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The effect of season, sex and feeding style on home range area versus body mass scaling in temperate ruminants

Abstract Sex-specific estimates of the summer and winter home range area of 19 species of temperate ruminants were collated from the literature. It was predicted that there should be a shallower slope for the home range area against body mass relationship during winter than during summer, as large ruminants can meet more of their energy requirements from the fat reserves deposited during summer than small ruminants. Consequently, relatively large species do not need to range as widely during winter. There was a significant positive relationship between body mass and summer and winter home range area in both females and males. This relationship remained significant when analysed within feeding styles (browser, mixed feeder, grazer), except in mixed feeders in winter. As predicted, slope estimates were significantly lower during winter (b=0.59) than during summer (b=1.28), both before and after controlling for phylogeny. After controlling for phylogeny, browsers had a steeper slope (summer: b=1.48; winter: b=1.07) of the home range area against body mass relationship than did mixed feeders (summer: b=0.75; winter: b=–0.11) or grazers (summer: b=1.10; winter: b=0.34). There was no effect of sex after body mass was controlled for. The effect of season, sex and feeding style on the home range area versus body mass relationship in temperate ruminants is discussed.

Keywords Allometry · Fat reserves · Phylogeny · Resource availability · Resource distribution

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Introduction

Considerable effort has been made to determine how the home range area (HR) of mammals scales with body mass (M) for a wide range of taxonomic groups (HR=aM^b; McNab 1963; Harestad and Bunnell 1979; Damuth 1981; Mace and Harvey 1983; Lindstedt et al. 1986; Swihart 1986; Swihart et al. 1988; Gompper and Gittleman 1991). For energetic demands the scaling coefficient (b) is expected to be 0.75 (McNab 1963). However, most studies have recorded a slope steeper than this ($1<b<1.4$ e.g. Harestad and Bunnell 1979; Mace and Harvey 1983; Lindstedt et al. 1986). The discrepancy between the prediction and the observation has been hypothesised to result from declining rates of production of utilizable energy per unit area of habitat with increasing body mass (Harestad and Bunnell 1979), size-dependent biological time (Lindstedt et al. 1986) and the fact that group size increases with body mass (Damuth 1981). In large herbivores for example, Owen-Smith (1988) reported a home range-body mass slope of 1.25 for 29 species in Africa, but the coefficient declined to 0.83 after accounting for group size (*sensu* Damuth 1981). Du Toit (1990) reported a home range-body mass coefficient of 1.38 for four sympatric African ungulates, while Garland et al. (1993) found a slope of 1.32 for 30 ungulates from both tropical and temperate regions. Less attention has been paid to how factors other than body mass affect home range scaling in ungulates. Grant et al. (1992) showed that male ungulates that defended territories used smaller ranges than those with undefended home ranges.

No study has made predictions regarding possible seasonal differences in the home range versus body mass scaling of large herbivores. In this study we test a new hypothesis concerning the allometry of home range in temperate herbivores. The hypothesis is derived from the observation that fat content scales approximately isometrically with body mass in herbivorous mammals (Calder 1984; Taylor and Murray 1987), while the allometric slope of basal metabolic rate is 0.75 (Kleiber 1975). This

suggests that depletion of fat reserves takes longer in large mammals (Calder 1984; Lindstedt and Boyce 1985; Millar and Hickling 1990). We, therefore, predict that the slope of the relationship between body mass versus home range area of temperate ruminants should be steeper during summer than during winter (i.e., $b_{summer}>b_{winter}$), since depletion of fat reserves takes longer in larger ruminants which thus do not need to range as widely during winter.

It could be argued that the slower rate of depletion of fat reserves for larger animals would confer a greater advantage in their being able to seek out food with higher availability or quality over a larger home range. In temperate climates winter is the main season of food shortage: quality and quantity decrease dramatically (Gordon 1989; Pérez-Barbería et al. 1997). Decreases in food quality affects species of different size in different ways since larger species are able to use forage of poorer quality than smaller species (Illius and Gordon 1991; van Wieren 1996). Thus, larger species could range less widely than smaller species utilising poorer quality food than do small animals.

