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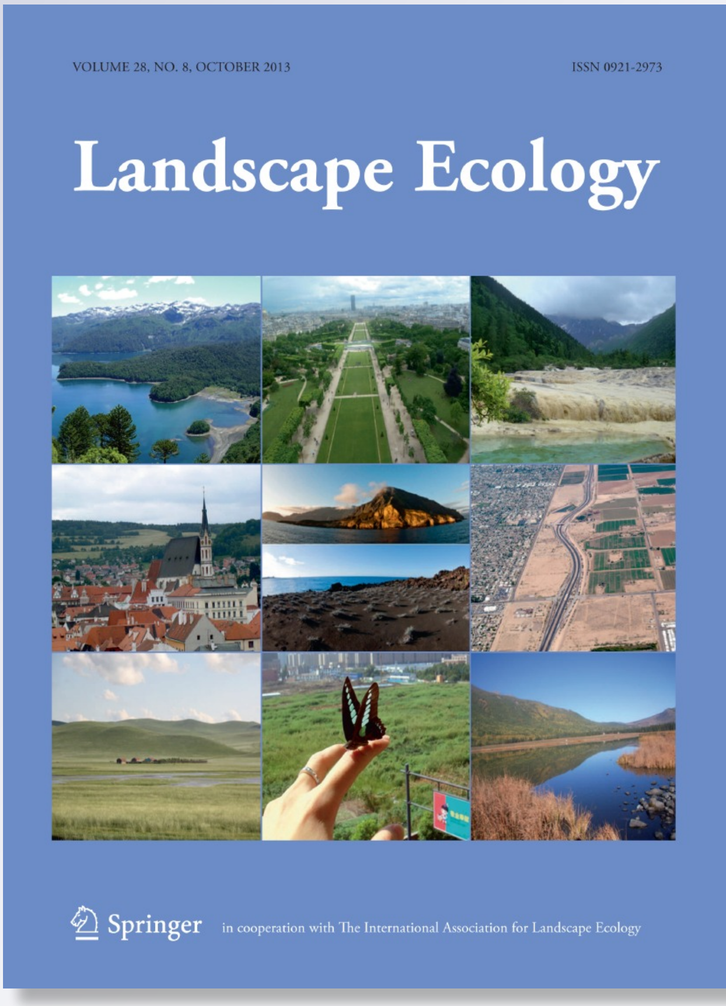

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RESEARCH ARTICLE

Characterizing wild ass pathways using a non-invasive approach: applying least-cost path modelling to guide field surveys and a model selection analysis

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Abstract Movement of animals is a key process affecting population dynamics. Information on factors that affect pathway use is essential for identifying and protecting pathways, and important for maintaining connectivity among populations. We present an innovative, non-invasive, approach for predicting pathways of reintroduced Asiatic wild ass (*Equus hemionus*) in Israel, which is based on understanding the effects of landscape factors on pathways use. The approach includes: Predicting pathways, by employing a least cost pathway (LCP) GIS models based on several landscape factors, so as to efficiently direct a field survey and explore the wild ass's general preferences of pathway types; Collecting empirical data by surveying the dung density of wild ass along each of the predicted pathways and using the data as an index of pathway use; Evaluating the predicted pathways against the empirical data collected, to estimate the general pathway preferences of the wild ass; and Developing and evaluating alternative generalized linear models, according to a priori hypotheses based on empirical data so as to quantify the effect of different landscape factors on pathway use. The analyses were conducted for the entire landscape, and then for two distinct landscape types, open landscape and landscape-barriers (mountain ridges), as subsets of the entire landscape. There were clear differences in the mean number of faeces counts between the LCPs, indicating that the wild ass prefers certain pathway types as a function of landscape features. We further found that the factors affecting *E. hemionus* pathway usage—vegetation; slopes; canyons; and 4-wheel drive routes—varied largely between the two major landscape types studied, demonstrating the importance of studying space use patterns at different landscape terrains. This information can be applicable to landscape planning measures that aim to enhance protection of the species. This approach provides a framework for studying animal space-use patterns of a variety of species, including elusive species, in a heterogeneous landscape.

