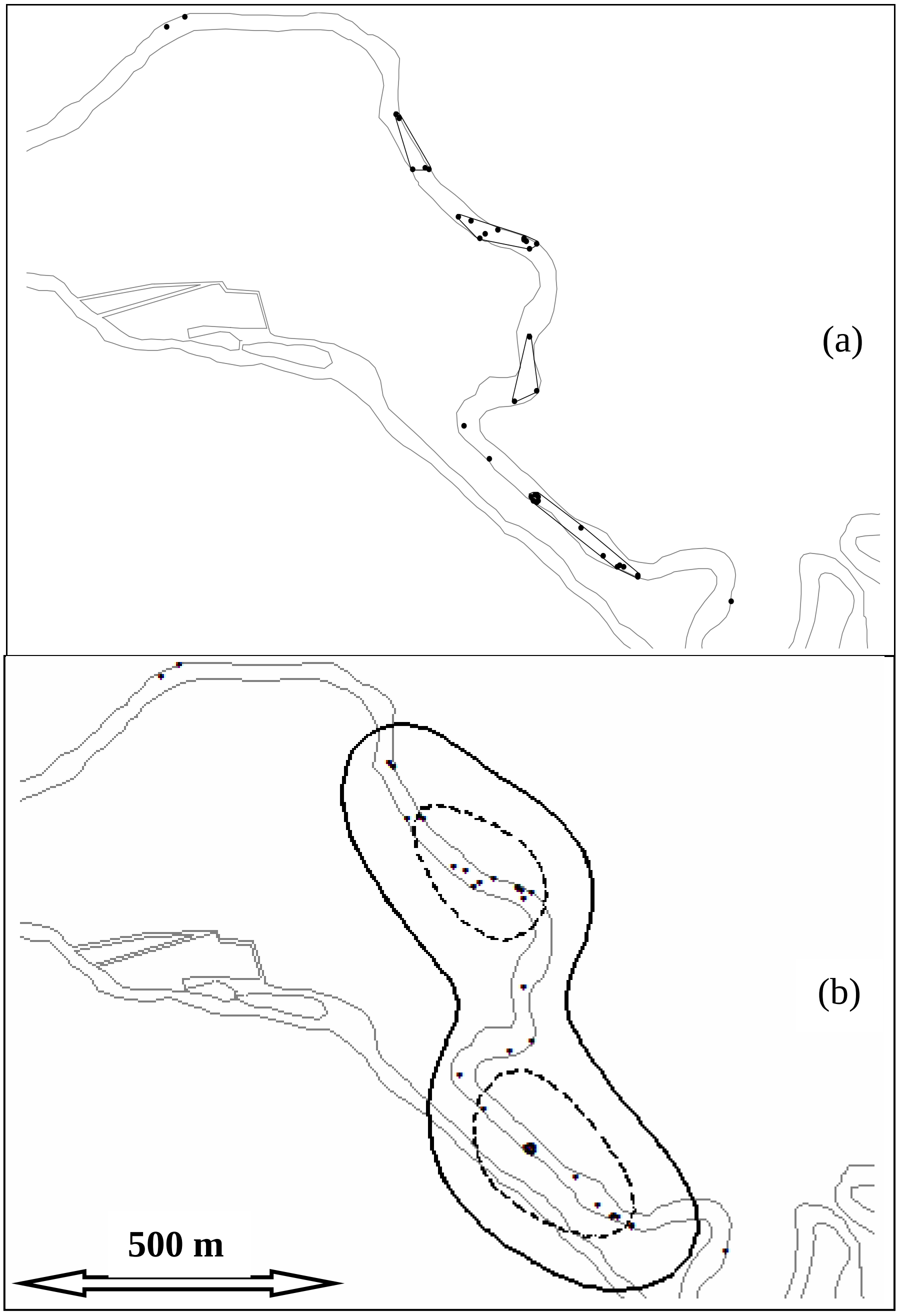

Figure 1

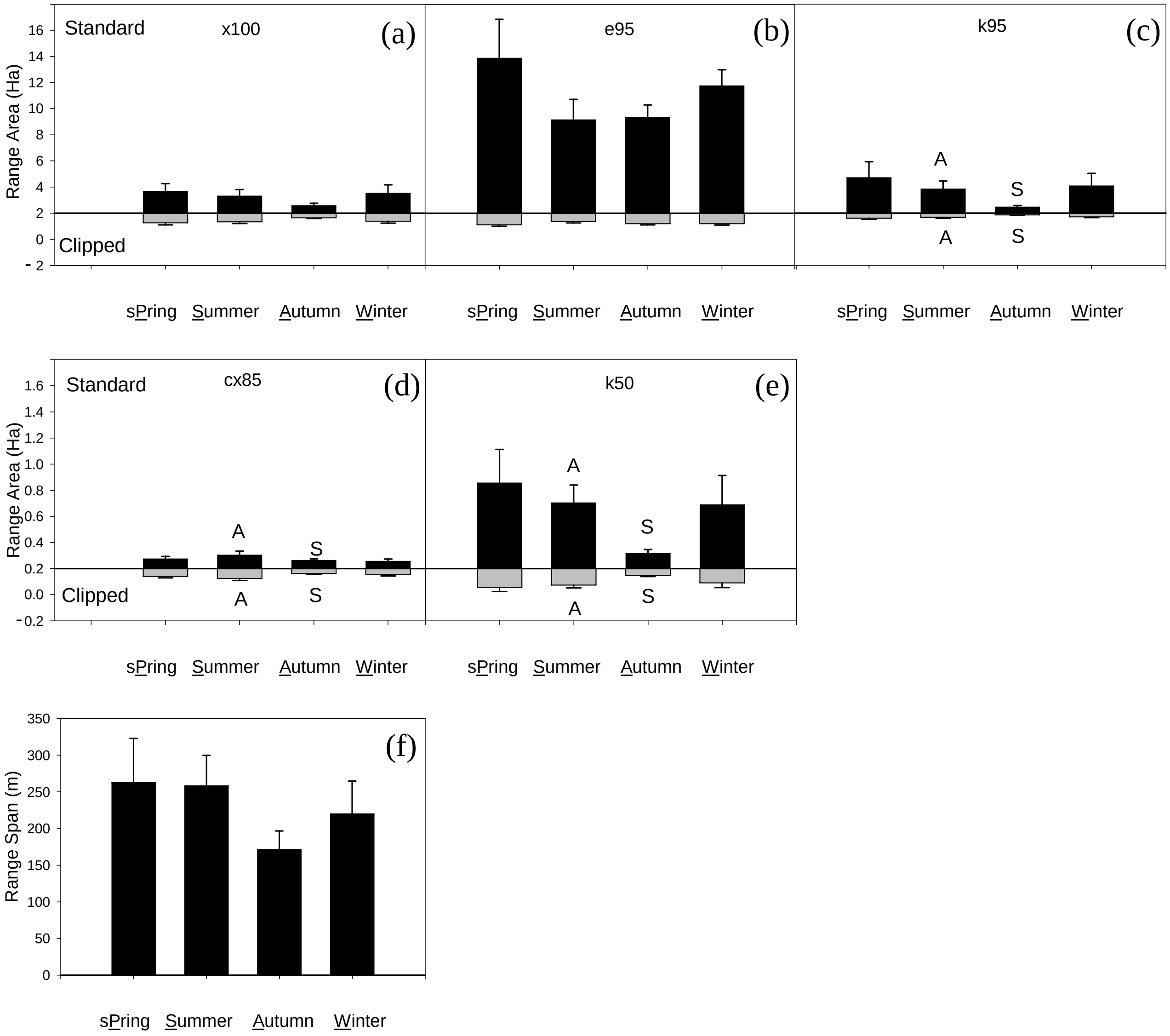
Standard
x100
(a)
e95
(b)
k95
(c)
Range Area (Ha)
16
14
12
10
8
6
4
2
0
- 2
Clipped
A
S
A
S
sPring Summer Autumn Winter
sPring Summer Autumn Winter
sPring Summer Autumn Winter
Standard
cx85
(d)
k50
(e)
Range Area (Ha)
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
Clipped
A
S
A
S
A
S
A
S
sPring Summer Autumn Winter
sPring Summer Autumn Winter
(f)
Range Span (m)
350
300
250
200
150
100
50
0
sPring Summer Autumn Winter