In the ruminants males are generally larger than females (Weckerly 1998; Loison et al. 1999; Pérez-Barbería and Gordon 2000), and males would, therefore, be expected to range more widely than females. After body mass is accounted for, there should be no effect of sex if home range size is determined only by a simple allometric relationship to body mass. However, because the fat reserves in males tend to be lower than those of females in autumn, due to strenuous rutting activity (red deer *Cervus elaphus*: Mitchell et al. 1976; Cantabrian chamois *Rupicapra pyrenaica*: Pérez-Barbería et al. 1998), we predict a higher intercept of the body mass versus home range relationship for males than females during winter.

Species of ruminants can be classified as browsers, mixed feeders and grazers based on their feeding style (Robbins et al. 1995). It has been predicted, but not tested, that browsing species should range more widely than mixed feeder or grazing species (i.e., differences in intercepts), because browse is more patchily distributed than grass (Bunnell and Gillingham 1985; Owen-Smith 1988). Further, browsers operate in a more three-dimensional world than grazers, in relation to food exploitation. We therefore predict that the slope of the home range area versus body mass relationship will be shallower for browsers than for grazers.

In this study, we estimate the allometric relationship between home range area and body mass for temperate ruminants of different feeding styles using sex-specific estimates with winter and summer home range area. We control for possible effects of phylogeny and group size, as with increasing group size, the home range, and thus resources, is shared by more individuals (Damuth 1981; Owen-Smith 1988).

Materials and methods

Data on home range areas of 19 temperate ruminants ranging from 12 to 470 kg were collated from the literature (Appendix). We recorded data on summer (preferably June-July; May and August also included) and winter (preferably January-March; December also included) home range area for adult females and males. Home ranges calculated using the minimum convex polygon method (Mohr 1947) were preferred because of the widespread use of this technique. Since, within species, home range values from different sources showed an asymmetric distribution, we opted to use the median of the home range values from the range of sources rather than the arithmetic mean. Since data on home range area are derived from two main methods, radio-telemetry and direct observation, we calculated a "method index" to control for the possible confounding effect of method [calculated as(number of studies with radio-telemetry)/(total number of studies) for each sex of a species]. A second problem was the large variation in number of radio-fixes used to give a home range estimate. To solve this, the estimates of home range area for each sex of a species were weighted in the analyses by the total number of fixes summed over all studies (square-root transformed; hereafter referred to as "weighting factor"). Data on male and female body mass were derived from Loison et al. (1999), except for *Bison bonasus* (Pucek 1985), *Bos taurus*, *Capra hircus* (Mason 1981; Sæther and Gordon 1994), *Capreolus pygargus* (Danilkin 1996) and *Ovis ammon* (Pfeffer 1967). Data on feeding type were retrieved from Hofmann (1989) and Loison et al. (1999), while data on group size were derived from a number of sources (Appendix).

Prior to carrying out the analyses, home range area, body mass and group size were log_{10}-transformed in order to stabilise variance and to produce linear relationships between the response and predictor variables.

Species
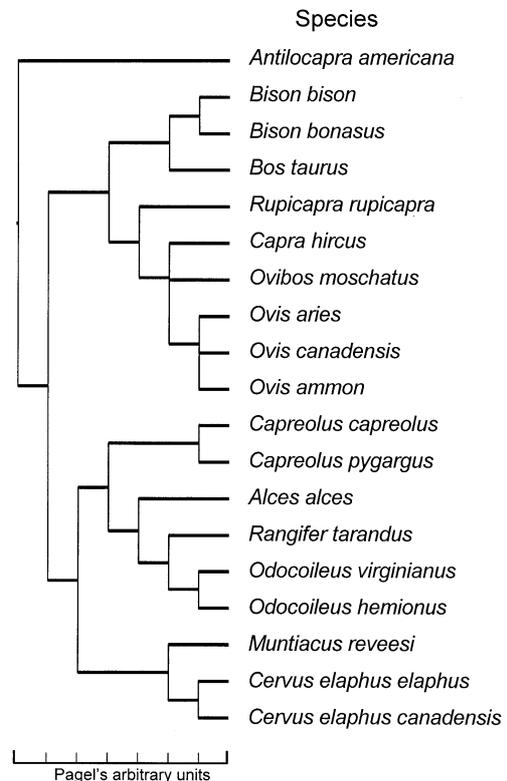
Fig. 1 Phylogenetic relationships between the 19 temperate ruminants included in this study. The branch lengths were estimated using Pagel's arbitrary method (Pagel 1992)

