Estimating habitat selection of badgers - a test between different methods

Authors: Kauhala, Kaarina, and Auttila, Miina

Estimating habitat selection of badgers - a test between different methods

Kaarina KAUHALA[1] and Miina AUTTILA[2]

[1] *Finnish Game and Fisheries Research Institute, Turku Game and Fisheries Research, Itäinen Pitkäkatu 3A, FI-20520 Turku, Finland; e-mail: kaarina.kauhala@rktl.fi*

[2] *Ecological Research Institute, Faculty of Biosciences, University of Joensuu, Finland; e-mail: miina.auttila@joensuu.fi*

Abstract. The aim of the present paper was to compare the picture of habitat selection obtained by using 1) different home ranges and core areas and 2) different methods (compositional analysis, Jacobs index and selection ratio), in radio-tracking studies of mammals. The experimental animal was the Eurasian badger *Meles meles*, radio-tracked in southern Finland in 2006-2007. The total home ranges used in the study, minimum convex polygon (MCP) and 95% fixed kernel home range (K95) differed in size, MCP being larger. Therefore its habitat composition resembled more that of the landscape, and comparison between K95 and the study area revealed better habitat selection within the landscape (second order selection). The proportions of two common habitat types (fields and spruce forests) differed between the core areas used in the study. Comparison between the smallest core area (K50) and MCP revealed best habitat preferences within the home range (third order habitat selection). Comparing the distribution of individual location points in different habitats to the habitat composition of home ranges did not reveal habitat preferences of badgers. The use of compositional analysis together with Jacobs index in habitat selection studies is recommended, because the simple selection ratio was not very sensitive.

Introduction

In radio-tracking studies, habitat selection of mammals is often examined by comparing the habitat compositions in the 'core area', in the 'total home range' and in the landscape (e.g. Hulbert et al. 1996, Brøseth et al. 1997, Rosalino et al. 2004, Dahl 2005). However, both the total home range and the core area can be defined in several ways (e.g. Samuel et al. 1985, Harris et al. 1990). The size and habitat composition of home ranges and core areas may differ greatly according to the method used to estimate them (synthesis of different methods in Harris et al. 1990). Depending on how they are defined, highly different pictures of the most frequently selected habitats in the landscape or the most favoured habitats within the home range (second *vs* third order selection, Johnson 1980) may be obtained. When comparing the results from different studies it is thus essential to know how the home ranges and core areas were calculated (e.g. Laver & Kelly 2008).

Minimum convex polygon (MCP, Mohr 1947) is still commonly used as the total home range (e.g. Cresswell & Harris 1988, Lucherini et al. 1995, Weber & Meia 1996, Elmeros et al. 2005, Kaartinen et al. 2005). Also 95% kernel home range (Worton 1989) is often used as the total home range (e.g. McLoughlin et al. 2003, Bender et al. 2004, Prange et al. 2004, Kauhala et al. 2006, Drygala et al. 2008, Palphramand et al. 2007). Some people recommend the use of a global smoothing parameter when calculating kernel home ranges (Whorton 1989, Kenward 2001, Hemson et al.

2005). Kernel 95% home range, calculated with a smoothing parameter < 1 (the default value = 1), is then used as a core area (e.g. Dahl 2005). However, 50% kernel home range is more often used as a core area (e.g. Okarma et al. 1998, Baghli & Verhagen 2004, Dahl 2005, Elmeros et al. 2005). The core area can also be determined from the utilization distribution curve of kernel or harmonic mean home ranges (% area plotted against % fixes, e.g. Jennrich & Turner 1969, Harris et al. 1990, Kauhala et al. 2005): the slope discontinuity indicates, which percentage value of fixes constitutes the core.

The distribution of location fixes in different habitats in the home range is also often compared with the habitat composition of the home range, usually MCP, in studies of habitat selection (Lucherini et al. 1995, Weber & Meia 1996, Brøseth et al. 1997, Revilla et al. 2000, Elmeros et al. 2005, Kaartinen et al. 2005, Palphramand et al. 2007, Drygala et al. 2008).

