RESEARCH PAPER

How landscape dynamics link individual- to population-level movement patterns: a multispecies comparison of ungulate relocation data

Thomas Mueller[1,2]*, Kirk A. Olson[3], Gunnar Dressler[1]†, Peter Leimgruber[2], Todd K. Fuller[3], Craig Nicolson[3], Andres J. Novaro[4], Maria J. Bolgeri[5], David Wattles[6], Stephen DeStefano[6], Justin M. Calabrese[7,2] and William F. Fagan[1]

[1]*Department of Biology, University of Maryland, College Park, MD 20742, USA,* [2]*Smithsonian Conservation Biology Institute, National Zoological Park, 1500 Remount Road, Front Royal, VA 22630, USA,* [3]*Department of Environmental Conservation, University of Massachusetts, Amherst, MA 01003-9285, USA,* [4]*Argentine Research Council and Patagonian and Andean Steppe Program-Wildlife Conservation Society, Carilafquen 51, Junin de los Andes, 8371 Neuquén, Argentina,* [5]*Argentine Science Agency and Patagonian and Andean Steppe Program-Wildlife Conservation Society, Carilafquen 51, Junin de los Andes, 8371 Neuquén, Argentina,* [6]*US Geological Survey, Massachusetts Cooperative Fish and Wildlife Research Unit, University of Massachusetts, Amherst, MA 01003, USA,* [7]*Department of Ecological Modelling, Helmholtz Centre for Environmental Research-UFZ, Permoserstrasse 15, 04318 Leipzig, Germany*

*Correspondence: Thomas Mueller, Department of Biology, BioPsych-Building, Room 3205, University of Maryland, College Park, MD 20742, USA.
E-mail: muellert@gmail.com
†Present address: University of Greifswald, Department of Mathematics and Computer Science, Robert-Blum-Strasse 2, D-17487 Greifswald, Germany.

ABSTRACT

Aim To demonstrate how the interrelations of individual movements form large-scale population-level movement patterns and how these patterns are associated with the underlying landscape dynamics by comparing ungulate movements across species.

Locations Arctic tundra in Alaska and Canada, temperate forests in Massachusetts, Patagonian Steppes in Argentina, Eastern Steppes in Mongolia.

Methods We used relocation data from four ungulate species (barren-ground caribou, Mongolian gazelle, guanaco and moose) to examine individual movements and the interrelation of movements among individuals. We applied and developed a suite of spatial metrics that measure variation in movement among individuals as population dispersion, movement coordination and realized mobility. Taken together, these metrics allowed us to quantify and distinguish among different large-scale population-level movement patterns such as migration, range residency and nomadism. We then related the population-level movement patterns to the underlying landscape vegetation dynamics via long-term remote sensing measurements of the temporal variability, spatial variability and unpredictability of vegetation productivity.

Results Moose, which remained in sedentary home ranges, and guanacos, which were partially migratory, exhibited relatively short annual movements associated with landscapes having very little broad-scale variability in vegetation. Caribou and gazelle performed extreme long-distance movements that were associated with broad-scale variability in vegetation productivity during the peak of the growing season. Caribou exhibited regular seasonal migration in which individuals were clustered for most of the year and exhibited coordinated movements. In contrast, gazelle were nomadic, as individuals were independently distributed and moved in an uncoordinated manner that relates to the comparatively unpredictable (yet broad-scale) vegetation dynamics of their landscape.

Main conclusions We show how broad-scale landscape unpredictability may lead to nomadism, an understudied type of long-distance movement. In contrast to classical migration where landscapes may vary at broad scales but in a predictable manner, long-distance movements of nomadic individuals are uncoordinated and independent from other such individuals. Landscapes with little broad-scale variability in vegetation productivity feature smaller-scale movements and allow for range residency. Nomadism requires distinct integrative conservation strategies that facilitate long-distance movements across the entire landscape and are not limited to certain migration corridors.

INTRODUCTION

Long-distance animal movements are a globally threatened phenomenon (Wilcove & Wikelski, 2008). To develop and implement better conservation strategies, population-level understanding of animal movements is critical. However, recent progress in understanding animal movement has mostly focused on the movement behaviours of individuals (Morales *et al.*, 2004; Holden, 2006; Forester *et al.*, 2007; Fryxell *et al.*, 2008; Nathan *et al.*, 2008; Schick *et al.*, 2008; Gurarie *et al.*, 2009) and our understanding of the emergent spatial dynamics at the population level has not increased at the same pace (but see Moorcroft & Lewis, 2006).

To quantify spatio-temporal dynamics in population distributions, the analysis of individual movement paths is not sufficient: ecologists must, in addition, attend to the relationships that exist among moving individuals. While much behavioural research has tackled mechanisms of leadership and group movement leading to the formation of herds and schools (e.g. Couzin *et al.*, 2005), little research has explored the inter-relationships among animal relocations at broad temporal and spatial scales. Likewise, whereas traditional research on population distributions has focused on static resource landscapes derived from habitat maps to explain spatial patterns of habitat use (e.g. habitat occupancy modelling and resource selection functions), the need to understand the effect of ecological and landscape dynamics on population distributions is widely recognized (Jonzén *et al.*, 2004; Mueller *et al.*, 2008; McLoughlin *et al.*, 2010). Long-term satellite data on vegetation productivity may be useful to quantify environmental dynamics and link them to individuals' movement paths and the resulting population-level movement patterns.

Population-level movement patterns, i.e. dynamics in population distributions, can be generally classified in three broad categories: (1) range residency, wherein individuals reside in home ranges or territories and in their lifetimes occupy relatively small areas compared to the population range; (2) migration, which is generally defined as a regular, long-distance pattern of movement to and from spatially disjunct seasonal ranges, and (3) nomadism, which occurs where individual animals exhibit long-distance movements (as in migration) but move across the landscape in routes that vary widely among individuals or from season to season (Mueller & Fagan, 2008). However, these general categories are non-exclusive, and more than one of these patterns may occur within populations of the same species (e.g. Hundertmark, 1998) or within the same species at different times (e.g. songbirds that are territorial at the breeding site, but migrate in groups between summer and winter ranges). In ungulates, underlying landscape dynamics are generally believed to be a major driver of these population-level movement patterns (Sinclair, 1983; Holdo *et al.*, 2009). Static landscapes or dynamics at small scales should favour sedentary ranges, dynamics that vary across broad scales but are predictable should facilitate migration, and broad-scale dynamics that are less predictable should support nomadism (Mueller & Fagan, 2008).

Although these different classes of movement dynamics are interesting from fundamental behavioural, ecological and evolutionary perspectives, animal movements in general, and long-distance movements in particular, also represent one of the greatest challenges in conservation (Wilcove & Wikelski, 2008). This situation is complicated even further when movements are not predictable in space and time (Fryxell *et al.*, 2005). Ungulates, which exhibit a tremendous plasticity in movement behaviours across and within species (Bolger *et al.*, 2008), constitute an excellent group of species in which to explore these issues.