Phylogeny and comparative method

It has been widely recognised that species cannot be treated as independent statistical units in inter-specific analyses (Felsenstein 1985; Harvey and Pagel 1991). We used independent contrasts (Felsenstein 1985; Garland et al. 1992) to test the contribution of phylogeny on the response variable. This method was applied to a phylogeny that was derived from different studies (Fig. 1). Unfortunately, there is no complete phylogeny for the Ungulata based on only one method (e.g. morphological or molecular techniques). Therefore, phylogenies for studies that include a large number of species had to be constructed based on various different phylogenetic studies (Pérez-Barbería and Gordon 1999). The phylogeny of bovids was based on recent studies that used molecular techniques (Essop et al. 1997; Gatesy et al. 1997; Pitra et al. 1997); information for the cervid phylogeny comes from Pérez-Barbería and Gordon (1999) who compiled the information from a variety of sources, mainly based on morphological and paleontological studies. Since information on branch lengths was not available for all nodes, or significant discrepancies occurred between divergence times estimated by palaeontological and molecular techniques, we used the arbitrary method of Pagel (1992) to assign branch lengths (i.e. all internode branch segments of the tree are set to equal one, but tips are constrained to be lined up across the top). The unresolved nodes were assumed to be soft polytomies (Purvis and Garland 1993). The efficacy of the contrasts for removing phylogenetic correlations was tested by examining the significance of the rank correlation coefficient of the contrasts with the original mean node values (Freckleton 2000).

Our group of variables contained either biological or ecological information (i.e. home range, body mass, group size and feeding style) and a second group of variables was constructed for purely analytical reasons (i.e. weighting factor and method index). Independent contrasts for the biological and ecological variables were calculated on the phylogeny as described above. However, because analytical variables did not evolve through the phylogeny, independent contrasts were calculated by collapsing the phylogenetic tree into a star (i.e. collapsing all of the inter-node branch lengths to zero and then making all of the branches linking with the tip-species equal to one: Wolf et al. 1998). The three feeding styles considered (browser, mixed feeder and grazer; *sensu* Robbins et al. 1995) were transformed into two dummy variables using mixed feeder as the reference category, and then independent contrasts were estimated. A similar procedure was applied to the season term, which was transformed into one dummy variable using summer as the reference category.

Independent contrasts assume a Brownian motion model of character evolution (Felsenstein 1985), and any violation of this assumption may result in inflated type I error rates. However, Díaz-Uriarte and Garland (1996) have demonstrated that even under extreme deviations from a Brownian motion model, if branch lengths are properly transformed, the maximum observed type I error is small. The validity of the branch lengths estimated using Pagel's arbitrary method was checked using the Pearson product-moment correlation (not through the origin) between the absolute values of standardised independent contrasts and their standard deviations, which was not significant and was, therefore, appropriate (Garland et al. 1992). The independent contrasts were standardised (i.e. by dividing by squared root of the branch lengths) and then used in regression analysis. The weighting factor was not used in the same way as the independent contrasts but as the nodal values (Bonine and Garland 1999). Independent contrasts were carried out with PDAP 5.0 software (Garland et al. 1993).

Statistical analyses

Since our data set contains pseudoreplication at the species level (i.e. information about the same species is available in winter and summer and in females and males), regression analysis cannot be used since it partitions the variance into a large number of degrees of freedom. Consequently we used residual maximum likelihood (REML, Patterson and Thompson 1971) which allows the vari-

ance due to species or contrasts to be assigned to a random effect. REML was used to analyse the effect of body mass, season, sex and feeding style on home range area controlling for group size, the method index and the weighting factor. This method was applied to our data set prior to controlling for phylogeny (conventional approach) and also to the independent contrasts (phylogenetic approach). Residual plots were examined in order to verify the assumptions of normality and homoscedasticity, which were met once the data were $\log_{10}$-transformed. Garland et al. (1992) pointed out the necessity of using regression through the origin when independent contrasts are being analysed in a regression model. The estimate of the constant term was, therefore, omitted when REML was applied to the phylogenetic approach. Furthermore, our REML approach should use the same restriction as regression, but, unlike regression, REML can also account for more than one source of variation in the data, providing an estimate of the variance components associated with the random terms in the model (Genstat 5 Committee 1993).

