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Spatial mismatch between management units and movement ecology of a partially migratory ungulate

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ABSTRACT

1. Population-level management is difficult to achieve if wildlife routinely crosses administrative boundaries, as is particularly frequent for migratory populations. However, the degree of mismatch between management units and scales at which ecological processes operate has rarely been quantified. Such insight is vital for delimiting functional population units of partially migratory species common in northern forest ecosystems.
2. We combined an extensive dataset of 412 GPS-marked red deer (*Cervus elaphus*) across Norway with information on the size and borders of two administrative levels, the governmental level (municipality) and landowner level (local management units; LMUs) to determine the timing and scale of mismatch between animal space use and management units. We analysed how landscape characteristics affected use of management units and the timing and likelihood of crossing borders between them, in an effort to delineate more appropriate units in various landscapes.
3. Median municipality size could potentially cover 70% of female and 62% of male annual ranges, while only 12% and 4% of LMUs were expansive enough to accommodate migratory routes in females and males, respectively. Red deer migrate along elevational gradients and are more likely to find both suitable lowland winter habitat and higher summer habitat within management units with variable topography. Consistent with this, the likelihood of border crossing decreased with increasing diversity of elevations.

4. *Synthesis and applications.* We demonstrate a considerable mismatch between animal space use and management units. Far-ranging movements and frequent administrative border crossings during autumn migration coincides with the period of active management (hunting season). Our study also highlights that, due to extensive movements of males, coordination of management aims may provide a more realistic avenue than increasing sizes of local management units. A more general insight is that the degree of mismatch between range use and management units depends on the season and landscape type. This needs to be accounted for when delimitating functional population units of migratory populations.

Keywords: border crossing, red deer, home range, hunting, migratory populations, partial migration, population management, movement ecology, range use, local management units

Introduction

The management of natural resources across space tends to follow administrative boundaries that are results of political rather than ecological considerations. Chief among the challenges in defining administrative units (jurisdictions) is the issue of their size. On the one hand, the “Convention on biological diversity” recommends that management should occur at the lowest practical level (UNEP 1999), and the EU’s Subsidiarity principle suggests that “within a political system, decisions should be made at the lowest possible level which is compatible with effective action” (Linnell 2005). On the other hand, ecologists are documenting that mammalian populations may have geographically large annual ranges (Berger 2004; Milner-Gulland, Fryxell & Sinclair 2011). The extensive space use of such populations represents a considerable challenge for management and conservation due to a mismatch between the size and spatial delimitation of administrative units (Linnell et al. 2001; Bischof, Brøseth &

Gimenez 2016). Despite this knowledge, management of “moving targets” and delimitation of functional population units represent recurrent challenges, particularly for migratory species (Singh & Milner-Gulland 2011; Bull et al. 2013).

In many areas, the extensive migration systems of ungulates are threatened due to loss of suitable habitats and obstruction of migration corridors (Bolger et al. 2008; Harris et al. 2009). Retaining connectivity is the main management challenge when facing expansion of human infrastructure. The conservation targets may then be easy to identify. In contrast, many cervids in Europe and North America have increased both in number and distribution over the past decades (McShea & Underwood 1997; Apollonio, Andersen & Putman 2010). At northern latitudes, these deer populations typically show patterns of partial migration where some animals remain resident, while others migrate between separate summer and winter ranges (Myserud 1999; Ball, Nordengren & Wallin 2001; Myserud et al. 2011; Bischof et al. 2012; Singh et al. 2012). The elusiveness of deer in the forest and mix of space use tactics, make it difficult for managers to assess landscape connectivity and what constitutes a functional population unit. Migratory behaviour depends on a range of environmental factors and vary greatly among forest deer populations (Myserud et al. 2011; Cagnacci et al. 2011; Singh et al. 2012). A lack of knowledge of space use relative to management borders remains a main hurdle to achieving population level management of partially migratory populations, as the migration movements are directional leading to changes in the relative abundances of deer locally. The extent of management border crossings will depend on the space use patterns determined by both environmental and landscape characteristics and on the management organization.