Keywords Akaike's information criterion (AIC) · Conservation · *Equus hemionus* · Faeces · GIS · Landscape barriers · Landscape connectivity · Least-cost models · Reintroduction

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Introduction

Movement of animals in a heterogeneous landscape is a key process (Wiens et al. 1993) affecting population dynamics (Saccheri et al. 1998). It has a direct effect on gene flow among populations (Clobert et al. 2001), genetic diversity within populations (Tallmon et al. 2004), and on the persistence of populations that are naturally connected by dispersal (Brown and Kodric-Brown 1977; Rueness et al. 2003; Nathan et al. 2008). However, our understanding of animal movements, especially large-scale movements, in diverse landscapes, is very limited (Wennergren et al. 1995; Koenig et al. 1996; Turchin 1996; Trakhtenbrot et al. 2005; Holyoak et al. 2008). Thus, information on factors influencing space use patterns is essential for comprehending behaviour and accurately predicting the use of travel corridors (Bruggeman et al. 2007) and landscape connectivity between a population's core areas (Beier et al. 2005). Moreover, monitoring and analysing movement patterns can help predict resource use (Taylor and Taylor 1977; Dobson and Jones 1985; Buchmann et al. 2012). Therefore, conservation planners need detailed information on space use patterns and the factors affecting them, in order to protect those landscape features which are important for ensuring a population's performance.

Movement of animals in complex landscapes is a function of multiple factors (Dickson and Beier 2007). Different landscape factors, such as topography, water and forage, have been shown to affect the pathways of mammals (Johnson et al. 2008). For example, mountain ridges can function as complete or semi-permeable landscape barriers to movement, affecting both individual behaviour and population dynamics (Clobert et al. 2001). Hence, pathways that cross barriers may be crucial for the connectivity within and among populations (Murtskhvaladze et al. 2010). The characterization of landscape factors that affect the location of pathways may facilitate the identification of pathways that cross barriers, which due to their critical role in maintaining connectivity should be protected (Long et al. 2010).

Human-induced factors are also known to have important effects on the movement of animals. For example, studies have shown that roads may constitute obstacles that limit animal crossings (Trombulak and Frissell 2000; Riley et al. 2006). On the other hand, roads can also facilitate movement, especially when animals use roads which extend along natural travel corridors (Bruggeman et al. 2007).

Understanding landscape factors that affect movement patterns and determine the location of the pathways of large-scale movements is of a particular interest for reintroduced species. Reintroduced populations are expanding their range as part of their establishment process. Individuals disperse from release sites, establish their home ranges and, later on, may shift their home ranges or disperse to new areas (Dunham 1998; Dolev et al. 2002; Bar-David et al. 2005). Knowledge of the biology of reintroduced populations is often limited due to their rarity (Sarrazin and Barbault 1996; Saltz et al. 2000). Consequently, monitoring of individuals post-reintroduction, e.g. by direct observations and telemetry, can provide valuable information on their space use patterns (Yott et al. 2011; Dolev et al. 2002; Perelberg et al. 2003). This information could be further used for identifying and predicting—with the use of models—pathways which are important for the population's connectivity, for its future/potential range expansion, and, hence, for long-term persistence of the species in the wild.

However, monitoring of movement patterns is problematic, especially when it is difficult to directly observe the species or track it by radio or GPS telemetry in a rugged terrain (Lunney et al. 1998). Telemetry tracking methods are invasive, requiring the capturing and handling of individuals, a procedure which is complicated when the species is either rare (Lozano et al. 2003) (as is usually the case with small reintroduced populations) or elusive (Sharp et al. 2001). Hence, there is a need for indirect observation methods by which to obtain information on movement patterns and pathway use and reveal the factors affecting them.