In the conventional approach a first model accounted for the effects of body mass, season, sex, feeding style and their interactions as fixed terms and body mass of each sex was nested within species as a random term. This model was then refined by removing the non-significant terms. In the conventional approach the final model comprised the following terms in this order: group size+method+body mass+season+body mass×season+feeding style+feeding style×season+body mass×feeding style and body mass nested within species as the random term. In the phylogenetic approach, REML was applied to the independent contrasts data set, but because independent contrasts require the analysis to be fitted through the origin only the slopes of each term were fitted in the model:group size+method+body mass+body mass×season+feeding style×season+body mass×feeding style. When using independent contrasts species disappeared as branch tips to become contrasts between pairs of species and then contrasts between internal nodes of the phylogenetic tree. As a consequence we used body mass nested within contrasts as a random term in the REML model; this allowed us to remove pseudoreplication within species between seasons.

Intercepts and slopes of the regression lines were obtained using the conventional approach by plotting the fitted home range area values predicted by REML. No graphic representation of the regression lines was given in the phylogenetic approach, because independent contrasts do not allow the graphing of points from regression models that contain more than one covariate in the original data space (although this is possible using simple regression with one covariate; Garland and Ives 2000). Instead we used the REML predicted values of effects to estimate the slopes of home range area against body mass between seasons and feeding styles. Since dummy variables fitted after independent contrasts become a group of continuous variables that indicates the degree of the feeding style of each species, prediction of home range area for each feeding style depends on the value of the continuous dummy variable feeding style chosen in the calculation. To avoid ambiguity in the estimate of the slopes we predicted home range area for the value of dummy variables equal to 1 and then we used these estimates to make relative comparisons between feeding styles. We refrained from presenting absolute slope values. It can be argued that these predictions come from a value out of the range of the dummy variables from independent contrasts; however, the relative comparisons between feeding styles were not affected.

REML tests each term using the Wald statistics, which has an asymptotic chi-squared distribution with degrees of freedom equal to those of the fixed model term. Wald statistics are calculated in the input order specified in the model, ignoring terms fitted later in the model. The model in Table 1 treats the categories "mixed feeders" and "summer" of the terms feeding style and season, respectively, as the reference categories (see Table 1 to clarify how comparisons are carried out). To test differences among the three feeding styles, the order in which the feeding styles were fitted in the model was modified and REML was re-run, the output obtained was consistent with the results described in this paper and Table 1. Statistical analyses were performed using Genstat 5 for Windows release 4.1 statistical software package (Genstat 5 Committee 1993).

Table 1 Residual maximum likelihood analysis, weighted for the number of fixes, of the home range area of 19 temperate ruminants constructed by adding terms in the order shown. Conventional approach: phylogeny was not taken into account. Phylogenetic approach: phylogeny was taken into account using independent contrasts analysis (see Materials and methods for further details). The Wald statistic is asymptotic to a χ^2 distribution. All Wald statistics are calculated ignoring terms fitted later in the model, therefore, for example, the term *browser* compares the intercept of browsing species against the intercept of grazing and mixed feeder species pooled together, whereas the term *grazer* compares the intercept of grazing species against the intercept of mixed feeder species. The same explanation is valid for the terms *body mass × browser* and *body mass × grazer* but in this case slopes are compared instead of intercepts. The random terms to model were body mass nested within species and body mass nested within contrasts in the conventional and phylogenetic approaches respectively

Fixed term to model	Conventional approach			Phylogenetic approach		
	Wald statistic	*df*	*P*	Wald statistic	*df*	*P*
Group size	44.8	1	<0.0001	37.0	1	<0.0001
Method index	16.1	1	<0.0001	0.0	1	≅1.0
Body mass	23.3	1	<0.0001	12.3	1	0.0005
Season (winter)[a]	1.2	1	0.273	–	–	–
Body mass×season (winter)	10.9	1	0.001	6.7	1	0.010
Browser[a]	8.8	1	0.003	–	–	–
Grazer[a]	0.5	1	0.480	–	–	–
Season (winter)×browser	0.9	1	0.343	0.0	1	≅1.0
Season (winter)×grazer	0.3	1	0.584	1.0	1	0.317
Body mass×browser	3.4	1	0.065	6.4	1	0.011
Body mass×grazer	1.8	1	0.180	2.0	1	0.157