The method used to estimate habitat selection within the landscape or within the home ranges may also affect the picture of habitat selection. Different preference indices have been used (e.g. Storch et al. 1990, Lucherini et al. 1995, Kauhala 1996, Revilla et al. 2000, Dahl 2005, Drygala et al. 2008). Also compositional analysis (Aebischer et al. 1993, Smith 2006) is nowadays commonly used in studies of habitat selection (e.g. Hulbert et al. 1996, Revilla et al. 2000, Rosalino et al. 2004, Elmeros et al. 2005, Kaartinen et al. 2005, Palphramand et al. 2007, Rosalino et al. 2008).

The aim of the present paper was to compare the picture of habitat selection obtained by using 1) different home ranges and core areas and 2) different methods (compositional analysis, Jacobs index and selection ratio), in radio-tracking studies of mammals. The experimental animal was the Eurasian badger *Meles meles* (Linnaeus, 1758), radio-tracked during summer in southern Finland. Although badgers have been studied a lot in Britain and in southern Europe, little is known about the northern badgers. Here the aim was to test the methods used to study habitat selection in order to choose the best methods before examining larger data from several areas near the northern limit of badger distribution area in Europe.

Material and Methods

Study area

The study area (50.4 km²) was located in Tuulos (61°10'N, 24°50'E), southern Finland (province of Häme). The study area was a polygon, which included all badger home ranges. It was formed by connecting the outermost corners
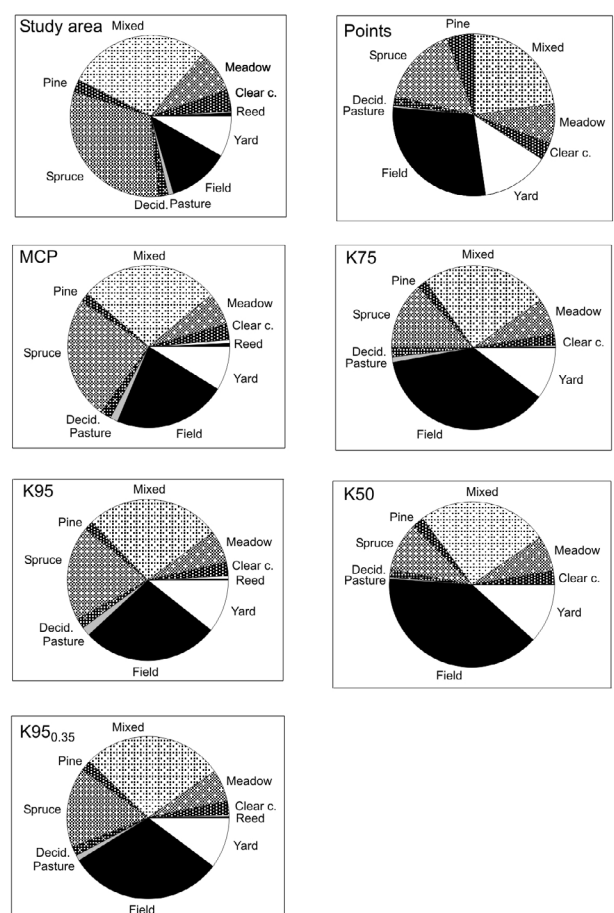
Fig. 1. Habitat composition of the study area and the mean proportions of different habitats in the total home ranges (MCP and K95), and in the core areas (K75, K50 and $K95_{0.35}$) of nine badgers radio-tracked in southern Finland in 2006-2007. The mean proportion of location points in different habitats is also given. K95 = 95% fixed kernel home range, $K95_{0.35}$ = 95% fixed kernel home range with smoothing parameter 0.35, K75 = 75% fixed kernel home range, K50 = 50% fixed kernel home range and MCP = minimum convex polygon.

of the home ranges. The western part of the area consisted of a mosaic of fields, pastures, meadows, farmhouses and patches of deciduous and mixed forests, whereas the eastern part of the area consisted mainly of spruce dominated coniferous forests and some clear cuttings, sapling stands and small bogs (Fig. 1). There were also few small lakes and rivers in the area, bordered by reed beds. The mean temperature of the year is 4.5 °C (Finnish Meteorological Institute 2008). The warmest month is July (17.2 °C) and the coldest February (-4.9 °C). Winter (i.e. the period when the mean daily temperature remains below 0 °C) usually begins in November and ends in April. Permanent snow cover falls on open ground about two weeks after winter begins, and snow melts during April.