In this article, we present an innovative, non-invasive approach for predicting the pathways of a species, by understanding the effects that landscape factors have on the species' use of pathways connecting between a population's core areas. We apply our approach to the endangered Asiatic wild ass (*Equus hemionus*) reintroduced into the Negev Desert, Israel. The approach is comprised of the following stages: (1) Predicting and mapping pathways of the wild ass between core areas, using least-cost path models (LCPs, McCoy and Johnston 2001; Chetkiewicz and Boyce 2009) to efficiently direct the (stage 2) field survey and explore the wild ass's general preferences of pathway types. The LCP function evaluates potential movement routes between a destination and a source in 'cost units' of movement, according to the specific landscape factor, and determines the 'cheapest route' (McCoy and Johnston 2001). Each LCP model took into account a single landscape factor. In the current study, we examined five main factors which, according to a literature survey and expert knowledge, have a considerable effect on the wild ass' pathways: steep slopes, narrow canyons, vegetation cover, water sources, and 4-wheel drive (4WD) routes. The LCPs were constructed using a Geographic Information System (GIS). (2) Collecting empirical data, by surveying dung density of wild ass in the field, along each of the mapped predicted pathways, as an index of pathway use. (3) Evaluating the predicted pathways against the empirical data to estimate the wild ass general pathway preferences. (4) Developing and evaluating alternative generalized linear models (GLMs) constructed according to a priori hypotheses, based on empirical data, in order to quantify the effect of the landscape factors on pathway use. The analyses were conducted for the entire landscape, and then for two distinct landscape types, open landscape and landscape-barriers (mountain ridges), as subsets of the entire landscape.

Methods

Study species

Equus hemionus is an endangered species (IUCN 2001), belonging to the horse (Equidae) family and weighing ~200 kg. Its distribution is mainly in arid environments throughout Asia (Saltz and Rubenstein 1995). The subspecies endemic to the Middle East (*E. h. hemippus*) became extinct at the beginning of the twentieth century (Groves 1986). In 1982, the Israeli Nature and Park Authority (INPA) began reintroducing Asiatic wild asses from a breeding core founded in 1968 in Hai-Bar Yotvata Reserve to the Negev Desert. The breeding core was established from six animals from the Persian subspecies (*E. h. onager*) and five animals from the Turkmen subspecies (*E. h. kulan*) (Saltz et al. 2000). Between 1982 and 1992, 17 males and 21 females of *E. hemionus* spp. were released in Makhtesh Ramon and in Wadi Paran, Negev Desert (Saltz and Rubenstein 1995). Currently, the population is estimated to be at least 200 individuals, distributed throughout the Negev (Fig. 1). Little is known about the reintroduced wild ass's movement patterns and pathway use.

The study area

The study was conducted in the Negev Desert (Fig. 1). The study area is diverse in elevation, from 1,000 m in the northwest to −200 m in the Arava Valley. Likewise, annual rainfall varies from 95 mm in the northwest to 30–40 mm in the rest of the region (Stern et al. 1986). The study area is characterized by steep and long mountain ridges, e.g. Makhtesh Ramon, Lotz cliffs and Arif-Hadav cliffs (Fig. 1).

There are three permanent water sources within the distribution area of the wild ass, which are artificial troughs that are maintained by the INPA: Ein Sharonim, Paran and Borot Lotz (Fig. 1). Around the three troughs, there is intensive activity of the wild ass, more so than in any other place in the Negev (Nezer 2011). Therefore, these areas were considered the three main core areas of the wild ass population in the Negev. In addition, (Nezer 2011) identified smaller core areas of the population, located in the Karkom Mountain, Wadi Ashosh, and the Chason Valley (Fig. 1).

Predicting and mapping least-cost pathways

Six LCP models in GIS (Ganskopp et al. 2000; McCoy and Johnston 2001) were constructed a priori, to predict and map wild ass pathways between the population's core areas. The LCP models' outputs, i.e. the predicted pathways, directed the field survey (see below). We assumed that evaluating the models' outputs against empirical data would clarify whether there are pathway-types that are used more intensively than others and, if so, which are the ones preferred.

The models were based on the main landscape factors which, according to a literature survey and expert knowledge, have a considerable effect on wild ass pathway use: steep slopes; narrow canyons; vegetation cover; water sources, and 4WD routes. Five LCP models took into account a single main landscape factor, and the sixth model was based on the shortest geographic distance between the population's core areas. The models were constructed using a least-cost function implemented in GIS software. For each