[a] These terms were not fitted to the model in the phylogenetic approach (see Statistical analysis)

Fig. 2 Home range size-body mass relationships for temperate ruminants of different feeding styles during summer and winter. Values predicted by residual maximum likelihood analysis (see Materials and methods)
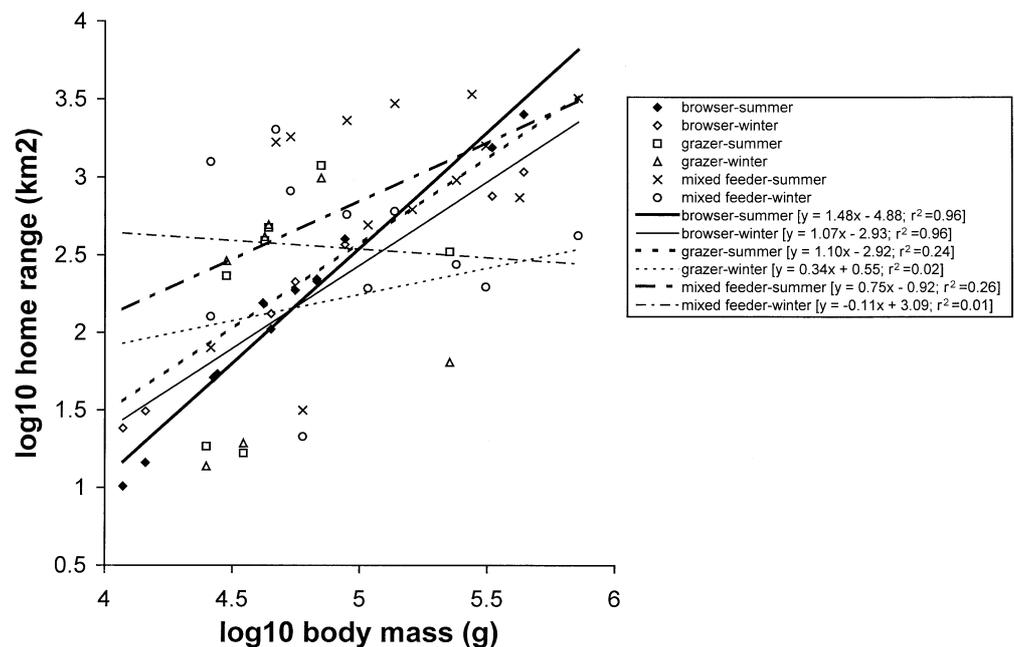
Results

Body mass was a significant predictor of home range area ($P<0.0001$; Table 1), both when using the conventional approach (CA) and the phylogenetic approach (PA). Home range area and body mass were positively correlated for most feeding styles and seasons, except for mixed feeders in winter where the slope did not differ from zero ($b=-0.11$; Fig. 2). There were no significant differences in the intercept of the regression line between winter and summer (CA: $P=0.273$; Table 1). However, as predicted, the relationship between body mass and home range area had a significantly steeper slope in summer ($b=1.28$) than in winter ($b=0.59$; CA: $P=0.001$; PA: $P=0.010$; Table 1). No sex differences in intercepts and slopes (conventional approach) or in slopes (phylogenetic approach) were detected once body mass was accounted for ($P>0.50$, in all cases; model not shown).

Home range area was similar between summer and winter for all feeding styles (Wald statistic pooled within feeding styles; CA: $\chi^2=1.2$, $df=2$, $P=0.549$; PA: $\chi^2=1.0$, $df=2$, $P=0.607$; Table 1). In the conventional approach grazers and mixed feeders had similar intercepts and slopes ($P\geq0.180$; in all cases; Table 1), the intercept of

browsers was significantly lower than the pooled intercept of grazers and mixed feeders together (P=0.003) and the slope of browsers was almost significantly steeper than the pooled slope of grazers and mixed feeder (P=0.065, Fig. 2). In the phylogenetic approach the slope of browsers differed from the slope of mixed feeders and grazers together (PA: P=0.011) and the predicted effects from the REML analysis indicated that this slope of browsers was steeper than the slope of the other two feeding styles.