Here, we examined relocation data for four ungulate species: barren-ground caribou (Cervidae: *Rangifer tarandus granti*) of the Porcupine herd in Alaska and north-west Canada, Mongolian gazelle (Bovidae: *Procapra gutturosa*) of the Eastern Steppes in Mongolia, guanacos (Camelidae: *Lama guanicoe*) in the Patagonian Steppes of Argentina, and moose (Cervidae: *Alces alces*) in the north-eastern United States. These four species represent a wide range of different types of population distributions. Distributions of some of these species (i.e. migration in caribou and range residency in moose, see details below) have been well studied and will serve as benchmarks for evaluating the distributions of the lesser known species (guanaco and in particular Mongolian gazelle).

We developed this paper with three goals in mind: (1) to distinguish the different population-level movement patterns (range residency, nomadism and migration) in a quantitative fashion; (2) to examine variability in movement behaviours within populations and within years; and (3) to link the population-level dynamics to the underlying landscape vegetation dynamics. To accomplish these three goals, we focused not just on traditional analyses of individual movement paths but also on analyses of the *inter-relationship of relocations among individuals*. Only very few studies so far have considered inter-relationships of relocations (Dunn & Gipson, 1977, on home ranges; Cushman *et al.*, 2005, on elephants; Heupel & Simpfendorfer, 2005, on sharks), and none with the goals of this paper in mind.

We extended the framework and movement metrics proposed by Mueller & Fagan (2008) and used relocation data to demonstrate how to measure spatio-temporal variation in movement

at the population level. Finally, we linked our results on the spatial dynamics of populations to analyses quantifying the underlying environmental landscape dynamics based on long-term satellite imagery of vegetation productivity. Our efforts advance ecological theory at the interface between individual behaviours and population distributions, and in addition, provide important metrics that can inform integrative conservation strategies for species that exhibit different types of long-distance movements.

METHODS

Study regions

The barren-ground caribou of the Porcupine herd range across the Arctic National Wildlife Refuge in Alaska (USA) and the northern Yukon (Canada). These caribou are long-distance migrants; they use the northern coastal tundra plains as calving grounds and overwinter further inland where mountainous alpine and taiga vegetation dominates (Fancy *et al.*, 1989; Griffith *et al.*, 2002).

Mongolian gazelle (hereafter referred to as gazelle) chiefly inhabit the Eastern Steppes of Mongolia. The steppes, which are the largest intact temperate grasslands in the world, feature broad plains and rolling hills with a relatively homogeneous vegetation comprising mostly grasses and forbs with almost no trees (Olson *et al.*, 2005, 2009; Mueller *et al.*, 2008). Gazelle move long distances (Ito *et al.*, 2006), but to date relatively little is known about their general patterns of movement.

Guanacos inhabit south-western South America, with their largest remaining populations in the Patagonian Steppes of Argentina. Low shrubs and scattered grasses alternate with bare soil and rocks. Little is known about guanaco movement patterns, but they are believed to be partial migrants, with some portion of the populations migrating and other individuals being range residents (Ortega & Franklin, 1995).

Moose relocation data are from the north-eastern United States, a temperate forest ecoregion featuring heavily forested habitats dominated by rolling hills and extensive streams, lakes and other wetlands. Unlike the other three study regions, this area features a relatively dense human population. Moose in this region are range residents (Hundertmark, 1998).

Appendix S1 in Supporting Information provides additional details on habitats, capture techniques and relocation methods for all four species.

Movement data

In the main body of the paper we present results from year-long relocation data for five individuals for each of the four species. For these analyses, we used data from individuals that were all captured in a single small region of each landscape, such that, for each species, the mean pairwise distance between the initial locations of individuals was < 20 km.

Because the quantification of population-level movement patterns addresses long-term and broad-scale questions and

because species may differ greatly in how their movement distances are related to temporal scale, we focused on 16-day time intervals in which complete sets of relocation data for all individuals were available, and intentionally ignored finer temporal resolutions for the inter-individual analyses of this study (see Appendix S2 for details on movement data).

For the remainder of the paper we focus on the dataset of 20 individuals described above because it affords a standardized data structure, geographically constrained starting points and a constant sample size. However, as a check on concerns about sample size, we also analysed additional data for caribou, gazelle and moose (see Appendix S3), which all confirmed our original findings.

Quantifying individual movement

We quantified two measures for each individual movement path, namely *total annual movement* and *tortuosity*, which measures the lack of straightness of a movement path.

Annual movement

From data acquired at different temporal resolutions (see Appendix S2) we estimated the annual movement of each individual by calculating the sum of all movement distances for each temporal resolution. We filled data gaps by bootstrapping samples from each individual and repeated the sampling 1000 times to calculate the mean estimate of annual movement for each individual on each temporal scale.

Tortuosity

For caribou, gazelle and moose, we could examine inter-specific differences in annual movement as a function of temporal resolution. Because the data were line segments rather than complete movement paths we adapted the divider method, a conservative technique for detecting differences in movement behaviours, to calculate the fractal dimension of movement (Halley *et al.*, 2004; Nams, 2005; Roshier *et al.*, 2008). In using fractal dimension, we do not imply the existence of any superdiffusion or self-similarity of paths, but simply seek to examine inter-specific differences in path straightness (or lack thereof).

To investigate the interaction of temporal resolution and species on annual movement, we log transformed annual movement and temporal resolution and fitted a linear mixed model [assuming random slopes for individuals and random intercepts where individuals were nested within species using function lmer in R (R Development Core Team, 2009), library lme4 (Bates *et al.*, 2008)]. We conducted multiple inter-specific comparisons by changing the reference level of the indicator variable 'species' and refitting the regression. We estimated *P*-values using Markov chain Monte Carlo (MCMC) methods (function pval.fnc in R, library languageR; Baayen, 2008) and performed Bonferroni adjustments to account for multiple comparisons.

We calculated the fractal dimension of the movement path for each species as 1 – slope of the species effect of temporal resolution.

Quantifying population-level movement patterns

We quantified three measures for population-level movement patterns. First, the *realized mobility index* (RMI) reports the amount of habitat an individual occupies as a proportion of the population range calculated across all five individuals (modified from Roshier & Reid, 2003). Second, the *movement coordination index* (MCI) measures the degree to which movements among individuals are related in direction and distance. Finally, the *population dispersion index* (PDI) measures the inter-relation of relocation records across individuals within a species as a point pattern to detect whether individuals co-occur, are dispersed from each other or are independently distributed.

Realized mobility index

We calculated annual ranges of each individual and the annual range of each 'population' (i.e. combined annual range of the five individuals) using minimum convex polygons and computed the RMI as the area of each individual range divided by the area of the population range.

Movement coordination index

We calculated a MCI among the five individuals at each movement step. This index is based on the X and Y shifts among individuals, thus capturing variation in both direction and distance. If x_i and y_i represent the observed displacements of the ith individual along orthogonal axes in a movement step and N is the number of individuals, the index can be calculated as:

$$\text{MCI}_{16\,\text{day step}} = 1 - \frac{1}{2}\left(\frac{\sum_{i=1}^{N}|x_i - \bar{x}|}{\sum_{i=1}^{N}|x_i|} + \frac{\sum_{i=1}^{N}|y_i - \bar{y}|}{\sum_{i=1}^{N}|y_i|}\right). \tag{1}$$

Identical movements among individuals yield MCI = 1, while more independent and random movements have MCI values closer to 0 (see Appendix S4 for an in-depth analysis of the behaviour and expected values of the MCI under both independent and correlated movements among individuals). We calculated this index for caribou, gazelle and moose, but had too few samples to calculate it for guanaco. We tested for significant differences in MCI by performing a Kruskal–Wallis test and post hoc tests for multiple comparisons between treatments (function kruskalmc, R library pgirmess; Giraudoux, 2009). Instead of the MCI, one might perform cross-correlation analyses between pairs of X and Y shifts. However, the MCI is based on absolute deviation, rather than squared errors; consequently, it does not emphasize large deviations from the mean over small ones and is less sensitive to outliers. We demonstrate in Appen-

dix S4 that the MCI increases with increasing correlation among individuals' movements, and that this general behaviour is independent of the particular forms of the X and Y shift distributions.