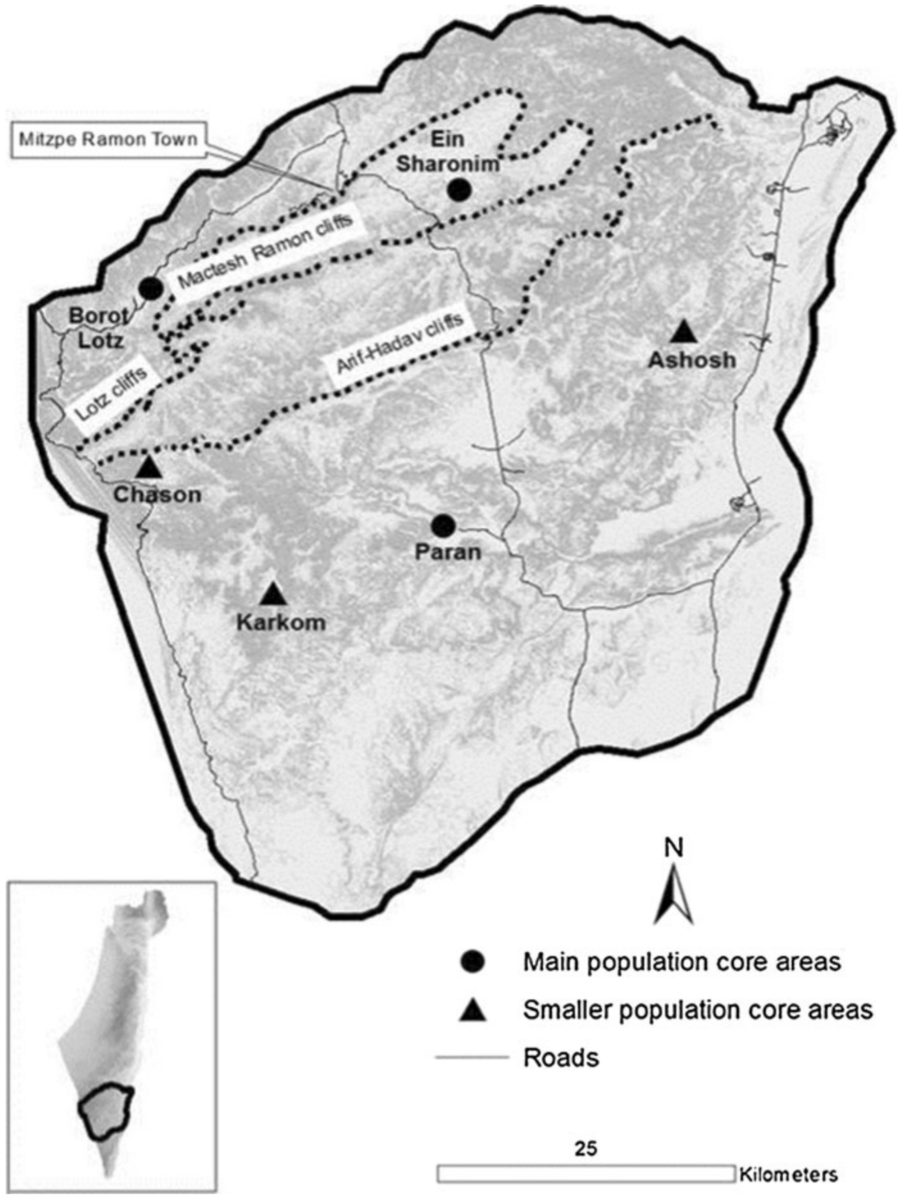

Fig. 1 The study area, Negev Desert, Israel, including the wild ass population's core areas. *Dotted lines* represent mountain ridges here considered as landscape barriers

given landscape factor, the least-cost function determines the shortest weighted distance path between a destination and a source in cost units, i.e. the 'cheapest route' for that factor (McCoy and Johnston 2001). The basis of this analysis is the cost raster maps that were constructed for each of the landscape factors: this is a GIS layer of the study area, in which every pixel has a cost assigned to it, according to the specific landscape factor (see details below). The outputs of the LCP models were respective LCP maps that connected the population's different core areas in a standard width of a single pixel (10 m). A description of the six LCP models follows.

