Home ranges, habitat and body mass: simple correlates of home range size in ungulates

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The spatial scale of animal space use, e.g. measured as individual home range size, is a key trait with important implications for ecological and evolutionary processes as well as management and conservation of populations and ecosystems. Explaining variation in home range size has therefore received great attention in ecological research. However, few studies have examined multiple hypotheses simultaneously, which is important provided the complex interactions between life history, social system and behaviour. Here, we review previous studies on home range size in ungulates, supplementing with a meta-analysis, to assess how differences in habitat use and species characteristics affect the relationship between body mass and home range size. Habitat type was the main factor explaining interspecific differences in home range size after accounting for species body mass and group size. Species using open habitats had larger home ranges for a given body mass than species using closed habitats, whereas species in open habitats showed a much weaker allometric relationship compared with species living in closed habitats. We found no support for relationships between home range size and species diet or mating system, or any sexual differences. These patterns suggest that the spatial scale of animal movement mainly is a combined effect of body mass, group size and the landscape structure. Accordingly, landscape management must acknowledge the influence of spatial distribution of habitat types on animal behaviour to ensure natural processes affecting demography and viability of ungulate populations.

1. Introduction

Any mobile organism faces the question of where to move. Individuals’ movement decisions affect what they can eat [1,2], who they get eaten by [3,4] and who they can mate with [5,6]. The pattern of movement may therefore strongly influence individual differences in fitness [7] and hence generate spatio-temporal variation in population dynamics [8–10]. Accordingly, numerous studies have analysed the causes and consequences of variation in animal movement patterns [11,12].

A fundamental characteristic of an individual’s movement pattern is its home range [13]. In one of the first attempts to relate home range to spatial scale of animal movement, it was defined as ‘that area traversed by the individual in its normal activities of food gathering, mating, and caring for the young’ [14]. This definition considers annual to multiannual temporal scales of movement of adult individuals, whereas restricted dispersal phases, e.g. by subadults, and shorter time periods, such as seasonal and diurnal ranges, do not necessarily capture all aspects of a species ‘normal activities’ [11, p. 351]. Some home range estimators, such as 100% minimum convex polygons (MCP), were found to be sensitive to ‘non-normal activities’, such as exploratory behaviour [15–17]. By contrast, estimators rejecting a certain proportion of the outermost locations (e.g. 95% MCP) or defining thresholds of probability of occurrence (e.g. 95% kernel density estimator [18])...
are more in accordance with the original definition [14], excluding movement patterns such as exploratory behaviour from an individual’s home range. Although choice of home range estimator may affect estimates of home range size, several studies suggest that home range estimators can provide valuable information about variation in animal space use [18–22], and that variation in estimated home range size owing to methodological differences is weaker than ecological signals with no qualitative influence on conclusions regarding ecological patterns ([23,24], but see [25]). Accordingly, knowledge about factors generating variation in home range size among populations and species may provide valuable information about the underlying ecological processes affecting intra- and interspecific variation in space use [26,27].

Ungulates, i.e. Perissodactyla and Artiodactyla, are a diverse group with respect to important ecological and behavioural traits. A large body of research on important factors such as relationships among metabolic requirements, diet, habitat preferences and social structures provides invaluable background knowledge about fundamental ecological processes [28–33]. Their potentially large impact on ecosystems [34] and high level of human–wildlife interactions [35] make them important parts of ecosystem management worldwide [36]. Ungulates are roughly classified as grazers, browsers or mixed foragers [37]. However, as with many other animal groups (e.g. [38,39]) diet and habitat use are often strongly associated, with grazers commonly found in open areas, whereas browsers more often use closed habitat [40–42]. Sexual size dimorphism is common among ungulates, with males being up to 2.6 times heavier than females [43]. Males do not take part in the care of offspring, and varying levels of polygamy by either harem-holding territorial males or tending males is the common mating system [44]. All the factors listed above are proposed to influence home range size in ungulates, as well as other animals (see figure 1 for predicted relationships). However, mechanisms may depend on each other, causing potentially complex relationships among species characteristics, environmental characteristics and spatial scale of movement as measured by the home range size (figure 1).

Here, we review patterns and mechanisms of variation in home range size among ungulates, supplementing with a meta-analysis where we address several hypotheses simultaneously. Information about the meta-analysis can be found in the electronic supplementary material (S1: Data search for

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**Figure 1.** How interspecific factors are expected to affect home range size and the allometric relationship between body mass and home range size.