Population dispersion index

We analysed animal relocations as a statistical point pattern and calculated the bivariate k function between each individual's relocation data and the relocation data of all other individuals of that species. The bivariate k function (Rowlingson & Diggle, 1993) calculates the expected number of points of pattern 1 (relocations of one individual) within a distance s of an arbitrary point of pattern 2 (relocations of all other individuals), divided by the overall point density in pattern 1 (function k12hat, R library splancs; Rowlingson *et al.*, 2008). Values near zero indicate randomness, above zero dispersion, and below zero spatial clustering of relocation patterns. We calculated the mean and the range of estimates for individuals of each species at several spatial lags.

Because the PDI does not discriminate relocations across time (i.e. clustering may indicate individuals using the same space but not necessarily at the same time), we additionally examined the *pairwise distances* of individuals throughout the year and compared them with the distribution of 1000 simulated pairwise distances of five random points drawn from within the yearly range of that species (i.e. the minimum convex polygon calculated across all recaptures of all individuals of that species).

Quantifying landscape dynamics

To quantify spatio-temporal change in resources across the ungulates' landscapes, we used GIMMS (global inventory modelling and mapping studies) data, a normalized difference vegetation index (NDVI) product obtained from the advanced very high resolution radiometer (AVHRR) instrument onboard the NOAA satellite series (Tucker *et al.*, 2005). NDVI is a good estimator of vegetation growth and productivity, and numerous studies demonstrate it to be extremely effective in predicting resources for ungulates, including some of those species studied here (Pettorelli *et al.*, 2005, 2009; Mueller *et al.*, 2008). GIMMS data, which span 1981–2006, are provided in 8 km × 8 km resolution semi-monthly composites, yielding 24 composites per year. For all composites, we extracted subsets for each of the four study regions using the minimum convex polygons of each species' total annual movement data as a mask. In addition, we also buffered the minimum convex polygons of guanacos and moose with 25-km and 50-km wide regions, respectively, to extract the NDVI data, because without the buffers the polygons were too small for subsequent analyses of broad-scale vegetation dynamics.

We measured landscape dynamics with regard to temporal variability, spatial variability and unpredictability of vegetation productivity. Unpredictability characterizes the 'repeatability' of landscape-level variation in space and time (Mueller & Fagan, 2008). This distinction means that a resource landscape could be

variable but relatively predictable in its variability, or variable but in an unpredictable fashion. For each study region and each of the 24 semi-monthly periods we used the 25 years of GIMMS data to calculate three metrics. First, we calculated the mean NDVI across space to estimate resource phenology within years. Second, we calculated the temporal average of semi-variograms with lags from 10 to 50 km to estimate how resource variability varied across spatial scales in the different systems. Lastly, we calculated for each spatial location (i.e. each grid cell) the standard deviations of NDVI for all composites of a semi-monthly period. We used the spatial average across all spatial locations as an estimate for the unpredictability of landscape dynamics.

We investigated how these measures differed among the four study regions and to what extent they were related to our estimates of animal movements on the individual and population levels. We fitted linear mixed models to test whether: (1) the temporal average semi-variance of NDVI at broad scales (specifically, a 50-km lag) was related to annual movement (accounting for species with a random factor); and (2) whether any significant differences existed in landscape unpredictability across the four study regions (accounting for the time period of the composites with a random factor). Differences in vegetation dynamics among landscapes were most prevalent at the height of the summer growing season (June to August, for caribou, gazelle and moose; December to February for guanaco), so we also analysed landscape dynamics using NDVI data from these summer months. We again used the function lmer in R and estimated *P*-values using MCMC methods (function pval.fnc in R).

RESULTS

Individual movements

Caribou and gazelle ranged across large areas, while guanaco and moose had smaller ranges (Fig. 1). The effect of temporal resolution on the overall length of movement paths was significantly greater for moose than for caribou ($P = 0.003$) or gazelle ($P = 0.003$, Fig. 2), indicating that movements of caribou and gazelle were less tortuous with lower fractal dimensions than movement paths of moose (Table S5.1 in Appendix S5). Gazelle and caribou were not significantly different from each other ($P = 0.1$).

At 16-day resolution, annual movements for all five caribou were greater than 1200 km (mean = 1624 km, range = 1258–1962 km). One gazelle moved a distance similar to the caribou, and the other four gazelle all moved >700 km (mean = 946 km, range = 726–1525 km). Annual movements for guanaco (mean = 230 km, range = 125–358 km) and moose (mean = 58 km, range = 42–107 km) were significantly shorter (Fig. 3a; see Appendix S3 for data on additional animals).

Population-level movement patterns

The RMI, which contrasts the annual ranges of each individual against the total annual range of the five monitored individuals

in its population, indicated a high overlap among the ranges of individual caribou, with all individual caribou covering a substantial portion of the population range over the course of a year (Fig. 3b; mean = 0.630, range = 0.475–0.795). Among gazelle, two individuals behaved similarly to the caribou and ranged across the larger part of the population range; in contrast, the other three gazelle covered a smaller portion of the yearly population range (Fig. 3b; mean = 0.320, range = 0.141–0.621). Guanacos had the widest spread in RMI, with one individual covering almost 60% of the population range, while another individual only covered a small fraction of the population range (Fig. 3b; mean = 0.275, range = 0.050–0.570). Individual moose covered small proportions of the population range (Fig. 3b; mean = 0.095, range = 0.046–0.192).

The MCI, which gauges the similarity among individuals' movements on a per step basis, showed marked differences between the coordinated movement of the caribou and the almost random movements of the gazelle and moose. Caribou had a mean MCI of 0.326 that was significantly higher ($P < 0.05$) than both moose and gazelle, which did not differ from each other (mean of 0.109 and 0.097, respectively; Fig. 3c; this was also the case for the additional data, see Appendix S3).

The PDI showed dispersed patterns for moose, mostly independent relocation patterns for gazelle, and strongly clustered patterns for caribou and guanaco (Fig. 3d). A closer examination of pairwise distances across time (Fig. 4) revealed that the five caribou remained clustered during much of the year, with a distinct period of dispersion for about 2.5 months in the autumn. In contrast, the gazelle were effectively independently distributed with the exception of a period of close aggregation at calving time. Finally, moose were more widely separated from each other than expected by chance and remained dispersed from each other for most of the year (Fig. 4).