Radio-tracking

Badgers were captured using baited wire traps. The animals were anaesthetized with ketamine hydrochloride, sexed, weighed and fitted with radio transmitters (Biotrack, model TW-3, 138-138.5 MHz). One badger was radio-tracked in summer 2006 and eight badgers in summer 2007. Radio-tracking was done from a truck with a three-element Yagi-type antenna. Animals were located from at least two points, preferably within five minutes, the angle between the bearings being as near 90° as possible. If the angle was not close to 90°, we took a third bearing to make the location more accurate. Location error was tested earlier and was < 150 m in 77% of the cases (Kauhala & Tiilikainen 2002).

Badgers were radio-tracked mainly during late evening and at night, i.e. during their circadian activity bout (Kowalczyk et al. 2003), from the beginning of May to the end of August. Locations were taken at 15-20 minutes interval. Although successive locations of each animal may not be independent, they can be used in home range calculations if there are several tracking-nights per home range (Smith et al. 1981) and the time interval between successive locations is relatively constant (De Solla et al. 1999). Our data fulfilled these criteria. Data for

both sexes (three males and six females) were pooled because of small sample size.

Home range calculations

Home ranges were calculated using the fixed kernel method (Worton 1989). The 95% kernel home range (K95), calculated using the smoothing parameter 1, was one of the 'total home ranges', the other one being the minimum convex polygon (MCP) with 100% of fixes (Mohr 1947). The core areas, i.e. areas used more frequently than other parts of the home ranges, were estimated using the fixed kernel method. One core area was the 50% kernel home range (K50) frequently used in other studies, and one was estimated from the utilization distribution curve (% area plotted against % fixes). The point where the change in the gradient of the slope is greatest indicates the core (see e.g. Jennrich & Turner 1969, Harris et al. 1990, Kauhala et al. 1993, Rosalino et al. 2004, Kauhala et al. 2005, Palphramand et al. 2007). This point was most often at 75% of fixes. Thus the 75% kernel home range (K75) was used as another core area. The core areas were calculated using the reference value 1 of the smoothing parameter. Using this value may overestimate the home range size, because it may over-smooth the range edges (Worthon 1989, Seaman & Powell 1996, Kenward 2001). Using the fraction of the reference value results in a home range, the contours of which follow more accurately the area covered by the location fixes. Thus the 95% kernel home ranges were also calculated using the smoothing parameter 0.35 (K95$_{0.35}$), which was the median of the smoothing parameters calculated individually for each home range. This home range was then used as an additional core area. We calculated all home ranges using the software Ranges6 (Kenward et al. 2003).

Sample size may affect the estimate of home range size (e.g. Harris et al. 1990, De Solla et al. 1999, Seaman et al. 1999, Börger et al. 2006, Wauters et al. 2007). In the present study the number of locations per home range was almost constant (78-85). Furthermore, the aim was to compare results obtained using

different methods/home ranges/core areas and the same data set was used in all cases. The possible differences in the results cannot thus be a consequence of different sample sizes.

The proportion of location points in different habitats were also calculated, because they are often used in habitat selection studies.

Habitat selection

Nine habitat classes were used in the analyses: farmyards, fields, pastures, meadows, deciduous forests, spruce forests, pine forests, mixed forests and clear cuttings (including sapling stands). Reed beds and small bogs were excluded, because they were sparse and not all home ranges included them. Habitat selection within the landscape (second order selection) was studied by comparing the habitat composition in the total home ranges (MCP and K95) with that in the whole study area. Habitat selection within the home ranges (third order selection) was examined by comparing the habitat compositions of the core areas to those in the total home ranges. We also compared the proportion of location points in different habitats to the habitat compositions in the home ranges. The software ArcView 3.2 was used and the home ranges and core areas were overlaid on top of a digital habitat map to determine the habitat compositions of the total home ranges and core areas. The map (CORINE land cover data) was produced by the Finnish Environment Institute (SYKE; www. environment.fi).