Discussion

We found a significant relationship between home range area and body mass (Table 1, Fig. 2), as has been found in other studies (see Introduction). This relationship remained significant for both summer or winter ranges or both sexes. The allometric relationship of summer home range area against body mass had a slope (b=1.28) that was similar to the slopes presented in the literature for tropical and temperate ungulates (b=1.25, Owen-Smith 1988; b=1.38, Du Toit 1990; b=1.32, Garland et al. 1993). However, as predicted, the slope of the home range area against body mass in winter was shallower (b=0.59) for the temperate ruminants. This was due, particularly, to the contribution of mixed feeders in winter, which had a slightly negative slope (b=-0.11; Fig. 2). Large-bodied ruminants have a slower rate of depletion of fat reserves than smaller-bodied species (Calder 1984; Lindstedt and Boyce 1985; Millar and Hickling 1990). Hence, large ruminants may choose to range over relatively smaller areas during winter.

All the covariates, except Method Index, were significant in the two approaches used in this study. Method Index was significant in the conventional approach but had no effect on home range area when it was used in the phylogenetic approach. This may be because of its analytical nature; its predictive power on home range area may have vanished after applying independent contrasts because of its arbitrariness in relation to the species in which this controlling factor was applied.

As males are generally larger than females in the ruminants (Weckerly 1998; Loison et al. 1999; Pérez-Barbería and Gordon 2000), males are expected to range more widely than females if home range size is determined solely by a simple allometric relationship with body mass, but only when body mass is not accounted for. No difference in intercepts or slopes were detected between the sexes when adjusted for body mass. Furthermore, even though fat reserves in males are lower than those of females in autumn, due to strenuous rutting activity (Mitchell et al. 1976; Pérez-Barbería et al. 1998), there was no evidence for the predicted higher intercept for males than females during the winter after body mass was accounted for (i.e. the interaction between sex and season did not make a significant contribution to the final model).

There may be a dynamic relationship between forage quality, activity time and home range size. Moose (*Alces alces*) living in areas with low quality forage spent a longer time ruminating, and subsequently had a smaller total foraging area as compared to moose in areas with access to high quality forage (Sæther and Andersen 1990). Alternative hypotheses for the season-dependent slopes of the home range versus body mass relationship are, therefore, that seasonal variation in the distribution of forage of different quality relative to searching costs affects small and large ruminants differently, or that large ruminants eat a lower-quality diet during winter than during summer than small species (Demment and Van Soest 1985). If resource availability affects the interspecific pattern of home range sizes, we would also expect differences due to feeding style. In the phylogenetic approach there was support for the hypothesis that browsing species generally range more than mixed feeder or grazing species, because browse is more patchily distributed than grass (Bunnell and Gillingham 1985; Owen-Smith 1988). The steeper slope of the relationship between body mass and home range area in browsers compared to grazers was contrary to our predictions regarding the different geometry of the food environment for the different feeding styles (see Introduction). Body size can be an important factor for how resources are perceived (Ritchie and Olff 1999), but it remains to be demonstrated whether resource perception relative to body size is different for grazers and browsers or not. The steeper slope of browsers compared to grazers and mixed feeders suggests that the more patchy distribution of browse may affect large and small-bodied browsers differently. We suggest that a small browser may cover its energy demands from a few concentrated patches, while a large browser will not be able to cover its higher absolute energy demands without including less aggregated patches.

Many parameters related to intake and digestion in ungulates, which had previously been associated with differences in feeding style (Hofmann 1989), have been shown to be product of body mass and phylogenetic relationships (oral morphology: Pérez-Barbería and Gordon 1999, 2000, F.J. Pérez-Barbería and I.J. Gordon, unpublished work; stomach morphology: F.J. Pérez-Barbería and I.J. Gordon, unpublished work). In contrast, differences in some behavioural parameters associated with feeding style remain even after controlling for both body mass and phylogeny (group size: Brashares et al. 2000; home range area: this study). This suggests that natural selection has not favoured extreme morphological traits specifically adapted to a narrow range of food resources in environments where forage quality and availability are variable and unpredictable (F.J. Pérez-Barbería and I.J. Gordon, unpublished work); however, behavioural parameters show greater adaptive flexibility.