Wildlife crossing of boundaries and management unit delimitation is a problem mainly when 1) there are spatial mismatches between management objectives and/or 2) the distribution of costs and benefits between stakeholders is compromised by boundary

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crossings. An example of the first is bird migration that frequently occurs at an inter-continental scale often with stark contrast in management and conservation efforts in summering and wintering areas. European raptors such as the Montagu's harrier (*Circus pygargus*) are sufficiently protected in their summer range, but limited by often poverty-driven habitat deterioration in their winter range (Liminana et al. 2012). At smaller scales, lynx (*Lynx lynx*) in central Europe (Müller et al. 2014) and elk in Yellowstone, USA (Hebblewhite et al. 2006) move between protected areas and human dominated landscapes with different management goals. An example of the second problem is management of red deer that tends to revolve around two main motifs: renewable resource use (harvest; sport- and meat hunting), and damage control mitigation (Milner et al. 2006). A practice of neglecting migration across borders may lead to an asymmetry of the browsing damage cost and harvesting benefit distribution across management units (Skonhøft 2005). With movement across management borders, a lower overall yield may result if harvesting is optimized at a local level instead of the population level (Milner-Gulland, Coulson & Clutton-Brock 2000; Clutton-Brock et al. 2002).

No previous study has used large scale GPS-data of ungulate movements across a range of environmental conditions assessing explicitly their match or mismatch to current management structures, which would provide an important basis to suggest more appropriate management units. Here we use data from 412 GPS-marked red deer (*Cervus elaphus*) across seven regions in Norway, all of which harbour partially migratory populations (Mysterud et al. 2011). Summer ranges of red deer are situated further inland and at higher elevation than winter ranges (Bischof et al. 2012). Importantly, the fall migration return to low elevation winter ranges coincides with the hunting season (Rivrud et al. 2016). Red deer cause substantial economic losses due to grazing damages at pastures in both winter and summer ranges (Lande et al. 2014). However, landowners in wintering areas often get a larger share

of the hunting revenue, because most deer migrate back to winter ranges early in the hunting season before landowners in the summer ranges can profit by harvesting them (Skonhøft et al. 2013; Loe et al. 2016). This asymmetry in hunting benefit often causes disagreement between landowners in winter and summer ranges regarding hunting quotas and targets for population sizes.

Theoretical studies clearly document that increased harvest yield and a more unified management of migratory populations can be attained through improved collaboration at larger scales in such a situation (Skonhøft et al. 2013). In our study system, formation of management units that cover both typically winter and summer ranges could solve this issue, potentially reducing conflicts by reaching common goals for population development and appropriate hunting quotas. Management of red deer in Norway occurs hierarchically at two spatial levels, the municipality and local management units (LMUs). Central authorities (Norwegian Environment Agency) make general laws and regulations for red deer management that are implemented by the local authorities at the scale of municipalities, which in turn give quotas to the different LMUs within each municipality. Landowners have exclusive hunting rights of ungulates and more than 80% of the land area is privately owned. Large landowners can have their own LMU, but it is far more common that many landowners unite in a common LMU. LMUs are the legal entity among landowners and their rights is regulated in the national legislation. The level and scale of the mismatch can influence on possible solutions, and the type of border may be important for how difficult it is to change management units' size. It may be unrealistic to change political boundaries such as municipalities, while it may be an easier task at landowner level (LMU).

Here, we (1) quantify red deer space use and relate the space use pattern to the size of administrative management units at these two levels i.e. landowners level (LMU) and public administration level (municipalities). We then (2) quantify the effect of environmental factors

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and individual characteristics for the probability of crossing administrative borders (LMU) during the year. We discuss the challenges related to attaining sustainable management of large ungulates when administrative units clearly deviate from biologically meaningful subdivisions, we give explicit advice regarding scales of management in different landscape contexts, and discuss the issues of scale relative to alternative management options such as coordination of aims across boundaries.