Figure 2

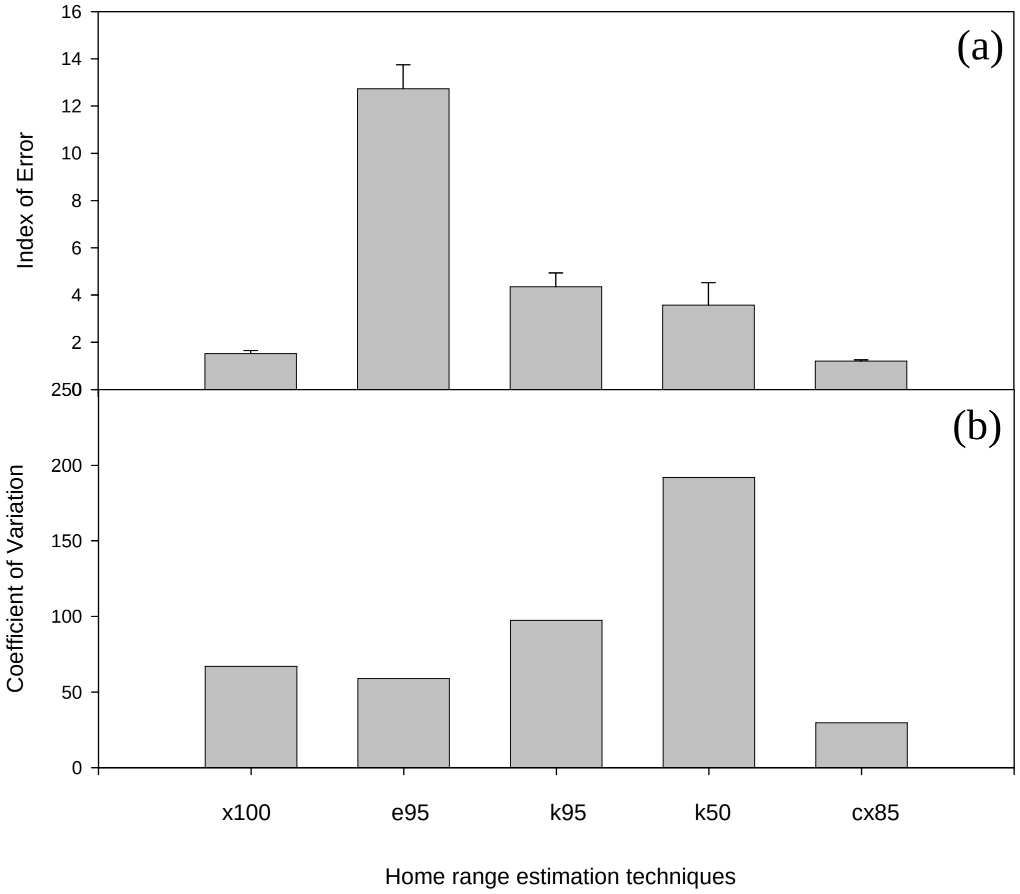
16
14
12
10
8
6
4
2
0
Index of Error
(a)
250
200
150
100
50
0
Coefficient of Variation
(b)
x100
e95
k95
k50
cx85
Home range estimation techniques

Figure 3

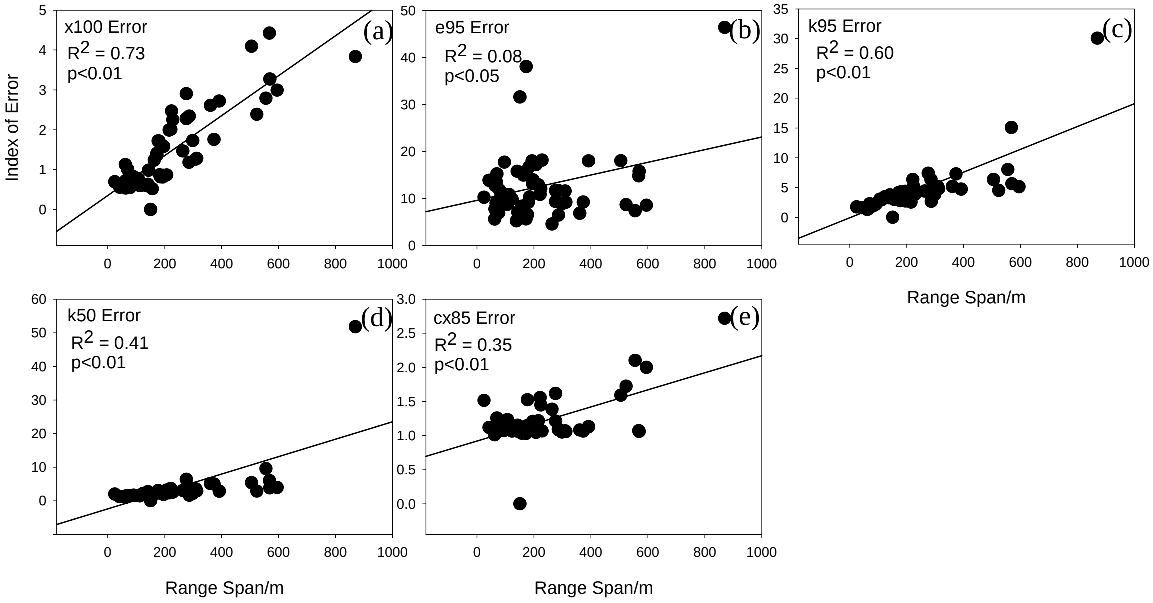
x100 Error
$R^2 = 0.73$
$p<0.01$
(a)
e95 Error
$R^2 = 0.08$
$p<0.05$
(b)
k95 Error
$R^2 = 0.60$
$p<0.01$
(c)
k50 Error
$R^2 = 0.41$
$p<0.01$
(d)
cx85 Error
$R^2 = 0.35$
$p<0.01$
(e)
Index of Error
Range Span/m
Range Span/m
Range Span/m
0
200
400
600
800
1000