Habitat selection was studied by using the compositional analysis (Aebischer et al. 1993), selection ratios (% habitat used / % habitat available) and Jacobs index (index D in Jacobs 1974), used in habitat selection studies by Revilla et al. (2000) and Drygala et al. (2008). Contrary to the selection ratio, Jacobs index is independent of the relative abundance of each habitat available to the animals (Jacobs 1974). Jacobs index was calculated according to the formula: $D = (r - p)/(r + p - 2rp)$, where r is the proportion of habitat used and p the proportion of habitat available. D varies from -1 (strong avoidance) to +1 (strong preference), and values close to zero indicate that the habitat is used in proportion to its availability. An individual was the sample unit in all analyses.

Statistical tests

The normality of the distributions of different variables was tested with Kolmogorov-Smirnov one sample test. When distributions were not normal or the variances of different samples were not homogenous, nonparametric tests were used. The 95% confidence limits for the means were calculated for Jacobs indices and selection ratios to test whether they differed significantly from the 'neutral' value 0 (Jacobs index) or 1 (selection ratio). If 0 or 1, respectively, was not included within the range of confidence limits, the use of the habitat type was considered not random but the habitat was either favoured or avoided ($P < 0.05$).

Results

Total home ranges and core areas

MCP was larger than K95 (paired t-test: $t = 2.34$, df = 8, $P = 0.048$). $K95_{0.35}$ was smaller than MCP ($t = -6.93$, $P < 0.001$) and K95 ($t = -8.28$, $P < 0.001$; Fig. 2). K75 was larger than K50 ($t = 4.84$, $P = 0.001$) but almost equal in size with $K95_{0.35}$.

The habitat compositions of the total home ranges (MCP and K95) were fairly similar (Fig. 1). The proportion of farmyards tended, however, to be larger in K95 (Wilcoxon signed ranks test, $P = 0.051$) and the proportion of spruce forests and clear cuttings tended to be larger in MCP ($P = 0.066$ for spruce forests and $P = 0.051$ for clear cuttings).

The proportions of fields (Friedman two-way analysis of variance, $P = 0.003$), pastures ($P = 0.003$), spruce forests ($P = 0.035$) and pine forests ($P = 0.003$) differed between the different core areas and location points, the proportion of fields being the largest in K50 and that of pastures and spruce forests in $K95_{0.35}$. The proportion of pine forests was the largest when estimated on the basis of the location points.

19
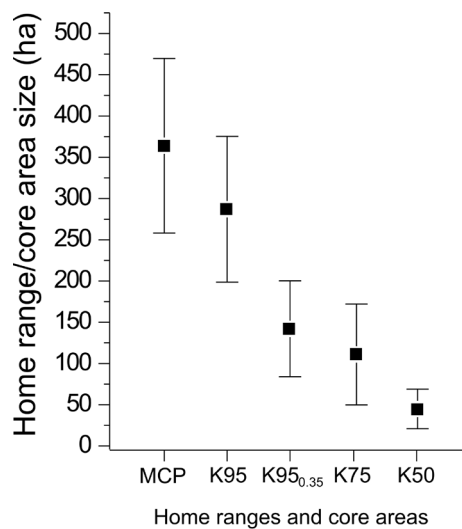
Fig. 2. Sizes (mean ± SD) of total home ranges (MCP and K95), and core areas (K75, K50 and $K95_{0.35}$) of nine badgers radio-tracked in southern Finland in 2006-2007. K95 = 95% fixed kernel home range, $K95_{0.35}$ = 95% fixed kernel home range with smoothing parameter 0.35, K75 = 75% fixed kernel home range, K50 = 50% fixed kernel home range and MCP = minimum convex polygon.

Habitat selection within the landscape (second order selection)

Comparison K95/study area was the only one which gave a significant result (randomised $P < 0.05$) according to compositional analysis (Table 1). Fields, pastures and farmyards were ranked highest, whereas pine and spruce forests and clear cuttings were ranked lowest.

According to Jacobs index, fields were favoured when K95 was compared to the study area, whereas coniferous forests, meadows and clear cuttings were avoided (Table 2). The index MCP/study area failed to reveal any habitat preferences. These results were equal to those obtained with compositional analysis.

Both selection ratios showed that fields were favoured but the ratio MCP/study area failed to reveal avoidance of coniferous forests indicated by the comparison K95/study area (Table 3).