Materials and methods

STUDY AREA AND DEER MANAGEMENT

The study area covers most of the red deer distribution range in Norway and was divided into seven different regions representing different counties (Myrsterud et al. 2011, see Fig. S1 in Supporting Information). Population density has increased substantially during the last decades and is highest in the coastal western regions and lowest in the eastern regions, and more than 95% of the annual harvest in Norway (35 135 deer in 2014) occurs in the five western counties along the coast. The regions cover a broad range of environmental conditions related to topography and climate. The topography along the west coast is more heterogeneous than in the eastern region. Mountainous areas account for approximately 30-50% of the area in the western regions. Agricultural areas, roads, towns and other human infrastructure are mainly located at lower elevations (Meisingset et al. 2013). More detailed description of the study area can be found elsewhere (e.g. Myrsterud et al. 2000).

The size of LMUs varies substantially, but need to be larger than the “minimum required area” (the smallest area required to harvest one animal) to get access to a hunting quota (usually between 0.5 to 2.0 km²). Typical property sizes range from 0.3 to 1.0 km² and less than 3% are >20 km². The minimum required area is set by each municipality based on estimated deer population density, and it can be varied within the municipality. However,

Norwegian governments have encouraged landowners to create larger LMU, to cover large enough areas to manage their “own” deer population. For smaller LMUs (less than 20x “minimum required area”), municipalities decides the yearly hunting quotas. Larger LMU usually make their own management plan for 3-5 year ahead with goals for population development and suggestion/application for annual hunting quotas divided into sex and age classes (calves, yearling and adults). The municipalities must approve this management plan. Until 2011, the hunting season lasted from 10 September until 15 November. From 2012, the hunting season was extended to last from 1 September to 23 December.

RED DEER DATA

We had access to GPS data from 114 male and 349 female red deer marked in 72 municipalities from 7 counties of Norway in the period 2002-2012 (subsets used in Myrsterud et al. 2011; Bischof et al. 2012). Deer were captured through chemical immobilization (darting) following standard procedures approved by the Norwegian Animal Research Authority (Sente et al. 2014). GPS-collars suitable for red deer females and males were used (Tellus from Followit, Sweden and GPS ProLite from Vectronic, Germany). Capture and marking were carried out from January to April each year. Collars were programmed to record positions every one to two hours. We included only the first monitoring year, and only deer which yielded sufficient data to designate annual space use patterns (females: n=316; males: n=96; Table S1, see next subsection).

ESTIMATION OF SPACE USE

We excluded all locations collected within 24 hours after marking. If deer were shot during hunt, we excluded all data acquired at the date of death. GPS-position outliers were removed (following Bjørneraas et al. 2010), causing deletion of less than 0.05% of the locations. Mean

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GPS fix rate was 90.2% (range 45.2-100%) and median location error has earlier been estimated to 12 m (Godvik et al. 2009). We classified red deer space use tactic (“resident”, “migratory”, “irregular” or “dispersal”) and extracted the timing and distance of migration (migrants only) following Bischof et al. (2012). This approach involves fitting logistic functions to displacement profiles, allowing discrimination of movement tactics and extraction of key parameters (Bunnfeld et al. 2011). Individuals classified as “irregular” and “dispersal” were excluded from all further modelling. We estimated home range size by using the fixed kernel technique (Worton 1989), using the R-package adehabitat (Calenge 2006). To get suitable estimates of the smoothing factor h , we divided the data into two groups based on individual space use tactics, i.e. migrating deer in one group and the rest in another group (resident, irregular and dispersal). We first calculated individual h -values for each deer using the reference method (Worton 1989). The final h -factor was calculated as the median value of the individual h -factor in each group, and this value was used when calculating the 95% kernel home range. For annual home range analysis, we included only animals that were marked before April 1 (still in their winter range) and provided positions at least until 1 November and/or had completed their autumn migration.