Landscape dynamics and animal movement

Landscapes with caribou and gazelle exhibited pronounced spatio-temporal variability in vegetation productivity, whereas the landscapes with moose and guanaco exhibited far less variability (Fig. 5). Variability generally increased at broader spatial scales and was especially large for caribou and gazelle during the summer months. Variability at broader spatial scales was comparatively low for guanaco and moose. The seasonality for range resident moose was different from the other three systems in that the variability of the moose landscape peaked in winter, not summer (Fig. 5). Seasonality of vegetation dynamics was strongest for the caribou landscape (in part due to its being almost entirely snow-covered from November to May), followed by landscapes of gazelle and moose. Seasonality of the guanaco landscape was not as pronounced (Fig. S5.1a in Appendix S5). For gazelle, unpredictability of the landscape peaked in summer at the height of the vegetation season. For caribou and moose, unpredictability peaked in spring at the beginning of vegetation green-up. In contrast, no prominent peaks in unpredictability existed for guanacos (Fig. S5.1b in Appendix S5).
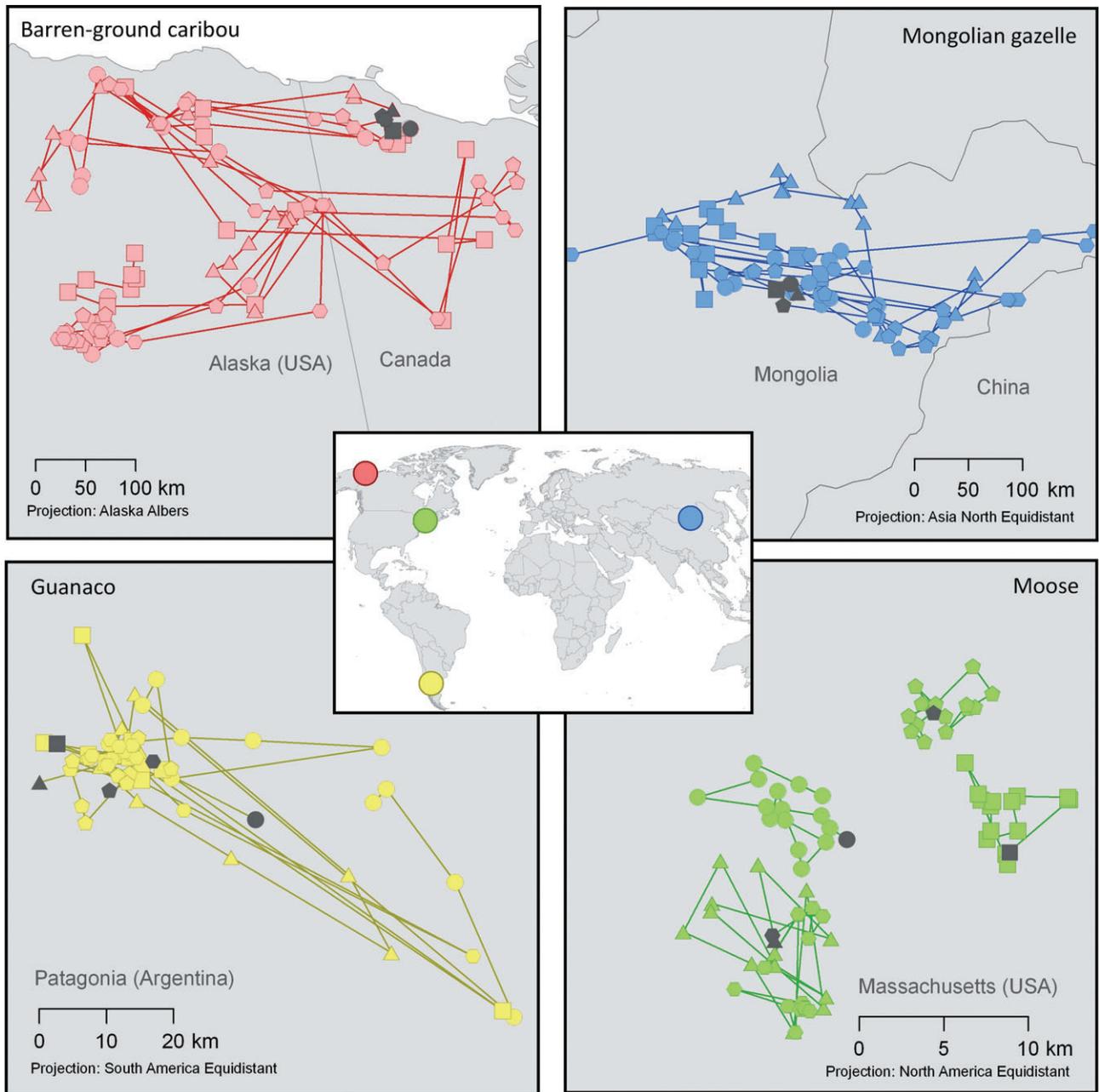
Figure 1 Yearly relocation data of caribou, Mongolian gazelle, guanaco and moose, sampled at a 16-day scale. Initial locations of each individual are in grey (each with a different symbol).

Landscape dynamics and animal movements covaried on the individual and population levels. On the individual level, long-distance annual movements were significantly positively related to broad-scale resource variability, in particular variability occurring at the peak of summer vegetation growth (Fig. 6a, Table S5.2 in Appendix S5). Across the entire year, the link between movement and resource landscape dynamics was considerably weaker (Table S5.2 in Appendix S5). We found similar results for the fractal dimension of animal movements, which were substantially lower in highly variable gazelle and caribou landscapes in summer compared with the more uniform moose landscape (Fig. S5.2 and Table S5.3 in Appendix S5). On the

population level, landscape unpredictability was associated with a lack of movement coordination. The gazelle landscape was significantly more unpredictable than landscapes of caribou, moose and guanaco during the summer, and remained different from caribou and guanaco (but not moose) when the entire year was considered (Fig. 6b for summer months and Table S5.4 in Appendix S5).

Overall, broad-scale landscape variability was associated with the long-distance movements of caribou and gazelle whereas low landscape variability was associated with the range resident movement pattern of moose and the relatively short-distance migration of guanaco (Fig. 6a). In addition, relatively low land-
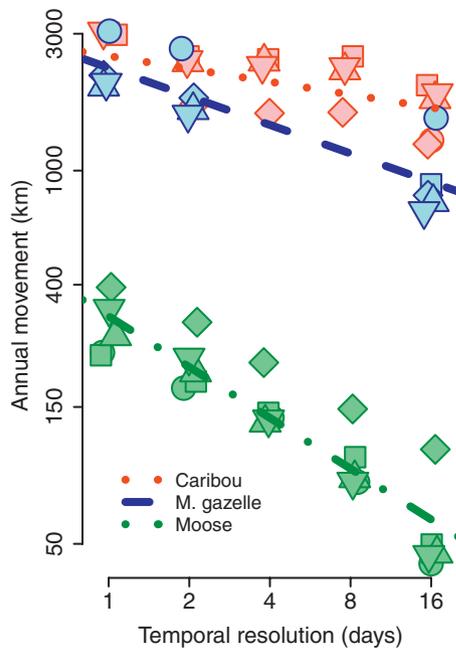
Figure 2 Annual movement in relation to temporal resolution of recapture data for caribou, Mongolian gazelle and moose. Data for guanaco were only available at the 16-day timescale and were thus excluded from this analysis. Symbols indicate individuals. Regression lines are species estimates from a linear mixed model (see Table S5.1 in Appendix S5).

scape unpredictability (compared with gazelle) was characteristic of caribou, which move in a coordinated migratory fashion (Fig. 6b). Taken together, these results suggest that broad-scale landscape variability coupled with landscape unpredictability may be the key ingredients underlying the nomadic movements of gazelle.