Table 1. Habitat preferences of nine badgers, radio-tracked in southern Finland in 2006-2007, according to compositional analysis. The ranked habitat sequence and test statistics lambda (λ), χ^2, P and randomised P are given. >>> indicates a significant difference between the use of two consecutive habitat types. The comparisons, which gave significant results (randomised $P < 0.05$) are included. K95 = 95% fixed kernel home range, K50 = 50% fixed kernel home range and MCP = minimum convex polygon.

Comparison	Ranked habitat sequence	λ	χ^2	P	Rand P
Second order selection:					
K95/study area	field>pasture>yard>deciduous>mixed>>>meadow>pine> clear c.>spruce	0.0004	71.2	<0.001	0.039
Third order selection:					
K50/MCP	field>yard>meadow>mixed>clear c.>deciduous>pine >spruce>pasture	0.000	73.0	<0.001	0.047

Habitat selection within the home ranges (third order selection)

The picture of third order selection differed somewhat depending on which of the core areas or total home ranges we used in the comparisons but only the comparison K50/MCP was significant according to compositional analysis (Table 1). Fields, yards and meadows were ranked highest and pastures and coniferous forests lowest.

All Jacobs indices, except those based on location points, indicated that fields were favoured and spruce forests avoided within the home ranges (Table 2). The other indices (points/MCP and points/K95) did not reveal any habitat preferences.

Also five selection ratios revealed the preference for fields. The two ratios based on location points differed from the others and indicated that pine forests were favoured (Table 3). The ratio $K95_{0.35}$/K95 failed to reveal any habitat preferences.

20

Table 2. The habitats preferred and avoided by nine badgers, radio-tracked in southern Finland in 2006-2007, according to Jacobs indices. The habitat was included in the list, when $P < 0.05$ (the 'neutral' value 0 was not within the 95% confidence limits of the mean Jacobs index for that habitat). K95 = 95% fixed kernel home range, $K95_{0.35}$ = 95% fixed kernel home range with smoothing parameter 0.35, K75 = 75% fixed kernel home range, K50 = 50% fixed kernel home range and MCP = minimum convex polygon.

Index	Habitats preferred	Habitats avoided
Second order selection:		
K95/study area	field	meadow, pine forest, clear cutting, spruce forest
Third order selection:		
K50/MCP	field	spruce forest, pasture
K50/K95	field	spruce forest, pasture
K75/MCP	field	clear cutting, spruce forest
K75/K95	field	spruce forest, pasture
$K95_{0.35}$/MCP	field	spruce forest
$K95_{0.35}$/K95	field	spruce forest, pasture

Table 3. The habitats preferred and avoided by nine badgers, radio-tracked in southern Finland in 2006-2007, according to selection ratios. The habitat was included in the list, when $P < 0.05$ (the 'neutral' value 1 was not within the 95% confidence limits of the mean selection ratio for that habitat). K95 = 95% fixed kernel home range, $K95_{0.35}$ = 95% fixed kernel home range with smoothing parameter 0.35, K75 = 75% fixed kernel home range, K50 = 50% fixed kernel home range and MCP = minimum convex polygon.

Index	Habitats preferred	Habitats avoided
Second order selection:		
K95/study area	field	meadow, pine forest, clear cutting, spruce forest
MCP/study area	field	meadow, clear cutting
Third order selection:		
K50/MCP	field	
K50/K95	field	pasture
K75/MCP	field	clear cutting, spruce forest
K75/K95	field	spruce forest, pasture
Points/MCP	pine forest	pasture
Points/K95	pine forest	pasture
$K95_{0.35}$/MCP	field	

Discussion

Selecting the total home range for habitat analysis

When studying second order selection, using K95 reveals better than MCP the habitats the animal selects from the landscape, because the habitat composition of MCP differed less than that of K95 from the habitat composition of the whole study area (Fig. 1). Furthermore, Kernel home range probably is the most accurate estimator of the area the animal uses during its normal activities (Worton 1989). Using K95 also excludes some outliers, such as the worst location errors.

However, MCP may reflect more neutrally than K95 the area available for an individual, because it covers roughly the area where the animal has moved but does not weigh any sub-areas inside it, i.e. there is no indication of the intensity of range use (Harris et al. 1990). K95

21

gives a better picture of range use, especially if the range use is patchy, and therefore its habitat composition resembles those of core areas. Consequently, when third order habitat selection was studied only the comparison K50/MCP gave a significant result according to compositional analysis. It can be assumed that the habitat use of an animal is never random. All animals prefer some habitats to other habitats (e.g. Samuel et al. 1985, Harris et al. 1990). The comparisons, which do not reveal any habitat preferences, are thus unlikely to be the best. Therefore, when studying third order habitat selection, it is better to use MCP instead of K95 as the total home range to which the habitat composition of the core area is compared.