ENVIRONMENTAL AND MANAGEMENT DATA

The Norwegian Institute of Bioeconomy Research (www.nibio.no) provided land resource maps, while digital terrain models and data on municipality borders were obtained from the Norwegian Mapping Authority (www.statkart.no). Data on LMU borders were obtained from each municipality in two of the seven study populations (Møre & Romsdal and Sør-Trøndelag, Fig. S2). We quantified environmental characteristics at the scale of municipality and values for each deer was linked to the municipality that had the largest part of the winter home range (before migration or first of June in resident individuals). The proportion of

forested habitat (all types) and proportion of agricultural areas (hereafter pastures) was quantified based on classified land cover using overlay analyses and raster operations in ArcGIS 9.3 (ESRI, USA). We calculated the distance to coast as the shortest distance from the centre of each municipality to the coastline, as well as latitude and topographic diversity (diversity of elevations; Mysterud et al. 2001). We used the proportion of high elevation deer habitat (segments between 250–700 m; Loe et al. 2012) as a measure for high elevation habitats. The number of harvested red deer per km² counting area (the basis for harvest quotas) in each municipality was used as a proxy for population density (Mysterud et al. 2007).

STATISTICAL ANALYSES

We grouped the analyses into: (1) red deer space use in relation to the size and use of administrative units (containing GPS positions from individual deer) at two levels (LMU and municipalities), and (2) temporal variation in the probability of crossing LMU borders.

All statistical analyses were performed in R (R Development Core Team 2011). We used generalized linear mixed-effects models (GLMM) with negative binomial response distributions when analysing number of used municipalities and LMU used by each deer (count data). GLMMs were fitted with the function `glmmadmb` in the R package `glmmADMB` vs. 0.8.4. We tested for inclusion of random effects using likelihood-ratio tests by sequentially removing one random effect at a time in a null model (no fixed effects except intercept) fitted with Restricted Maximum likelihood (REML; Pinheiro & Bates 2000). After establishing the random effects structure, we fitted full models using maximum likelihood, to allow for fixed-effects model selection. Likelihood-ratio tests were used to test for the inclusion of candidate fixed effects (Pinheiro & Bates 2000). At the municipality scale, the full model included sex, space use tactic (migratory or resident), diversity of elevations,

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proportion of high elevation habitats, latitude, population density, proportion of forested habitats, proportion of pastures, and whether the municipality was an island or not. At the LMU scale, the full model included sex, space use tactic, proportion of high elevation habitats, population density, distance to coast, proportion of forested habitats, proportion of pastures, and whether the municipality was an island or not. Exploratory plotting of Generalized Additive mixed models (GAMM) indicated that diversity of elevations had a non-linear relationship with several of the response variables. We therefore included a polynomial (2nd order) term for this variable in all initial models. All continuous fixed effects were standardized to allow for direct comparison of effect sizes.

To analyse the temporal variation in the probability to cross LMU borders, we used GAMM fitted with the `gamm` function in the library `mgcv` in R (Wood 2006). We considered a border crossing (binomially distributed response variable; 1=yes, 0=no) when successive GPS-positions were found in different LMUs. We evaluated the results visually based on predicted effect sizes and confidence limits. Julian date was fitted as a spline variable and individual as random effect. Separate models were fitted for all four combinations of sex and space use tactic. This analyses were only run for areas with digitized LMU maps (Møre & Romsdal and Sør-Trøndelag, Fig. S2).