Appendix

Summer and winter home range area (ha) of female (*F*) and male (*M*) temperate ruminants

Data were collected by radiotelemetry (*RT*) or direct observation (*DO*) and range areas were calculated using the minimum convex polygon (*MCP*; *mMCP* modified version of MCP), kernel (*Ker*), ellipse (*Ell*) methods or grid-cell count (*GCC*). A number after the method (e.g. MCP95) indicates that the outermost fixes were excluded (e.g. 5%). Information on body weights, feeding styles (*FST*; *BR* browser, *MF* mixed feeder, *GR* grazer), and group size (*GS*) was also retrieved from the literature (source for group size cited on the same line as the species name)

Species	Body weight (kg)		FST	GS	Summer GS		Winter GS		Summer home range area		Winter home range area		Data	Method	Reference
	M	F			F	M	F	M	F	M	F	M			
Alces alces	440	331	BR	2											Molvar and Bowyer 1994
									1735	1476	363	311	RT	MCP	Phillips et al. 1973
											200	1200	RT	MCP	Addison et al. 1980
									5700	5700	3000	3000	RT	MCP	Hauge and Keith 1981[a]
									2600		1500		RT	MCP	Mytton and Keith 1981
									210		755		RT	MCP	Doerr 1983
									740				RT	MCP	Cederlund et al. 1987
									910		490		RT	MCP95	Cederlund and Okarma 1988
									2790	2790			RT	MCP	Leptich and Gilbert 1989
											1080	1330	RT	MCP	Sweanor and Sandegren 1989
										3630		750	RT	MCP	Garner and Porter 1990
									1403				RT	Ker95	Andersen 1991
									10300		11300		RT	MCP	Ballard et al. 1991
									5530	3405	390	830	RT	MCP	Miller and Litvaitis 1992
									895		250		RT	mMCP	Histøl and Hjeljord 1993
									550	800	500	1000	RT	MCP	Cederlund and Sand 1994
									717				RT	MCP70	Nelin 1995
									1630	1520	2120	1230	RT	MCP95	Van Dyke et al. 1995
									580	750	500	1450	RT	MCP	Kufeld and Bowden 1996
									5500	9300	6800	5200	RT	MCP	MacCracken et al. 1997
Antilocapra americana	54	47	MF		10	10	25	4							Kitchen 1974
											1150		RT	MCP	Bayless 1969
									1363	1362	3224	2214	RT	MCP	Hoskinson and Tester 1980
									1240	1122			RT	MCP	Reynolds 1984
Bison bison	470	275	MF	22											Van Vuren 1983
									5220				RT	MCP	Van Vuren 1983
Bison bonasus	718	423	MF		20	2	80	5							Krasinska et al. 1987; Krasinska and Krasinski 1995
									1963				DO	MCP	Krasinska et al. 1987[a]
										2288		426	DO	MCP	Krasinska and Krasinski 1995
Bos taurus		225	GR	48											Lazo 1994
									86				RT	MCP95	Loft et al. 1993
									180		210		DO	MCP	Lazo 1995
Capra hircus	67	60	MF	99											O'Brien 1984
									17		25		DO	GCC	O'Brien 1984
Capreolus capreolus	28	27	BR		2	2	5	5							Hewison et al. 1998
									95	97	115	154	RT	MCP	Cederlund 1983
									44	44			RT	GCC	Thor 1990
									38	35			RT	mMCP	Bjar et al. 1991
									15	17			RT	MCP	Cederlund et al. 1993
									38	19	91	75	RT	MCP	Chapman et al. 1993
									28	42	34	16	RT	MCP	Koubek 1995
											60		RT	MCP	Guillet et al. 1996
									73	114	508	508	RT	MCP?	Danilkin 1996[a]
									9				RT	Ker90	Tufto et al. 1996
									86	139			RT	MCP	Mysterud 1998
											46	52	RT	MCP	Mysterud 1999
Capreolus pygargus	42	39	BR		1	1	3	3							Danilkin 1996
										114			RT	MCP?	Danilkin 1996
Cervus elaphus canadensis	312	239	MF		4	2	6	3							Bender and Haufler 1996
									967		152		RT	MCP	Craighead et al. 1973
									820		210		RT	mMCP	Irwin and Peek 1983[a]
									9520	11770			RT	MCP	McCorquodale et al. 1989

