Rangeland Ecology & Management xxx (2017) xxx–xxx

Contents lists available at ScienceDirect

Rangeland Ecology & Management

journal homepage: http://www.elsevier.com/locate/rama

Original Research

Does Scale Matter? Variation in Area Use Across Spatiotemporal Scales of Two Sheep Breeds in Two Contrasting Alpine Environments☆

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ARTICLE INFO

Article history:
Received 18 November 2016
Received in revised form 16 October 2017
Accepted 6 November 2017
Available online xxxx

Keywords:
core areas
dBBMM
home ranges
pasture
utilization distribution

ABSTRACT

Animal-by-environment interaction creates space use patterns, which characterize an animal's utilization distribution (UD) area. We fitted 51 ewes of the two Norwegian breeds Norwegian White Sheep (NWS) and Spælsau (SP) with Global Positioning System collars in two contrasting environments (Spekedalen; poor pasture and Bratthøa; rich pasture) during the 2013 and 2014 summer grazing seasons. We explored effects of spatiotemporal scales on UD sizes of the sheep in these environments. We defined the temporal scales as 5-, 10-, 15-, 20-, 30-, and 60-d intervals and spatial scales as 95% and 50% UD using the dynamic Brownian Bridge Movement Model. Our results showed that, in general, sheep had larger UDs in the poor area compared with the rich area and the SP had larger UDs compared with the NWS. We found 95% UD differences between the two environments at all temporal scales, except 60 d, whereas differences were found between breeds at all but the finest temporal scale. The 50% UD differed between breeds and environments on all temporal scales except between-study areas at the 5-d scale. The lack of environment by breed interactions suggest that the two breeds respond equally to range quality at all spatiotemporal scales. We conclude that scale has to be considered when comparing UD differences across spatial and temporal scales in contrasting environments and between sheep genotypes. Our findings are thus important for management of grazing resources in multipurpose land use planning.

Introduction

Animal-by-environment interplay creates space use patterns (Morales et al., 2010). This can be used to characterize how an animal utilizes its surroundings (Tufto et al., 1996). Animals often restrict themselves to a certain area, their home range, and are likely to increase their forage efficiency and subsequent fitness as familiarity with that area increases (Van Moorter et al., 2009). Animals operate on different functional scales, and causes for variation in home range size may differ within and between species. Differences between species are generally driven by body mass (Carbone et al., 2005). Intraspecific variation may be caused by a number of intrinsic factors such as age (Saïd et al., 2005, 2009), sex (Main and Coblentz, 1996), body mass (van Beest et al., 2011), and reproductive status (Tufto et al., 1996), as well as social organization (Wronski et al., 2006) and activity patterns (Owen-Smith et al., 2010). Indeed, extrinsic factors such as range quality and population density (Dussault et al., 2005; Saïd et al., 2005, 2009) may also cause variation.

Landscape characteristics including heterogeneity (Bartlam-Brooks et al., 2013), topography (Mysterud et al., 2001), and elevation (Killeen et al., 2014) can influence how individuals in spatially structured populations interact with the environment. However, studies that address spatiotemporal processes affecting area use are scarce (Bjørneraas et al., 2012), but see van Beest et al. (2011) that aimed to quantify the relative effect of various individual, forage, and climatic determinants of variation in home range size across multiple spatiotemporal scales in moose *(Alces alces)*. Because spatial and temporal scales may co-vary (Wiens, 1989), it is imperative to include both when analyzing ecological processes and to select the most informative scales of analysis (Dayton and Tegner, 1984; Mayor et al., 2009). Indeed, a multiscale approach is often imperative to unravel scale-sensitive ecological processes (e.g., an animal's area use and at which spatiotemporal scales it is operating on).

An animal's space use can be characterized by its utilization distribution (UD), which can be calculated using statistical methods like kernel density estimation (Worton, 1989) and Brownian bridge movement models (Horne et al., 2007) or variations thereof

☆ This work was supported by Småfefondet, NMBU and Norwegian Research Council (NFR 208036/010).

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https://doi.org/10.1016/j.rama.2017.11.001

Please cite this article as: Jørgensen, NH., et al., Does Scale Matter? Variation in Area Use Across Spatiotemporal Scales of Two Sheep Breeds in Two Contrasting Alpine Environments, Rangeland Ecology & Management (2017), https://doi.org/10.1016/j.rama.2017.11.001

(i.e., dynamic Brownian bridge movement model) (Kranstauber et al., 2012). The 95% and 50% areas used represent the most commonly used spatial estimators (see e.g., van Beest et al., 2011). Both of these UD estimates may vary in extension and overlap both spatially and temporally. However, the two spatial scales need not conform to a certain percentage of the estimated UD, per se, and may depend on the species' or breed's range behavioral patterns. Animals may thus have the same home range sizes, but with different ratios of intensively used foraging patches because resources are distributed differently within the areas (Vander Wal and Rodgers, 2012). Indeed, core areas may be more important within heterogeneous home ranges with greater forage availability or quality than in areas with fewer or homogeneously distributed resources (McLoughlin and Ferguson, 2000). One would thus expect that differences in UDs, at any temporal scale, between the homogeneous Spekedalen and the heterogeneous Bratthøa study area would be more pronounced at a finer spatial scale (e.g., 50% UD). Further, an animal's use of space within a short time-span should intuitively be smaller than the area used during a longer period within a specific environment (WallisDeVries et al., 1999; Fortin et al., 2003).