Results

RED DEER SPACE USE

Among females, 55.1% were classified as migrants, 39.9% as resident, 1.9% as dispersers and 3.2% with irregular space use (n=316). Among males, 56.3% were classified as migrants, 28.1% as resident, 6.3% as dispersers and 9.4% with irregular space use (n=96). In the subsequent analyses, deer with irregular space use and dispersers were excluded. Males had generally a more extensive space use than females. Fewer males were found to be resident

($z=3.06$, $p=0.002$), males had longer migration distances (males: mean=28.8 km, range=3.6-101.4 km, females: mean=21.1 km, range=2.5-75.8 km, $t=2.71$, $p=0.007$), and larger annual home ranges than females (migratory males: mean=149.8 km², range=58.3-426.9 km², migratory females: mean=115.1 km², range=46.6-384.1 km², $t=4.00$, $p<0.001$; resident males: mean=9.1 km², range=3.0-64.8 km², resident females: mean=4.9 km², range=1.0-13.9 km², $t=6.16$, $p<0.001$).

SIZE OF ADMINISTRATIVE UNITS RELATIVE TO DEER SPACE USE

A medium-sized municipality (median=282.5 km², range=19.5-1902 km²) was large enough to contain 98% of female annual home ranges and 94% of male annual home ranges (Fig. 1a), whereas median diameter of municipalities encompassed 70% and 62% of female and male migration distances, respectively (Fig. 1b). In contrast, both home range size and migration distances clearly exceeded the size of LMU. A medium sized LMU (median=14.3 km², range=1.2 km²-195 km²) was large enough to contain 39% of female home ranges and 21% of male home ranges (Fig. 1a), whereas only 12% and 4% of LMU were wide enough to encompass migration distances in females and males, respectively (Fig. 1b).

INFLUENCE OF INDIVIDUAL AND ENVIRONMENTAL FACTORS ON THE EXTENT OF MANAGEMENT AREA USE

The number of used municipalities (i.e. containing GPS positions) was higher in migrating (mean=2.1, $SD\pm 1.18$, $n=227$; range=1-6) than resident red deer (mean=1.2, $SD\pm 0.42$, $n=153$; range=1-3; Table 1) with no additional difference between the sexes. While 86% of resident red deer used only one municipality, only 37% of migrants did the same. Correspondingly, migratory deer (mean=6.6, $SD\pm 4.70$, $n=83$; range=1-20) used a substantially higher number of LMUs than resident deer (mean=2.0, $SD\pm 1.31$, $n=69$; range=1-8), and males (mean=6.0,

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SD±5.22, n=50; range=1-20) used a higher number than females (mean=3.7, SD±3.46, n=102; range=1-18; Table 2). While resident deer of both sexes spent about 93% of their time in their core LMU, migratory females spent 64% and migratory males 56% of their time in one LMU. When excluding deer that used only one LMU (males n=11; females n=29), resident females (n=30) and males (n=4) spent respectively 99% and 88% of their time within two LMUs. For the migratory deer, females (n=43) spent 89% of their time in only two LMUs, whereas migratory males (n=35) spent 86% of their time in only two LMUs. The number of municipalities used were negatively associated with diversity of elevations (Table 1). Proportion of forest contributed to increasing number of used municipalities (Table 1). Red deer on the mainland used more municipalities (Table 1) and LMUs (Table 2) compared to those on islands. Red deer used more LMUs in municipalities with a high proportion of high elevation habitats and with decreasing distance to coast (Table 2).

TIMING OF MIGRATION AND ADMINISTRATIVE BORDER CROSSINGS

Probability of crossing management borders differed greatly between resident and migratory deer, with migrants having much higher probability to cross a border throughout the year (Fig. 2). Migrating deer of both sexes showed a bimodal distribution in border crossing probability, with peaks in the probability of crossing coinciding with timing of seasonal migration. The mean date of spring migration was 6 May for females (SD=17.0 days, n=174) and 9 May for males (SD=16.8 days, n=54). Compared to the spring migration, autumn migration was spread over a longer period (females: mean=21 September, SD=29.8, n=174; males: mean=22 September, SD=23.9, n=54), and 20% of the deer started migration before the onset of the hunting season 1 September (Fig. 3). Further, the peak in border crossing frequency in autumn was overlapping with first half of the hunting season (Fig. 2).