(a) Because of higher predation risk in open habitats, species living in open habitats will have overall larger home ranges than species in closed habitats. However, the higher movement efficiency between foraging patches with increasing body size will result in a shallower allometric slope between body size and home range size in open compared to closed habitats. (b) Because of the more patchily distribution of browse compared with grass, browsers will have larger home ranges compared with grazers. However, larger bodied browsers have higher energetic demands and will need to include more and larger patches, which will be more dispersed and heterogeneous compared with the spatial distribution of food resources of larger grazers. This will give a steeper allometric slope between body mass and home range size for browsers than for grazers. (c) Females will have smaller home ranges than males owing to more selective foraging in heterogeneous landscapes, and because of movement constraints by calf at heel. However, increasing group size decreases sex difference in home range size (not shown in figure). (d) Owing to costs of defence and loss of mating benefits with increasing area, territorial males should have smaller home ranges than tending males.
home range size in ungulates, S2: Statistical procedures and methodological considerations for analysing home range size variation in ungulates and S3: Detailed presentation of results from a meta-analysis of home range size variation in ungulates).

2. Metabolic requirements and home range size

The variation in home range size among [45] and within species [46] was originally considered to be a function of metabolic rate. Accordingly, the scaling between body mass and home range size should be comparable to the body mass scaling of forage intake rate of approximately 0.75 at the logarithmic scale [33,47,48]. On an arithmetic scale, this means that the positive relationship between home range size and body mass is steeper at smaller body masses, and decelerates with increasing body mass. Later studies found support for steeper allometric slopes of approximately 1.0 [20,24,47,49–52], which was explained by dietary differences [51], length of the biological time scale included in the study [47] and higher level of scramble competition from conspecifics for species with larger body mass [20]. Our meta-analysis revealed an overall allometric slope of 1.06 (95% CI = 0.67; 1.41, electronic supplementary material, table S4), which is in accordance with previous estimates among large herbivores of 1.06 [52], 1.02 [20] and 1.08 [53]. Hence, the predicted relationship between home range size and body mass of 0.75 [45] seems not to be valid in ungulates. The larger coefficient could be the result of environmental and/or species characteristics, other than body mass, affecting the cost–benefit ratio of movement. However, it can also be related to the fact that digestion efficiency increases with body mass [28]. The increased digestion efficiency of larger animals comes at the costs of a more time-restricted activity budget [29], which again may increase the home range [54]. This emphasizes how the complex interactions between body mass and ecological factors may amplify or cancel out each other’s effects on home range size, and should therefore be considered jointly (see sections below).

For group-living animals, the functional unit at which space use scale is measured becomes the group rather than the individual [52]. Through increased scramble competition one therefore expects a similar relationship between home range and group size as for body mass [47]. Previous studies of home range size have often omitted or controlled for variation in group size prior to analyses [20,47,55,56], making it difficult to determine its effect. In our meta-analysis, we found a decelerating increase in home range size with increasing group size, but with a high uncertainty in the parameter estimate (electronic supplementary material, table S4). This could be because a group’s size is an imprecise measure of the costs of scramble competition [52], and hence that group size is not a suitable measure for relating metabolic requirements to home range variation in animals.

3. Habitat

The habitat explains important factors of the foraging niche, such as the quantity and quality of forage [57,58]. It also encompasses a range of other biotic and abiotic variables and their spatial distribution so that different foraging strategies may lead to the same habitat [59]. However, within a habitat different diets may result in different energy trade-offs [59], or alternatively the habitat may determine the diet [60], making the distinction between the two important. Moreover, habitat affects the mortality risk associated with predation [39,61], and exposure to extreme weather conditions [62,63]. Habitat composition also affects movement among foraging patches [64,65], and thereby factors such as resource encounter rate and scale of perception [66]. Scale of perception, which is increased in low-dimensional patches such as open areas [64], may strongly reduce distance moved between patches [65,67]. As such, in combination with body mass (figure 1), habitat composition may strongly affect individual movement patterns and thereby shape the spatial scale of space use [64,68].