DISCUSSION

Using a suite of spatial statistical probes, we demonstrated striking links between landscape vegetation dynamics and movement patterns for four ungulate species. Long-distance ungulate movements, which were related to broad-scale summertime resource dynamics, exhibited substantial variability both within and among species. We systematically differentiated among different types of long-distance movement by quantifying how the spatio-temporal unpredictability of resources mapped onto the coordination (or lack of coordination) in movement among individuals in a population. Nomadism, as exhibited by Mongolian gazelle, was an especially remarkable form of movement in that individual animals captured in close proximity to one another subsequently moved across many hundreds of kilometres in a seemingly uncoordinated fashion that was statistically distinguishable from seasonal migration. Our study is novel because it compares standardized relocation data across species, because it considers inter-individual relationships of relocations, and

because it relates among-species differences in movement to the dynamics of resource landscapes. The spatial statistical metrics that we developed and applied effectively distinguished among alternative types of population-level movement patterns (range residency, migration and nomadism).

## Quantifying differences among migration and nomadism and home ranges

Traditionally, ungulate populations have been classified simply as 'migratory' or 'non-migratory', and for migratory populations the standard metric has been roundtrip distance to and from disjunct seasonal ranges (Berger, 2004; Harris *et al.*, 2009; see Appendix S6 for a discussion of relevance of temporal resolution on roundtrip distance). While this simple dichotomy is sometimes appropriate, authors have noted wide variation in migratory patterns and emphasized the need for a more specific understanding of long-distance movements (Bolger *et al.*, 2008; Wilcove & Wikelski, 2008).

Here we provide quantitative evidence for the existence of nomadism in ungulates as a type of long-distance movement distinct from migration and find fundamental differences in long-distance movements of caribou and gazelle. Traditionally both, caribou and gazelle, were referred to as migratory and classified as such according to roundtrip distances (Leimgruber *et al.*, 2001; Berger, 2004; Harris *et al.*, 2009). Roundtrip distances however are insufficient for comparisons because caribou and gazelle differed critically in 'movement coordination' among individuals. Movements of individual gazelle were significantly more independent from each other than were movements of individual caribou (note that this was the case even if caribou were not caught in the same region, see Appendix S3). In fact, the low level of movement coordination observed among gazelle did not differ from the movement coordination of moose that resided in separate home ranges and moved far smaller distances (Figs 1 & 3). The PDI indicated random, rather than clustered, distributions of relocation patterns between individual gazelle when measured at spatial scales up to 20 km (Fig. 3d). Despite being captured in very close proximity to each other, individual gazelle did not occur significantly closer to one another than expected by chance except at calving time.

Although we could not calculate movement coordination for guanaco, analyses of relocations as point patterns revealed that some guanacos, like caribou, remained clustered throughout the year. In contrast, other species were either more randomly distributed (gazelle) or evenly dispersed (moose). Thus our analyses suggest that guanacos moved together in a migratory fashion but over far shorter distances than did caribou. However, guanaco are believed to be partial migrants, with only some portion of the populations migrating and other individuals being range residents (Ortega & Franklin, 1995). The RMI confirmed this, as some guanacos covered almost the entire population range (similar to caribou and gazelle) while others covered only a small fraction (yielding small RMI values similar to resident moose).
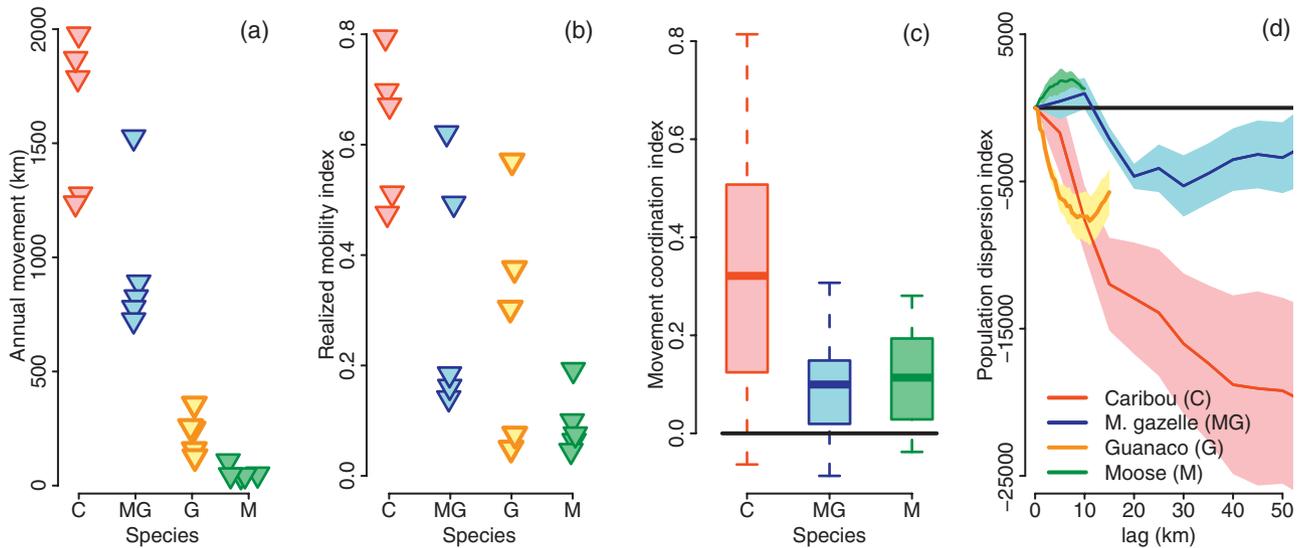
Figure 3 Annual movements (a) and inter-relations between individuals (b, c, d) based on 1 year of relocation data from five individuals of each of four species (C, caribou; MG, Mongolian gazelle; G, guanaco; M, moose) measured in 16-day intervals. (b) Realized mobility index*: quantifies the annual range of an individual as a proportion of the annual range of the 'population' (i.e. the range of all five individuals of that species). Values close to 1 indicate that individuals range over the entire population range. (c) Movement coordination index (MCI) measures the movement variation among individuals in terms of the relative distance and direction moved at each time step. Identical movements across individuals have a MCI value of 1 whereas random movements have an MCI closer to 0 (see Appendix S4). (d) Population dispersion index (PDI) reports the bivariate *k*-function between each individual and relocation points of all other individuals of the same species as a function of spatial lag. The solid line indicates the mean and shaded areas show the range of all PDI estimates. Positive values (above the solid black line at *y* = 0) indicate dispersion and negative values indicate clustering between relocations of different individuals. For further details on each statistic see Methods.
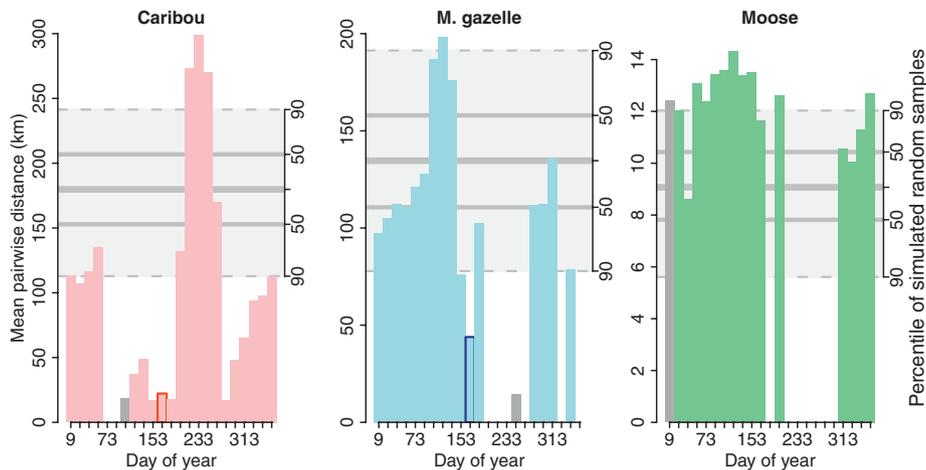