Discussion

Animal movements across administrative borders can have major impact on conservation or management of populations (Singh & Milner-Gulland 2011). There has been an increasing body of literature regarding animal space use and migrations during the last decades (Cagnacci et al. 2010), but surprisingly few attempts to link movement data with applied issues related to scale of management (Linnell 2005). Delimiting populations that occupy continuous habitats into biologically meaningful units for management is difficult partly due to the elusiveness of animals in forested areas and partial migration. We show that migratory red deer frequently cross management borders and use several municipalities and management units throughout the year. Such a sharing of individuals across management units makes it difficult to achieve population level deer management.

LANDSCAPE AND SCALE OF MANAGEMENT

The relevance of scaling issues varies depending on extent of movements within species and populations relative to size of management units, whether there are conflicting aims, and whether the costs and benefits are evenly or unevenly distributed between management units. In our study, the current main concern of fragmented management is not a lower population growth rate than could optimally be achieved (Hebblewhite et al 2006). Instead, the concern is on a fair share of revenue and costs among landowners with different proportions of summer and winter range to red deer (Skonhøft et al 2013). Main drivers of migration in the northern hemisphere are often linked to snowfall in autumn and forage maturation in spring (Hebblewhite, Merrill & McDermid 2008; Cagnacci et al. 2011; Mysterud 2013). Summer ranges are often found at higher elevations (Mysterud et al. 2011; Hebblewhite, Merrill & McDermid 2008). A topography with access to a range of elevations prolongs the favourable spring period (Bischof et al. 2012), and high topographic diversity are often linked to higher

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proportion of migrants (Mysterud et al. 2011). Interestingly, red deer used fewer management units in municipalities in areas with diverse topography. In line with this, occurrence of migration and migration distance in roe deer (*Capreolus capreolus*) across Europe was a function of a combination of topography (slope) and habitat characteristics (occurrence of forest; Cagnacci et al. 2011). Environmental factors such as snow depth were important in describing migrating patterns in moose across a large latitudinal gradient in Sweden (Singh et al. 2012), whereas spatial and temporal dynamics in resource availability and snow depth explained the variation in movement distances in a population of Norwegian moose (Van Moorter et al. 2013). These movement patterns are probably explained by large-scale variation in topography. Our finding of less used municipalities in areas with diverse topography, and higher use of LMU with increasing proportion of high elevation habitats demonstrate that landscape and habitat patterns should be taken into account when forming LMUs for populations with partial migration. However, red deer used more LMUs along the coast, and this was due to smaller LMU sizes in these areas rather than the deer space use.

COMMON MANAGEMENT OF TWO SEXES WITH DIFFERENT RANGE USE

Our results show that average sized LMUs are too limited in size to manage the male segment of the population, and even municipalities are small when considering the migration distances of males. Sexual segregation is a common phenomenon in ungulates (Ruckstuhl & Neuhaus 2005), but rarely accounted for in population management. In Slovakia, the minimum extent of hunting grounds is 20 km², partly to account for long-distance movements of male red deer (Kropil, Smolko & Garaj 2015). In Sweden, males migrated outside an open red deer conservation reserve of 440 km² during rut, which complicated the management goal to increase the proportion of mature males in the local management area, as males crossed borders into other areas (Jarnemo 2008). Even if migration patterns are well known,

management may fail because of different hunting regimes and competition over mature males between hunting units (Clutton-Brock et al. 2002). The case of the extensive male space use questions whether population level management within LMUs is realistic.