However, Jacobs index and selection ratio revealed similar preferences (third order selection) irrespective of the total home range used. Thus, depending on the method, also K95 can sometimes be used as the total home range.

Selecting the core area for habitat analysis

Choosing the right core area is important in habitat selection studies, because the habitat compositions tended to differ to some extent between the core areas. For instance, the proportions of fields and coniferous forests, two abundant habitat types, were not equal in different core areas. As stated above, only the comparison between K50 and MCP gave a significant result of third order habitat selection according to compositional analysis. It thus seems that choosing a small core area, such as K50, probably reveals better than a larger core area the habitat preferences within the home range. However, all core areas revealed the preference for fields, when Jacobs index or selection ratio was used. It thus seems that compositional analysis is more sensitive as to the core area used in the comparisons.

If there were large data and no location error, the distribution of location points in different habitats would reveal the most favoured habitats. But when data are limited, there is some location error, and habitat patches are small, the use of single location points may give erroneous results (Kauhala & Tiilikainen 2002, Kauhala & Holmala 2007). In the present study, location points either did not reveal any habitat preferences or revealed different preferences than when kernel core areas were used in the analyses. The use of a kernel core area results in a more truthful picture of habitat use.

Selecting the best method

Compositional analysis compares the use of each habitat to the use of all other habitats and should thus give more reliable results than simple selection ratios (% used / % available). Compositional analysis takes into account the fact that the use of a certain habitat is not independent of the use of other habitats: for instance, if an animal is in the field, it cannot be at the same time in the forest (Aebischer et al. 1993). Compositional analysis ranks the habitat types in order of relative use. However, compositional analysis can be used only, if the number of individuals is at least equal to the number of habitat classes and in no case smaller than six. Furthermore, the number of locations per animal should not vary widely. If the number of individuals is too small for compositional analysis, Jacobs index (Jacobs 1974) should be used. In the present study the results for both second and third order selection (K95/study area and K50/MCP) obtained by using Jacobs index were equal to those obtained by using compositional analysis. Furthermore, if the aim is to study whether the use of a certain habitat type differs from random use, Jacobs index can be used to add information to that obtained by using compositional analysis (Revilla et al. 2000). Also, if one aims to compare habitat preferences with environmental variables, such as food availability, then the use of the Jacobs index is a good solution (Revilla et al. 2000).

Drygala et al. (2008) used Jacobs index in their study of raccoon dogs (*Nyctereutes procyonoides*) in Germany. According to their study, raccoon dogs used all habitat types opportunistically and Jacobs index was almost

neutral for most habitat types. The animals avoided some habitats (open farmland, meadows and settlements) but did not favour (significantly) any habitat. This is an unexpected result, because all animals certainly have some habitat preferences. The result may be due to the fact that they compared location points to K95, because the use of location points failed to reveal habitat preferences also in our study.

Selection ratio failed to reveal the avoidance of spruce forests and pastures when K50 was compared to MCP, although the comparison K50/MCP gave the most significant result according to compositional analysis. However, Jacobs index, selection ratio and compositional analysis gave similar results, when K95 was compared to the study area. Thus, also the selection ratio may reveal the habitat selection in some cases.

Conclusions

The total home range, core area and method used can all affect the results obtained in habitat selection studies. The comparison between K95 and the study area revealed the second order habitat selection better than comparison between MCP and the study area, whereas the comparison between the smallest core area (K50) and MCP revealed best the third order habitat selection. Unless the sample size is very large and no location error exists, individual location points should not be used when studying third order habitat selection: using the location points did not reveal habitat preferences. Compositional analysis and Jacobs index gave similar results and revealed the habitat preferences of badgers better than the simple selection ratio.