It seems to be a general pattern that species using open habitats have larger home ranges for a given body mass than species living predominantly in closed habitats [69, figure 2; electronic supplementary material, table S4]. Two mechanisms may explain this pattern (figure 1). Firstly, ungulate space use is not only a result of food, but may also be related to protection from predators and harsh weather [70]. Accordingly, ungulates foraging in open habitats may have to increase their home range to include habitats offering cover [71–75]. Secondly, plants growing under shady conditions, such as in closed habitats, develop fewer secondary compounds and have a lower fibre content, resulting in a higher quality herbivore forage [76–78]. This may lead to increased energy gain for a given intake rate [79] regardless of diet. As a consequence, closed habitats may provide sufficient food within smaller home ranges for a given body mass [49,80]. Our meta-analyses revealed that the size of home ranges of ungulates in mixed habitats was even smaller than that of ungulates in closed habitats (figure 2; electronic supplementary material, table S4). Possibly, this is because mixed habitats include more edges where animals can optimize the cost–benefit trade-off between food and cover at even smaller spatial scales than in open or closed habitats [81,82]. Because larger bodied herbivores are better at using low-quality forage, such as fibre-rich grass found in open areas, the scaling between body mass and intake rate is expected to be weaker in such habitats compared to habitats with...
high-quality forage where the nutritional benefit of a given intake rate is weaker related to body mass [28,33]. Interactions between habitat composition and animals’ movement patterns [66,67] can also lead to habitat-specific patterns in the allometric relationship between body mass and home range size. Specifically, a steeper allometric relationship is found for species in closed habitats compared to species in open habitats [69]: open habitats $\beta = 0.69$, closed habitat $\beta = 1.23$, or animals found in high- versus low-dimensional habitats [64,67]. This is confirmed by our meta-analysis ($\beta_{\text{open}} = 0.48 [-0.08; 1.09]$).

4. Diet
A broad classification used to explain differences in ungulates body-mass scaling properties, as well as other ecological factors, is to separate between browsers and grazers [33,37,87]. In general, grass is considered low-quality forage, but is normally abundant over large areas in open landscapes [37]. Browsers are considered easier to digest, but is more patchily distributed, and more abundant in closed habitats [37,88]. According to optimal foraging theory [89], increased spatial heterogeneity is expected to increase the movement rate between patches [90–92], resulting in larger home range size among browsers. In line with this, several studies have reported larger home ranges for browsers compared with grazers [56,93]. However, a larger home range among browsers compared with grazers may also be explained by grazers having a slightly higher retention time [94], resulting in less time spent on movement and a weaker allometric relationship among grazers than among browsers [33]. The allometric slope of browsers may be further steepened owing to the need of relatively larger patches to sustain larger bodied browsers [56,93]. A decreasing patch encounter rate with increasing patch size [64] makes it necessary to increase movement to obtain the required intake rate given the body mass. Diet and habitat use are inevitable linked; what you eat affects where you go and where you are affects what you can eat. For instance, grazers and browsers are often found in open and closed habitats, respectively [40], making it challenging to distinguish the relative contribution of these factors for explaining variation in the spatial scale of space use. The predicted relationship with home range size of habitat and diet differ; we expect species in closed habitat (i.e. typically browsers) to have smaller home ranges than species in open habitats, but also that a diet consisting mainly of browse should lead to a larger home range than a grass-dominated diet (figure 1). From theory, the predicted difference in the allometric relationship, however, is similar; browsers, which are mainly living in closed habitats, should have a steeper allometric relationship than open-living grazers (figure 1). Our meta-analysis, which is one of the first attempts of relating variation in home range size to habitat and diet simultaneously, suggests that habitat has a stronger explanatory power than diet (electronic supplementary material, S3 and table S3). Accordingly, it appears that when it comes to species variation in space use patterns, the browser–grazer dichotomy is not as suited as for other ecological phenomenon. Instead, observed relationship between scales of space use can be explained by habitat characteristics influencing the distribution of components of species’ foraging niche [69].