Figure 4

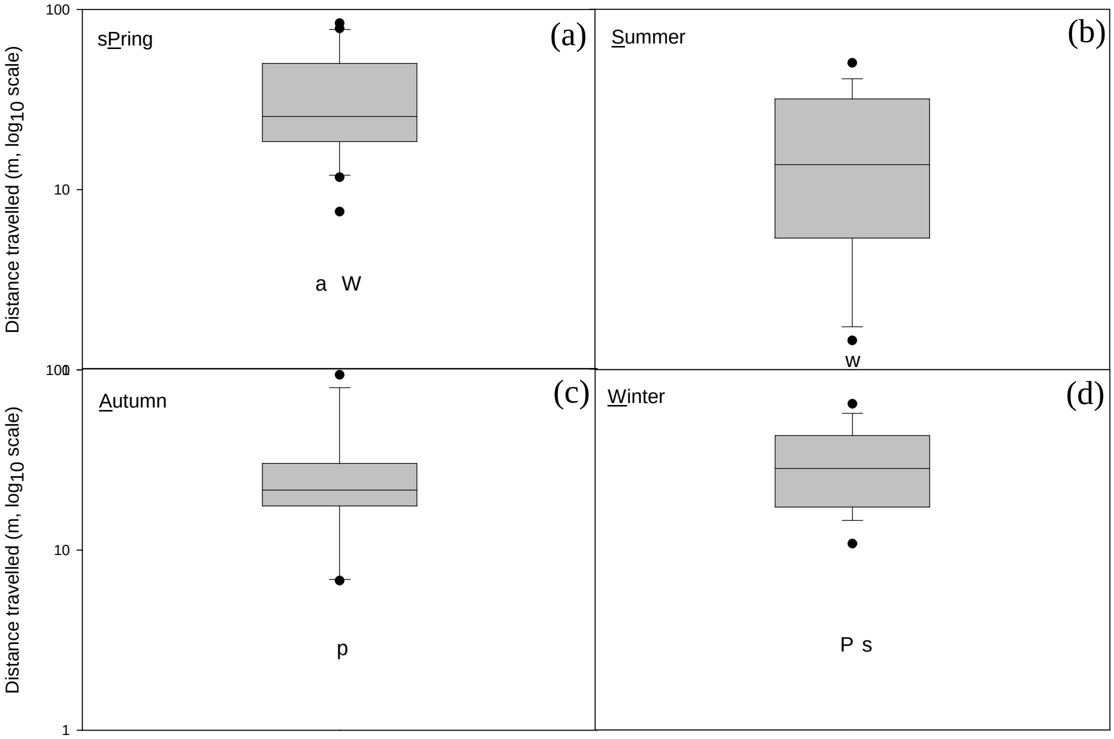
100
10
1
Distance travelled (m, log10 scale)
sPring
(a)
a W
Summer
(b)
w
Autumn
(c)
p
Winter
(d)
P s

Figure 5

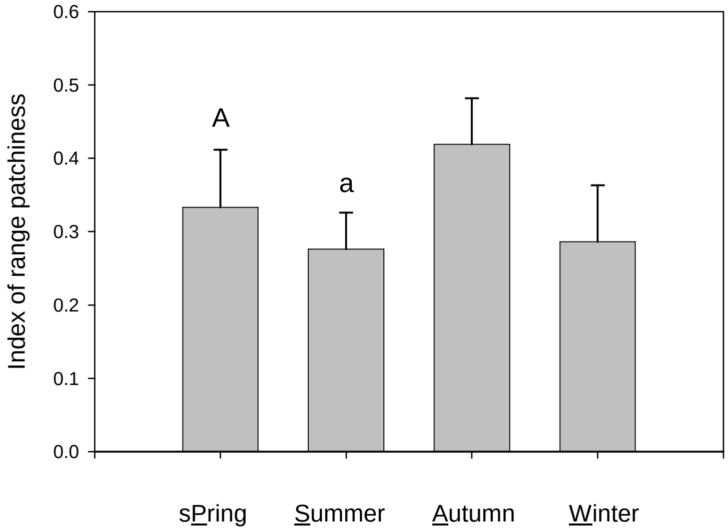
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Index of range patchiness
A
a
sPring
Summer
Autumn
Winter

Figure 6