LARGE OVERLAP BETWEEN MIGRATION AND HUNTING PERIOD

The timing of migration relative to the hunting season may dampen or increase the problem caused by migratory animals. The same animals may be subject to different harvesting regimes if management is not coordinated and migration coincides with hunting. In pronghorn (*Antilocapra americana*) in North Dakota, USA, movements over management boundaries were common, but few animals moved before or during the actual hunt (Kolar, Millspaugh & Stillings 2011). In contrast, red deer females in the Italian Alps migrated in the first week of the hunting season back to their protected winter range (Bocci et al. 2010). For the Jackson elk herd in the US, the implementation of a longer hunting season led to a higher harvest of late migrants (Smith 2007). Timing of hunting seasons varies largely across Europe, and may as well be altered within countries over time (Apollonio et al. 2011). In our Norwegian case, autumn migrations coincided with the current hunting season for 80% of the migratory deer resulting in peaked border crossings during the hunt, accentuating the need for a unified management in winter and summer ranges. Attempts to mitigate this by advancing the onset of the hunting season (in 2012) resulted in a moderate redistribution of hunting revenue (Loe et al. 2016), but any further advancement of the hunting season is restricted by ethics (the risk of orphaning dependent offspring in early autumn). Further progress in redistribution of this resource must therefore occur by reconsidering the extent of the spatial management units relative to deer space use, and our results provide a solid basis for such a process.

ALTERNATIVES FOR PRACTICAL MANAGEMENT

The space use of red deer in Norway found in this study would lead us to recommend management unit sizes of about 200 km², but depending on landscape. Theoretically, this will intercept more than 90% of the local red deer population. Hence, the main conclusion of our study is that current LMUs are clearly too small, while the scale of the municipality is close to capture functional population units of these partially migratory deer populations.

The first option is to merge LMUs guided by information of population connectivity, irrespective of the artificial boundaries set by current administrative borders. A trend of increasing sizes of LMUs has been an ongoing process over the last decades in Norway. However, our study document that current efforts have not been sufficient to capture the functional populations. Our results indicate that further increases in LMU sizes could be an option in areas with a diverse topography spanning both winter and summer ranges within reasonable distances. Where red deer mainly migrate along an elevational gradient, landowners could merge neighbouring LMUs along the same gradient, as a step in the direction towards management of functional population units. Even migratory males spent more than 85% of their time within two LMUs, suggesting that merging of only two neighbouring LMUs could be an important contribution. However, in areas with longer migration distances, management at a population level would require joining an additional 10-20 LMUs to create more relevant sizes, which would be close to a municipality scale.

A second option is therefore to only manage at the municipality scale and remove the LMU scale. This raises the question of whether deer management in Norway should reverse the process of local decision-making and decide quotas directly with strict municipal control. This was in many ways how deer were managed in the past. Though biologically meaningful, it has proven to lead to less interest in management and reduce local understanding of and ownership to management goals. Therefore, such a top down control is unlikely to achieve

the desired objectives of improved management, as local participation in processes appears a key feature of successful management.

A third option is coordination of management goals at larger scales. Coordination across LMUs regarding size and composition of hunting quotas may potentially decrease the need for larger formal LMUs. We see such efforts as a promising solution in particular regarding management of males with the most extensive movements. In many areas, there is an aim to increase mean age of males (and hence to save larger males), and this could be compromised if management aims are not coordinated across larger scales. In the case of males, it would be easier to see the benefits to all LMUs. However, whether there is willingness to solve the issue of how to get a more even share of revenue between winter and summer ranges remains more unclear, as this requires the LMUs dominated by winter ranges to accept a lower yield voluntarily. If they accept a redistribution of quotas towards being higher in summer ranges, it is uncertain if deer remain sufficiently long before migration, so that the increase in quotas actually leads to higher harvests.