5. Sex
If home range size was only a result of metabolic requirements, males and females would have similar home range sizes after accounting for differences in body mass, diet and habitat. However, several other factors are predicted to generate sex differences in ungulate space use patterns such as home range size, with mixed support from empirical studies [32]. First, females have the cost of lactation and fending for offspring. On the one hand, increased need for resources can increase home range size [71,95,96], whereas constrained movement and increased mortality risk have been found to decrease home range size [24,97,98]. Although the movement may be restricted only for a limited period after giving birth, the magnitude in differences between the males’ and females’ movement rate [24] may be sufficient to cause sex differences in annual home range size. Second, males are more willing to trade off forage quality for quantity if the costs of locating high-quality forage are high [49]. Accordingly, with decreasing forage quality males may compensate by increasing their home range, whereas females compensate by becoming more selective [4,32,99] and spend more time hiding or foraging to offset lactation costs [51]. Based on support from other studies on space use patterns in large herbivores [32], the general prediction is larger home ranges in males compared with females after accounting for sexual size dimorphism (figure 1c). Our meta-analysis did not support sex-specific variation in home range size after accounting for size (electronic supplementary material S3 and tables S3), and supports previous findings that sex differences in the spatial scale of movement are caused by sexual size dimorphism [32,56]. Moreover, the meta-analysis did not support sex differences in allometric slopes between home range size and group size. Accordingly, it appears that any difference in the spatial scale of space use of male and female ungulates is explained by body size, and that it relates similarly to variation in group size, body mass, habitat or any other characteristics of the species or environment. The lack of distinct sex-specific differences may, however, be caused by different factors cancelling each other’s effect on home range size. For instance, female movement may be constrained by calves at heel, but a calf may also increase the need for cover, forcing females living in open habitats to increase their space use to include more closed habitats to provide shelter for their offspring. However, such mechanisms have yet to be tested, but should be feasible with increasingly more available movement data at the individual level [100,101].

6. Mating system
The mating system of a population is expected to greatly influence animal space use patterns and vice versa through several
mechanisms [102]. These can have different strength on males and females. For instance, both harem-holding and territorial species are spatially polygynous owing to female clustering, and because of the benefit of occupying rutting sites in due time before the rutting season [103,104], males may have relatively small home ranges. By contrast, tending species are temporally polygynous as males roam about and sequentially guard and mate with females [102], resulting in the benefit of increasing home range size for males [6]. This suggests larger home ranges in tending males compared to territorial males (figure 1d), but with no predicted effects on females. This is supported by earlier studies covering the costs of defending a territorial home range across a range of taxa [105]. The increased costs of defending a larger home range outweigh the benefits, and resulted in a smaller home range for territorial species. Our meta-analysis did not provide support to the prediction that tending males have larger home ranges than territorial males. This may partly be due to interspecific correlation in characteristics such as habitat use and mating systems. For instance, it has been suggested that polygamy and diet co-evolved during the development of open grasslands [41,44]. Thus, monogamous species tend to be browsers and reside in closed habitats while polygamous species tend to be grazers in open landscapes. Still, the fact that habitat was included in all the highest ranked models whereas other species traits only were included sporadically in the top models (electronic supplementary material, table S3), supports that habitat use, rather than other traits, is the key driver for variation in home range size given that variation in body mass and group size is accounted for.

7. Concluding remarks
Conservation of threatened species must account for important processes shaping their spatial distribution. Our review of the literature on home range size in ungulates, supplemented with a meta-analysis, suggests that only habitat association of a species provide a significant effect after accounting for metabolic requirements (i.e. body mass and group size). Our study also emphasizes the importance of methodological and phylogenetical considerations when assessing ecological patterns based on meta-analyses (electronic supplementary material, S3, table S3 and table S4). Most importantly, several methodological factors such as accounting for estimate uncertainty or phylogeny, have only weak signals on the ecological patterns and can be considered ignored at the gain of increased sample size (electronic supplementary material, S2). This may increase the statistical power to detect general ecological relationships across species or taxa.

The impact of habitat elaborates the importance of landscape characteristics on essential ecological and evolutionary processes related to spatial scale, such as the spatial scale of population fluctuations [106], population viability [107] and gene flow [108,109]. Currently, habitat loss and fragmentation are among the biggest threats to global biodiversity [11], and like in many other studies [110–112], our results emphasize the importance of conserving areas of sufficient size and complexity for maintaining viable populations. Optimizing the costs and benefits associated with the conservation of populations and species therefore hinges on joined landscape and wildlife management [29].

Data accessibility. The studies included in the meta-analysis presented in figure 2 are listed in the electronic supplementary material, table S1.

Authors’ contributions. B.-E.S. initiated the study. E.G.O. performed the literature search, developed and ran all analyses. E.G.O., I.H., B.-E.S. and E.J.S. wrote the paper.

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References


79. Capreolus capreolus L. 1890/08-0162.1)


91. Rybicki J, Hanski I. 2013 Species – area relationships and extinctions caused by habitat loss and