Figure 4 Mean pairwise distances of five individual caribou, Mongolian gazelle, moose and guanaco. Grey bars indicate first pairwise distance in data set (for gazelle right after capture). Bars with a dark coloured outline indicate the calving time for caribou and Mongolian gazelle where only females were tracked. Grey horizontal bars indicate the mean, 50th and 90th percentiles of the mean of 1000 simulated pairwise distances of five points drawn randomly from within the minimum convex polygon of the yearly range of all individuals of that species. Note that *y*-axis scales differ among panels.

Landscape vegetation dynamics as a driver of ungulate movement

Here, we have focused on ungulate movements in the context of landscape-scale vegetation dynamics. This is a reasonable starting point because foraging resources are tightly linked to veg-

etation dynamics and NDVI (Hebblewhite *et al.*, 2008; Mueller *et al.*, 2008; Pettorelli *et al.*, 2009), and are widely considered the predominant factor determining ungulate movements (Sinclair, 1983). However, we recognize that exactly how NDVI translates into resource availability may depend on numerous factors
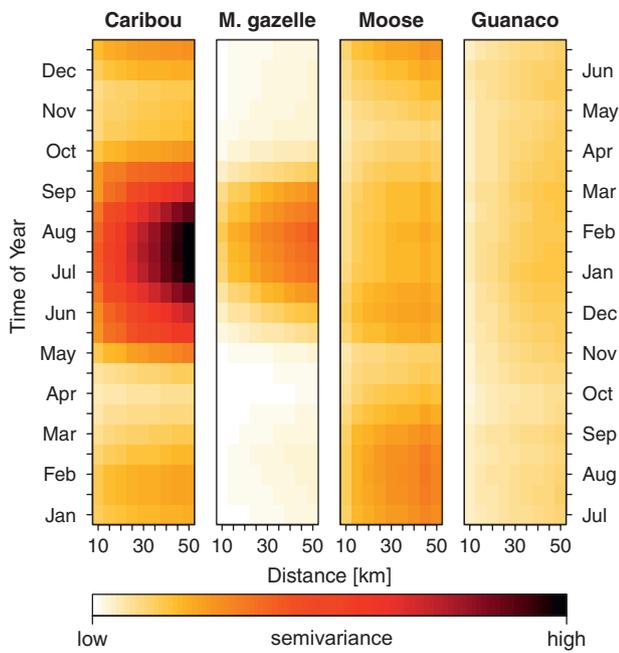
Figure 5 Semi-variance of vegetation productivity, based on 25 years of global inventory modelling and mapping studies (GIMMS) normalized difference vegetation index (NDVI) data, for resource landscapes of caribou, Mongolian gazelle, moose and guanaco. Because the resource landscape of guanacos is located in the Southern Hemisphere, the *y*-axis is shifted by 6 months to make the seasonality comparable to the other three landscapes in the Northern Hemisphere.

(such as habitat, vegetation and herbivore species, season). Consequently, we did not attempt to establish mechanistic links between movements and changes in resource distributions (as in Holdo *et al.*, 2009), but merely to demonstrate general associations between patterns of movements and patterns of vegetation productivity. Other factors such as predator avoidance, mate-finding and social structure may also influence movements. For example, aggregations at calving time may be an evolved predator swamping strategy (Young & McCabe, 1998, Fig. 4).

We conducted a multisystem comparison of links between ungulate movements and vegetation dynamics, demonstrating that long-distance movements were indeed related to broad-scale variability of vegetation productivity. However, because we generally found little variation of NDVI in the winter season, the link was strongest in summer. In combination with high variability at broad scales, unpredictability of resources was a key factor shaping long-distance ungulate movements. We found generally less predictability for the gazelle landscape than for the caribou landscape, which corresponds to the less coordinated movement of gazelle compared with caribou. Landscape vegetation dynamics for gazelle may be driven mainly by stochastic rainfall events. For example, a massive rainstorm in August 2007 (> 30 cm precipitation, which is abnormally high for the arid steppe) coincided with an unprecedented mass aggregation of 200,000 gazelle in the same

area several days later (Olson *et al.*, 2009). In contrast, the greater resource predictability for the caribou landscape arises due to a highly seasonal north–south coastal plain-to-mountains gradient. This dichotomy between stochasticity and seasonality in the gazelle and caribou landscapes, respectively, may explain the especially prominent difference in resource unpredictability during the growing seasons (Fig. 6b). In particular, we note that the only time the caribou landscape exhibited a greater unpredictability of resources than the gazelle landscape was in early summer at the beginning of vegetation green-up when unpredictability peaked for the caribou landscape (Fig. S5.2a,b in Appendix S5). That narrow peak in unpredictability is probably related to differences in the timing of snow melt among years and thus is not characteristic of the remainder of the growing season in the caribou landscape. Likewise, the smaller late-season peak in unpredictability in the caribou landscape may be associated with spatio-temporal heterogeneity in the arrival of the first heavy snowfall.

Conservation implications

Long-distance migration is particularly threatened by fragmentation and climate change (Bolger *et al.*, 2008; Wilcove & Wikelski, 2008; Sawyer *et al.*, 2009). Traditional conservation strategies for animals that move long distances have focused on the concept of migration, operating on the assumption that animals move regularly to and from seasonal ranges. As a consequence of that assumption, conservation efforts have focused on protecting habitats associated with perceived critical periods in life history, such as overwintering areas, calving ranges and the protection of specific migration corridors. Among ungulates, a focus on calving areas is especially important when populations have relatively well-defined areas where mass calving traditionally occurs [e.g. caribou, (Griffith *et al.*, 2002) and Tibetan antelope (Schaller, 1998)]. Likewise, a focus on migration corridors is appropriate for species that migrate along traditional routes and through bottlenecks [e.g. pronghorn (Berger, 2004) and saiga (Berger *et al.*, 2006)].