It is well documented that herbivores that use sparsely distributed resources are likely to operate on a larger spatial scale than those using richer environments (Searle et al., 2006). Further, differences between animal genotypes may exist—it is known that the Spælsau (SP) is more gregarious and active and should thus use larger areas compared with the Norwegian White Sheep (NWS) (http://www.nsg.no), which spread out in small groups. However, Jørgensen et al. (2016) were not able to show that sheep used larger home ranges (95% UD) in Spekedalen, a poor grazing area, as compared with Bratthøa, a rich area, or that SP used larger home ranges than NWS on a full summer season scale. We therefore set out to study:

1. how temporal scales affect sheep area use on 50% UD and 95% UD spatial scales in Spekedalen compared with Bratthøa;
2. how temporal scales affect breed area use on 50% UD and 95% UD spatial scales in Spekedalen compared with Bratthøa; and
3. if there is a genotype by environment interaction effect on area use across spatiotemporal scales.

Materials and methods

Study Area

Spekedalen study area (Fig. 1), a part of the Sølendalen grazing commons (hereafter called Spekedalen), is situated in the northern part of Rendalen municipality, Hedmark County, in southeastern Norway (11°21′E, 62°4016′N). Spekedalen covers 97 km^2 and reaches from 688 to 1604 m above sea level (m.a.s.l.). Pasture quality is generally poor (Rekdal, 2007) in terms of sheep grazing quality, with 1% classified as "Very Good," 21% as "Good," and 78% as "Less Good." Bratthøa commons study area (hereafter called Bratthøa) (see Fig. 1) in Vingelen (northern part of Tolga municipality) covers approximately 62 km^2 spanning from 790 to 1229 m.a.s.l. and has in general higher pasture quality (Rekdal, 2009): 12% "Very Good," 48% "Good," and 40% "Less Good." The difference in pasture quality is reflected in the mean lamb autumn weights (1993 − 2013) of 47 kg in rich Bratthøa as compared with 40 kg in poor Spekedalen (Sauekontrollen, available by appointment at: https://www.animalia.no/).

The total density of sheep in the Spekedalen study area was approximately 3 sheep per km^2 in both 2013 and 2014, while in Bratthøa density it was 38 and 40 sheep per km^2 in 2013 and 2014, respectively (www.nibio.no), below their estimated grazing capacities, especially in Spekedalen (Rekdal, 2007). See Jørgensen et al. (2016) for further details regarding the two study areas.

Study Animals

The free-range summer outfield grazing started on 23 June and lasted to 2 September in both 2013 and 2014. Fifty-one lactating ewes of the SP and NWS breeds, of known age and with two lambs at foot, were released into the two study areas, 23 and 28 ewes in Spekedalen (SP: 10, NWS: 13) and Bratthøa (SP: 13, NWS: 15), respectively. The study animals were recruited from six sheep farms that had used the study areas for summer grazing during several years before the study.

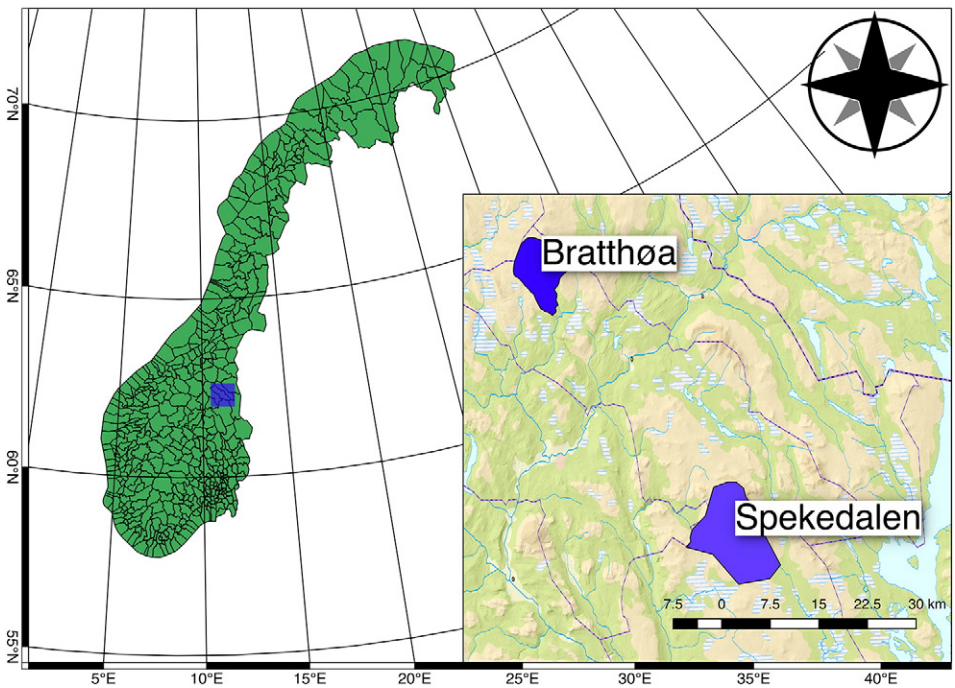

Figure 1. Study areas: Bratthøa study area in the northern part of Tolga municipality and Spekedalen study area in northern part of the Rendalen municipality, both in Hedmark County, Norway (Source: Statens Kartverk 2015). Map was generated using the QGIS version 2.16.3 print composer (QGIS Development Team, 2016).

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