LITERATURE

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

Baghli A. & Verhagen R. 2004: Home ranges and movement patterns in a vulnerable polecat *Mustela putorius* population. *Acta Theriol. 49: 247–258.*

Bender L.C., Anderson D.P. & Lewis J.C. 2004: Annual and seasonal habitat use of Columbian black-tailed deer in urban Vancouver, Washington. *Urban Ecosystems 7: 41–53.*

Brøseth H., Knutsen B. & Bevanger K. 1997: Spatial organization and habitat utilization of badgers *Meles meles*: Effects of food patch dispersion in the boreal forest of central Norway. *Z. Säugetierkunde 62: 17–22.*

Börger L., Franconi N., De Michele G., Gantz A., Meschi F., Manica A., Lovari S. & Coulson T. 2006: Effects of sampling regime on the mean and variance of home range size estimates. *J. Anim. Ecol. 75: 1393–1405.*

Cresswell W.J. & Harris S. 1988: Foraging behaviour and home-range utilization in a suburban badger (*Meles meles*) population. *Mammal Rev. 18: 37–49.*

Dahl F. 2005: Distinct seasonal habitat selection by annually sedentary mountain hares (*Lepus timidus*) in the boreal forest of Sweden. *Eur. J. Wildl. Res. 51: 163–169.*

De Solla S.R., Bonduriansky R. & Brooks R.J. 1999: Eliminating autocorrelation reduces biological relevance of home range estimates. *J. Anim. Ecol. 68: 221–234.*

Drygala F., Stier N., Zoller H., Boegelsack K., Mix H. & Roth M. 2008: Habitat use of the raccoon dog (*Nyctereutes procyonoides*) in north-eastern Germany. *Mamm. Biol. 73: 371–378.*

Elmeros M., Madsen A.B. & Prang A. 2005: Home range of the badger (*Meles meles*) in a heterogenous landscape in Denmark. *Lutra 48: 35–44.*

Finnish Meteorological Institute 2008: Weather and climate. *http://www.fmi.fi/weather/climate_4.html#2*

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

Hemson G., Johnson P., South A., Kenward R., Ripley R. & Macdonald D. 2005: Are kernels the mustard? Data from global positioning system (GPS) collars suggest problems for kernel home-range analyses with least-squares cross-validation. *J. Anim. Ecol. 74: 455–463.*

Hulbert I.A.R., Iason G.R. & Racey P.A. 1996: Habitat utilization in a stratified upland landscape by two lagomorphs with different feeding strategies. *J. Appl. Ecol. 33: 315–324.*

Jacobs J. 1974: Quantitative measurement of food selection. A modification of the forage ratio and Ivlev's electivity index. *Oecologia (Berl.) 14: 413–417.*

Jennrich R.I. & Turner F.B. 1969: Measurement of noncircular home range. *J. Theor. Biol. 22: 227–237.*

Johnson D.H. 1980: The comparison of usage and availability measurements for evaluating resource preference. *Ecology 61: 65–71.*

Kaartinen S., Kojola I. & Colpaert A. 2005: Finnish wolves avoid roads and settlements. *Ann. Zool. Fennici 42: 523–532.*

Kauhala K. 1996: Habitat use of raccoon dogs, *Nyctereutes procyonoides*, in southern Finland. *Z. Säugetierkunde 61: 269–275.*

Kauhala K. & Holmala K. 2007: Kissan elinympäristön käyttö kesällä Kaakkois-Suomessa - pohdintaa kissan merkityksestä luonnossamme [Habitat use of the domestic cat in summer in southeast Finland - discussion of the cat's role in the wild]. *Suomen Riista 53: 25–41. (in Finnish with English summary)*

Kauhala K. & Tiilikainen T. 2002: Radio location error and the estimates of home-range size, movements, and habitat use: a simple field test. *Ann. Zool. Fennici 39: 317–324.*

Kauhala K., Helle E. & Taskinen K. 1993: Home range of the raccoon dog (*Nyctereutes procyonoides*) in southern Finland. *J. Zool. 231: 95–106.*

Kauhala K., Hiltunen M. & Salonen T. 2005: Home ranges of mountain hares *Lepus timidus* in boreal forests of Finland. *Wildl. Biol. 11: 193–200.*

Kauhala K., Holmala K., Lammers W. & Schregel J. 2006: Home ranges and densities of medium-sized carnivores in south-east Finland, with special reference to rabies spread. *Acta Theriol. 51: 1–13.*