Species	Body weight (kg)		FST	GS	Summer GS		Winter GS		Summer home range area		Winter home range area		Data	Method	Reference
	M	F			F	M	F	M	F	M	F	M			
Cervus elaphus elaphus	160	108	MF		6	6	5	5							Clutton-Brock et al. 1982
									121		65		RT	GCC	Georgii 1980
										386		113	RT	GCC	Georgii and Schröder 1983
									371		956		RT	MCP	Jeppesen 1987
											318	318	DO	GCC	Schmidt 1993
									200	410	300	1180	RT	MCP	Lazo et al. 1994
									92	307	31	43	RT	MCP	Koubek and Hrabe 1996
Muntiacus reveesi	15	12	BR	1											Chapman et al. 1993
									12	26	14	28	RT	MCP	Chapman et al. 1993
Odocoileus hemionus	88	56	BR	2											Bowyer et al. 1996
										1940		2820	RT	MCP	Koerth and Bryant 1982
									162				RT	MCP95	Loft et al. 1984
									428		348		RT	MCP	Koerth et al. 1985
									70	90	83	76	RT	MCP	Schoen and Kirchhoff 1985
									392	1140	477	347	RT	MCP	Pac et al. 1988
											211		RT	MCP	Kufeld et al. 1989
									4400	3585	9070	3341	RT	MCP	Rautenstrauch and Krausman 1989
									226		479		RT	MCP	Livezey 1991
									45		32		RT	MCP95	Yeo and Peek 1992
									97				RT	MCP95	Loft et al. 1993
									25	35	36	86	RT	MCP	Weckerly 1993
									321	257	669	230	RT	MCP	Nicholson et al. 1997
Odocoileus virginianus	68	45	BR	3											Hirth 1977; Lagory 1986
											148	115	RT	GCC	Rongstad and Tester 1969
										465	182	467	RT	MCP	Drolet 1976
									83	319	19		RT	MCP	Nelson and Mech 1981
									120	204			RT	MCP	Nelson and Mech 1984
									221	233	132	150	RT	MCP	Tierson et al. 1985
									69		43		RT	MCP	Mooty et al. 1987
									160		309		RT	Ell95	Cohen et al. 1989
									39		25		RT	MCP	Hölzenbein and Schwede 1989
									32	94	55	127	RT	MCP	Beier and McCullough 1990
									85	323			RT	MCP	Nixon et al. 1991
									71				RT	MCP	Leach and Edge 1994
									17				RT	Ker95	Bertrand et al. 1996
									82	82	123	123	RT	MCP95	Leslie et al. 1996
Ovibos moschatus	334	260	MF		13	13	24	24							Heard 1992
											2550		RT	?	Reynolds 1992
Ovis ammon	43	30	GR	4											Bon et al. 1992
									247		244		RT	GCC	Dubois et al. 1992
										130		110	RT	GCC	Dubois et al. 1993
									179	194	203	203	RT	GCC	Dubois et al. 1994
Ovis aries	35	25	GR	32											Grubb 1974
									5	4	11	8	DO	MCP	Grubb and Jewell 1974
									39		20		DO	MCP	Lawrence and Wood-Gush 1988
									1020				RT	MCP	Warren 1996
Ovis canadensis	71	44	GR		3	2	3	2							Bleich et al. 1997
									650		480		RT	MCP	Leslie and Douglas 1979
									1140		1320		RT	MCP	Seegmiller and Ohmart 1981
									970	4000	880	3540	RT	MCP	Krausman et al. 1989
Rangifer tarandus	137	89	MF		1	1	5	5							Fuller and Keith 1981
									7700	6300	137	335	RT	MCP	Fuller and Keith 1981
Rupicapra rupicapra	39	26	MF		10	10	4	4							Lovari and Cosentino 1986
									207		70		DO	MCP	Clarke and Henderson 1984
									28				DO	MCP?	Pachlatko and Nievergelt 1985

[a] Estimates for males and females are pooled

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