However, the suitability of these alternative conservation approaches hinges on what form the long-distance movements actually take. Neither protection of seasonal ranges nor the protection of migration routes will suffice if populations exhibit a high level of nomadism, in which individuals move independently from one another and at large spatial scales that would make any movement corridors or protected areas unfeasible. Our analyses demonstrate that Mongolian gazelle exhibit this kind of nomadic movement (Figs 3 & 4). In addition, no traditional calving areas are known for gazelle and effective conservation of this species will require that the steppe remains an open habitat, which is increasingly challenging in the face of infra-structure development related to oil exploitation and fencing (Olson *et al.*, 2009). For other ungulates (e.g. guanacos in Argentina outside our study region, several African species), movement barriers have eliminated long-distance movements entirely and have caused once-migratory populations to become
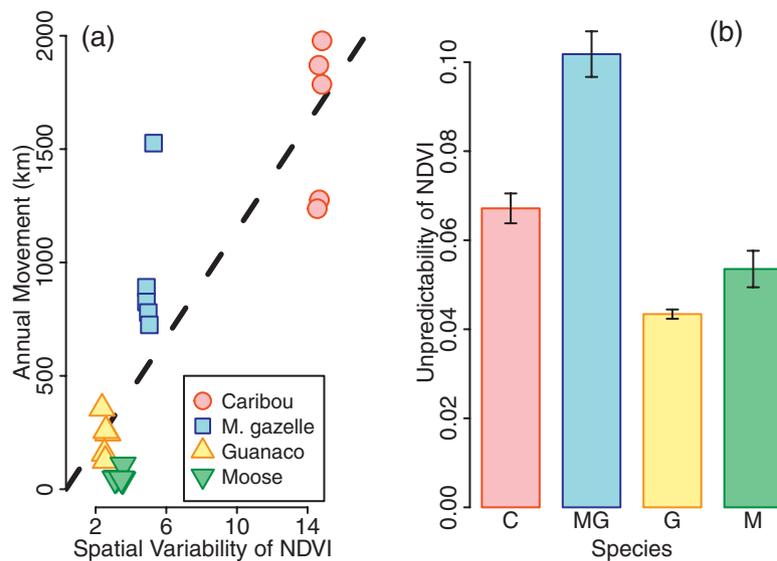
Figure 6 Multispecies comparison of ungulate movements as a function of landscape vegetation dynamics in summer (June to August for caribou, Mongolian gazelle and moose; December to February for guanaco). Panel (a) reports total annual movement as a function of the spatial variability of the normalized difference vegetation index (NDVI) for each species' landscape. Spatial variability was calculated as the average semi-variance of NDVI in summer based on images from 1981 to 2006 at a lag of 50 km. Each symbol represents an individual. The dotted line represents the average regression line of the mixed model analysis ($P = 0.002$; see Table S5.2 in Appendix S5). Panel (b) reports the unpredictability of vegetation dynamics in summer (calculated as the standard deviation of NDVI at the same time of year, see Methods for details). Mongolian gazelle exhibit significantly higher landscape unpredictability than caribou, guanaco or moose ($P < 0.001$ for each comparison; see Table S5.4 in Appendix S5).

sedentary. Such shifts in spatial population dynamics are often accompanied by dramatic decreases in population size (Newmark, 2008).

Future directions

Using a multispecies comparison of inter-individual relocation data, we demonstrated the existence of nomadism as a distinct type of long-distance movement that presents challenges for conservation and highlighted the importance of landscape variability and unpredictability as determinants of ungulate movement. For future studies, comparisons of movements of the same species in different ecosystems or of different species in the same ecosystem may provide a more mechanistic understanding of the relationships between individual movements and population-level movement patterns. Particularly interesting would be a multiyear study for species with long-distance movements that could investigate how inter-individual variability in movement paths shapes population-level patterns (e.g. the inter-individual concordance index; Mueller & Fagan, 2008).

REFERENCES

Baayen, R.H. (2008) *Analyzing linguistic data: a practical introduction to statistics using R.* Cambridge University Press, Cambridge.

Bates, D., Maechler, M. & Dai, B. (2008) *lme4: linear mixed-effects models using S4 classes.* R package version 0.999375-28. Available at: http://lme4.r-forge.r-project.org (accessed 1 March 2010).

Berger, J. (2004) The last mile: how to sustain long-distance migration in mammals. *Conservation Biology*, **18**, 320–331.

Berger, J., Cain, S.L. & Berger, K.M. (2006) Connecting the dots: an invariant migration corridor links the Holocene to the present. *Biology Letters*, **2**, 528–531.

Bolger, D.T., Newmark, W.D., Morrison, T.A. & Doak, D.F. (2008) The need for integrative approaches to understand and conserve migratory ungulates. *Ecology Letters*, **11**, 63–77.

Couzin, I.D., Krause, J., Franks, N.R. & Levin, S.A. (2005) Effective leadership and decision-making in animal groups on the move. *Nature*, **433**, 513–516.

Cushman, S.A., Chase, M. & Griffin, C. (2005) Elephants in space and time. *Oikos*, **109**, 331–341.

Dunn, J. & Gipson, P. (1977) Analysis of radio telemetry data in studies of home range. *Biometrics*, **33**, 85–101.

Fancy, S., Pank, L., Whitten, K. & Regelin, W. (1989) Seasonal movements of caribou in arctic Alaska as determined by satellite. *Canadian Journal of Zoology*, **67**, 644–650.

Forester, J.D., Ives, A.R., Turner, M.G., Anderson, D.P., Fortin, D., Beyer, H.L., Smith, D.W. & Boyce, M.S. (2007) State-space models link elk movement patterns to landscape characteristics in Yellowstone National Park. *Ecological Monographs*, **77**, 285–299.

Fryxell, J.M., Wilmshurst, J.F., Sinclair, A.R.E., Haydon, D.T., Holt, R.D. & Abrams, P.A. (2005) Landscape scale, heterogeneity, and the viability of Serengeti grazers. *Ecology Letters*, **8**, 328–335.

Fryxell, J.M., Hazell, M., Börger, L., Dalziel, B.D., Haydon, D.T., Morales, J.M., McIntosh, T. & Rosatte, R.C. (2008) Multiple movement modes by large herbivores at multiple spatiotemporal scales. *Proceedings of the National Academy of Sciences USA*, **105**, 19114–19119.

Giraudoux, P. (2009) *pgirmess: data analysis in ecology*. R package version 1.3.8. Available at: http://perso.orange.fr/giraudoux/ (accessed 1 March 2010).

Griffith, B., Douglas, D.C., Walsh, N.E., Young, D.D., McCabe, T.R., Russell, D.E., White, R.G., Cameron, R.D. & Whitten, K.R. (2002) The Porcupine caribou herd. *Arctic Refuge coastal plain terrestrial wildlife research summaries* (ed. by D.C. Douglas, P.E. Reynolds and E.B. Rhode), pp. 8–37. Biological Science Report USGS/BRD/BSR-2002-0001. US Geological Survey, Biological Resources Division. Available at: http://alaska.usgs.gov/BSR-2002/pdf/usgs-brd-bsr-2002-0001-sec03.pdf (accessed 1 March 2010).

Gurarie, E., Andrews, R.D. & Laidre, K.L. (2009) A novel method for identifying behavioural changes in animal movement data. *Ecology Letters*, **12**, 395–408.

Halley, J.M., Hartley, S., Kallimanis, A.S., Kunin, W.E., Lennon, J.J. & Sgardelis, S.P. (2004) Uses and abuses of fractal methodology in ecology. *Ecology Letters*, **7**, 254–271.

Harris, G., Thirgood, S., Hopcraft, J.G.C., Cromsigt, J.P.G. & Berger, J. (2009) Global decline in aggregated migrations of large terrestrial mammals. *Endangered Species Research*, **7**, 55–76.