Conclusions

A large portion of the deer populations in northern forests exhibits a space use pattern involving a substantial regular spatial redistribution due to partial migration. For migratory individuals, we found a substantial mismatch between annual space use and the average size of both landowner based management co-operation units (LMUs) as well as for municipality size. The current situation involves significant challenges related to carrying out a uniformed population management strategy, as well as related to a fair distribution between hunting revenues and costs related to foraging damages. Management units should therefore more closely reflect the biology of the populations rather than the human-defined jurisdictional

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boundaries. Our study highlights how GPS-data can be used to explicitly inform the spatial scale of population management also for more elusive forest living deer. However, the extensive movements of males suggest that also coordination across local management units may be needed, as it may not be practically realistic to have units sufficiently large to capture annual range use of males. Given the current organization of management structures, achievement of specific management goals will rely on extensive collaboration between management units sharing a common functionally linked deer population.

Data accessibility

Data set used available from the Dryad Digital Repository: doi:10.5061/dryad.h7v6v (Meisingset et al. 2017).

Authors' contributions

ELM, LEL and AM initiated the study. ELM, BZ and ØB organized data collection and database. ELM, LEL, RB, and IMR did various aspects of statistical analysis. ØB, USL and VV and constructed maps and did GIS-work. ELM drafted the paper with main input from LEL and AM. All authors edited and approved the final manuscript.

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Table 1. Coefficients of the top general mixed-effects model (GLMM; Negative binomial) predicting the number of municipalities annually used by GPS-marked red deer (n=380) in Norway. Marking municipality (n=70) was included as a random effect (SD=0.001). Negative binomial dispersion parameter: 403.43 (SE<0.001)

Variable	<i>B</i>	SE	<i>z</i>	<i>P</i> -value
(Intercept)	-0.110	0.142	-0.77	0.440
Space use tactic (migr. vs resi.)‡	0.548	0.092	5.97	<0.001
Diversity of elevations	-0.099	0.051	-1.93	0.051
Proportion of forests	0.136	0.039	3.48	<0.001
Island or mainland†	0.327	0.152	2.16	0.031

‡Reference for space use tactic is resident (=resi.; migr.=migratory)

† Reference category is island.

Table 2. Coefficients of the top general mixed-effects model (GLMM; Negative binomial) predicting the number of local management units (LMU) annually used by red deer (n=152) in Norway. Marking municipality (n=17) was included as a random effect (SD=0.0008). Negative binomial dispersion parameter: 6.561 (SE=1.722).

Variable	<i>B</i>	SE	<i>z</i>	<i>P</i> -value
(Intercept)	0.230	0.156	1.47	0.141
Sex*	0.283	0.112	2.53	0.011
Space use tactic (migr. vs resi.)‡	0.937	0.134	6.98	<0.001
Proportion of high elevation habitats	0.266	0.096	2.77	0.006
Distance to coast	-0.422	0.098	-4.28	<0.001
Island or mainland†	0.635	0.173	3.67	<0.001

*Reference sex is female.

‡Reference for space use tactic is resident (=resi.; migr=migratory)

† Reference category is island.

Figure legends

Fig. 1. Annual home range (95% kernel; a) and migration distances (migrants only; b) shown as accumulated proportion for each sex (solid line=females, broken line=males) in relation to area (km²) and diameter (km) of local management units (LMU; red) and municipalities (Munic; blue). Red and blue lines represent the median area (a) and diameter (b) of the units, and the coloured area the 25% and 75% quantiles. Note: Data for both red deer space use as well as LMU and municipality borders were only available from two populations (Møre & Romsdal and Sør-Trøndelag)

Fig. 2. Probability of red deer crossing borders of local management units (LMU, per hour) as a function of Julian date for each combination of sex and migration strategy (resident and migratory). Lines represent predicted effects from the final GAMM. Coloured shaded areas represent 95% confidence polygons of the predicted effects. Gray vertical shaded areas represent the hunting periods.

Fig. 3. Distribution of onset (timing) of autumn migration for female (solid line) and male red deer (broken line) in Norway shown as accumulated proportion of migratory deer of each sex in relation to Julian date. Gray vertical shaded areas represent the hunting periods (see text for details).