Kenward R.E. 2001: A manual for wildlife radio tagging. *Academic Press, London.*

Kenward R.E., South A.B. & Walls S.S. 2003: Ranges6 v1.2: For the analysis of tracking and location data. *Anatrack Ltd., Wareham, UK.*

Kowalczyk R., Jędrzejewska B. & Zalewski A. 2003: Annual and circadian activity patterns of badgers (*Meles meles*) in Bialowieża primeval forest (eastern Poland) compared with other Palaearctic populations. *J. Biogeogr. 30: 463–472.*

Laver P.N. & Kelly M.J. 2008: A critical review of home range studies. *J. Wildl. Mngmt. 72: 290–298.*

Lucherini M., Lovari S. & Crema G. 1995: Habitat use and ranging behaviour of the red fox (*Vulpes vulpes*) in a Mediterranean rural area: is shelter availability a key factor? *J. Zool. 237: 577–591.*

McLoughlin P.D., Cluff H.D., Gau R.J., Mulders R., Case R.L. & Messier F. 2003: Effect of spatial differences in habitat on home ranges of grizzly bears. *Ecoscience 10: 11–16.*

Mohr C.O. 1947: Table of equivalent populations of North American small mammals. *Am. Midl. Nat. 37: 223–249.*

Okarma H., Jędrzejewski W., Schmidt K., Sniezko S., Bunevich A.N. & Jędrzejewska B. 1998: Home ranges of wolves in Bialowieża primeval forest, Poland, compared with other Eurasian populations. *J. Mammal. 79: 842–852.*

Palphramand K.L., Newton-Cross G. & White P.C.L. 2007: Spatial organization and behaviour of badgers (*Meles meles*) in a moderate-density population. *Behav. Ecol. Sociobiol. 61: 401–413.*

Prange S., Gehrt S.D. & Wiggers E.P. 2004: Influences of anthropogenic resources on raccoon (*Procyon lotor*) movements and spatial distribution. *J. Mammal. 85: 483–490.*

Revilla E., Palomares F. & Delibes M. 2000: Defining key habitats for low density populations of Eurasian badgers in Mediterranean environments. *Biol. Conserv. 95: 269–277.*

Rosalino L.M., Macdonald D.W. & Santos-Reis M. 2004: Spatial structure and land-cover use in a low-density Mediterranean population of Eurasian badgers. *Can. J. Zool. 82: 1493–1502.*

Rosalino L.M., Santos M.J., Beier P. & Santos-Reis M. 2008: Eurasian badger habitat selection in Mediterranean environments: Does scale really matter? *Mamm. Biol. 73: 189–198.*

Samuel M.D., Pierce D.J. & Garton E.O. 1985: Identifying areas of concentrated use within the home range. *J. Anim. Ecol. 54: 711–719.*

Seaman D.E. & Powell R.A. 1996: An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology 77: 2075–2085.*

Seaman D.E., Millspaugh J.J., Kernohan B.J., Brundige G.C., Raedeke K.J. & Gitzen R.A. 1999: Effects of sample size on kernel home range estimates. *J. Wildl. Mngmt. 63: 739–747.*

Smith P.G. 2006: Compos analysis version 6.2. user's guide. Version 6.2.3. Smith Ecology Ltd., 1 Bettws Cottage, Bettws, Abergavenny, NP7 7LG, UK. i + 22 pp. *http://www.smithecology.com/software.htm*

Smith G.J., Cary J.R. & Rongstad O.J. 1981: Sampling strategies for radio-tracking coyotes. *Wildl. Soc. Bull. 9: 88–93.*

Storch I., Lindström E. & De Jounge J. 1990: Diet and habitat selection of the pine marten in relation to competition with the red fox. *Acta Theriol. 35: 311–320.*

Wauters L.A., Preatoni D.G., Molinari A. & Tosi G. 2007: Radio-tracking squirrels: Performance of home range density and linkage estimators with small range and sample size. *Ecol. Modelling 202: 333–344.*

Weber J.-M. & Meia J.-S. 1996: Habitat use by the red fox *Vulpes vulpes* in a mountainous area. *Ethol. Ecol. Evol. 8: 223–232.*

Worthon B.J. 1989: Kernel methods for estimating the utilisation distribution in home range studies. *Ecology 70: 164–168.*