Hebblewhite, M., Merrill, E. & McDermid, G. (2008) A multiscale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecological Monographs*, **78**, 141–166.

Heupel, M.R. & Simpfendorfer, C.A. (2005) Quantitative analysis of aggregation behavior in juvenile blacktip sharks. *Marine Biology*, **147**, 1239–1249.

Holden, C. (2006) Inching toward movement ecology. *Science*, **313**, 779–782.

Holdo, R.M., Holt, R.D. & Fryxell, J.M. (2009) Opposing rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti. *The American Naturalist*, **173**, 431–445.

Hundertmark, H.J. (1998) Home range, dispersal and migration. *Ecology and management of the North American moose* (ed. by A.W. Franzmann and C.C. Schwartz), pp. 303–335. Smithsonian Institute Press, Washington, DC.

Ito, T.Y., Miura, N., Lhagvasuren, B., Enkhbileg, D., Takatsuki, S., Tsunekawa, A. & Jiang, Z. (2006) Satellite tracking of Mongolian gazelles (*Procapra gutturosa*) and habitat shifts in their seasonal ranges. *Journal of Zoology*, **269**, 291–298.

Jonzén, N., Wilcox, C. & Possingham, H.P. (2004) Habitat selection and population regulation in temporally fluctuating environments. *The American Naturalist*, **164**, E103–E114.

Leimgruber, P., McShea, W.J., Brookes, C.J., Bolor-Erdene, L., Wemmer, C. & Larson, C. (2001) Spatial patterns in relative primary productivity and gazelle migration in the Eastern Steppes of Mongolia. *Biological Conservation*, **102**, 205–212.

McLoughlin, P.D., Morris, D.W., Fortin, D., Vander Wal, E. & Contasti, A.L. (2010) Considering ecological dynamics in resource selection functions. *Journal of Animal Ecology*, **79**, 4–12.

Moorcroft, P.R. & Lewis, M.A. (2006) *Mechanistic home range analysis*. Princeton University Press, Princeton, NJ.

Morales, J.M., Haydon, D.T., Frair, J., Holsiner, K.E. & Fryxell, J.M. (2004) Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology*, **85**, 2436–2445.

Mueller, T. & Fagan, W.F. (2008) Search and navigation in dynamic environments – from individual behaviors to population distributions. *Oikos*, **117**, 654–664.

Mueller, T., Olson, K.A., Fuller, T.K., Schaller, G.B., Murray, M.G. & Leimgruber, P. (2008) In search of forage: predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity. *Journal of Applied Ecology*, **45**, 649–658.

Nams, V.O. (2005) Using animal movement paths to measure response to spatial scale. *Oecologia*, **143**, 179–188.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P.E. (2008) A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences USA*, **105**, 19052–19059.

Newmark, W.D. (2008) Isolation of African protected areas. *Frontiers in Ecology and the Environment*, **6**, 321–328.

Olson, K.A., Fuller, T.K., Schaller, G.B., Lhagvasuren, B. & Odonkhuu, D. (2005) Reproduction, neonatal weights, and first-year survival of Mongolian gazelles (*Procapra gutturosa*). *Journal of Zoology*, **265**, 227–233.

Olson, K.A., Mueller, T., Bolortsetseg, S., Leimgruber, P., Fagan, W.F. & Fuller, T.K. (2009) A mega-herd of more than 200,000 Mongolian gazelles *Procapra gutturosa*: a consequence of habitat quality. *Oryx*, **43**, 149–153.

Ortega, I.M. & Franklin, W.L. (1995) Social organization, distribution and movements of a migratory guanaco population in the Chilean Patagonia. *Revista Chilena de Historia Natural*, **68**, 489–500.

Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.M., Tucker, C.J. & Stenseth, N.C. (2005) Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology and Evolution*, **20**, 503–510.

Pettorelli, N., Bro-Jørgensen, J., Durant, S.M., Blackburn, T. & Carbone, C. (2009) Energy availability and density estimates in African ungulates. *The American Naturalist*, **173**, 698–704.

R Development Core Team (2009) *R: a language and environment for statistical computing*. R foundation for statistical computing, Vienna, Austria. Available at: http://www.R-project.org (accessed 1 March 2010).

Roshier, D.A. & Reid, J.R.W. (2003) On animal distributions in dynamic landscapes. *Ecography*, **26**, 539–544.

Roshier, D.A., Doerr, V.A.J. & Doerr, E.D. (2008) Animal movement in dynamic landscapes: interaction between behavioural strategies and resource distributions. *Oecologia*, **156**, 465–477.

Rowlingson, B. & Diggle, P. (1993) Splancs – spatial point pattern-analysis code in S-Plus. *Computers & Geosciences*, **19**, 627–655.

Rowlingson, B., Diggle, P., Bivand, R., Petris, G. & Eglen, S. (2008) *splancs: spatial and space-time point pattern analysis*. R package version 2.01-24. Available at: http://www.maths.lancs.ac.uk/~rowlings/Splancs/ (accessed 1 March 2010).

Sawyer, H., Kauffman, M.J., Nielson, R.M. & Horne, J.S. (2009) Identifying and prioritizing ungulate migration routes for landscape-level conservation. *Ecological Applications*, **19**, 2016–2025.

Schaller, G.B. (1998) *Wildlife of the Tibetan steppe*. University of Chicago Press, Chicago, IL.

Schick, R.S., Loarie, S.R., Colchero, F., Best, B.D., Boustany, A., Conde, D.A., Halpin, P.N., Joppa, L.N., McClellan, C.M. & Clark, J.S. (2008) Understanding movement data and movement processes: current and emerging directions. *Ecology Letters*, **11**, 1338–1350.

Sinclair, A.R.E. (1983) The function of distance movements in vertebrates. *The ecology of animal movement* (ed. by I.R. Swingland and P.J. Greenwood), pp. 248–258. Clarendon Press, Oxford.

Tucker, C.J., Pinzon, J.E., Brown, M.E., Slayback, D.A., Pak, E.W., Mahoney, R., Vermotea, E.F. & El Saleousa, N. (2005) An extended AVHRR 8-km NDVI dataset compatible with MODIS and SPOT vegetation NDVI data. *International Journal of Remote Sensing*, **26**, 4485–4498.

Wilcove, D.S. & Wikelski, M. (2008) Going, going, gone: is animal migration disappearing? *PLoS Biology*, **6**, 1361–1364.

Young, D.D. & McCabe, T.R. (1998) Grizzly bears and calving caribou: what is the relation with river corridors? *Journal of Wildlife Management*, **62**, 255–261.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Study regions and data collection.
Appendix S2 Standardization of relocation data.
Appendix S3 Analyses using additional data for caribou, Mongolian gazelle and moose.
Appendix S4 Analysis and expectations of the movement coordination index.
Appendix S5 Additional figures and tables.
Appendix S6 The importance of temporal resolution of movement data.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be reorganized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

BIOSKETCH

Thomas Mueller is an ecologist at University of Maryland who is working at the interface of theoretical and applied questions. He is interested in processes explaining spatio-temporal population dynamics and has worked in a variety of systems including ravens in Poland, elephants in Myanmar and gazelles in Mongolia.

Editor: Joshua Lawlor