(1) *The slope model* was based on the assumption that steep slopes require high cost for movement, because they are energetically costly (i.e. the steeper the slope, the higher the cost). For model development, a digital elevation model representing the elevation of the study area was transformed so that each pixel was assigned a value corresponding to the maximum change in

elevation over the distance between that pixel and its eight adjacent neighbours (McCoy and Johnston 2001). To create the cost raster, each range of slopes was assigned a cost value, according to the energetic costs (oxygen consumption) measured for burros (*E. africanus asinus*) climbing uphill (Yousef et al. 1972) (Appendix 1.1 in Supplementary material). We assumed that the cost of going uphill is the same as going downhill.

(2) *The narrow canyons-slope model* was based on the assumption that narrow canyons are risky for the wild asses, due to limited escape options driving a higher risk of predation (i.e. the narrower and longer the canyons, the higher the cost). For model development, a GIS map which defined polygons that surrounded the narrow canyons (<160 m between the walls of the canyon) was created. Each pixel within these polygons was assigned a cost according to the width and length of the canyons. The model combined the cost of moving in canyons (Appendix 1.2 in Supplementary material) and the cost of moving on slopes (Appendix 1.1 in Supplementary material).

(3) *The vegetation cover model* was based on the assumption that higher vegetation cover reduces the cost on movement (Kaczensky et al. 2008). Every pixel on the vegetation cover map was assigned a cost inversely related to the amount of vegetation cover in it (Appendix 1.3 in Supplementary material). The source of this map was a 'vegetation map' which presented at each pixel (10 m^2) the percentage of all woody vegetation cover, shrubs, and trees with a radius larger than 0.2 m (Nezer 2011).

(4) *The water sources model* was based on the assumption that travel costs increase with the distance to water sources (Saltz et al. 2000). Each pixel on the temporary water sources map was assigned a cost according to its distance to the nearest permanent water source, using the Euclidean distance function in ArcGIS.

(5) *The 4WD pathway model* was based on the assumption that 4WD vehicle routes would constitute a preferred alternative for wild ass movement since, they are less rough than other trails (Trombulak and Frissell 2000; Riley et al. 2006; Bruggeman et al. 2007). Hence, the model pathways followed 4WD routes.

(6) *Shortest distance between the population's core areas* was based on the assumption that the wild ass selects the shortest way, i.e. no landscape factors affect its movement. The model generated the shortest straight lines (Euclidean distance) between the population's core areas.

Collecting empirical data: field survey

We conducted dung surveys along the LCP model outputs (the predicted pathways). We assessed dung density, counted as the number of faeces mounds along each of the LCPs outputs, as an index of pathway use (Laing et al. 2003). Faeces mounds remain detectable in the field for about a year.

The field survey was done on two landscape types: open landscape and landscape barriers (mountain ridges, see details below). This enabled us to conduct the analyses for the entire landscape, as well as for two subsets of the entire landscape.

Selecting transects for the field survey

Using GIS, transects were selected a priori (before the field survey) to be evenly distributed along the LCPs of each model. From the LCP model outputs, 128 transects were selected (along the pathways), between 14 and 24 for each model. Due to landscape constraints and limited vehicle traversability, it was not possible to collect an equal number of samples for the various transects. All transects were 500 m long by 10 m wide (5 m on each side of the transect) where faeces detection probability was 100 %. The location of transects in the field was done using a GPS/GIS arc pad system; whenever possible, the transect locations selected followed the wild ass's natural trails (Appendix 2 in Supplementary material).

Among these 128 transects, 54 were located within three main mountain ridges (Fig. 1). These ridges were assumed a priori to be landscape barriers to the movement of the wild ass, based on their topography and due to their steep slopes and their length (Henley et al. 2007; Sharma et al. 2004). Movement through barriers has energetic costs and risks (Bruggeman et al. 2007; Dickson and Beier 2007). Thus, we presumed that wild asses only move through barriers when traversing long distances between core areas. For this reason, these barrier areas are of particular interest and, hence, the 54 transects were analysed as a separate subset, referred to as the landscape barriers subset. Along the transects, we counted the number of faeces mounds and recorded their GPS location.

Transect characteristics

Each of the surveyed transects was characterized by: (a) the total of faeces counts along it; and (b) the main landscape factors. Specifically, using GIS techniques, each transect and the 10 m strip along it was characterized according to the landscape factors under study, namely, its mean slope, proportion of vegetation cover, its distance from the nearest water source, whether it was located along 4WD routes, and whether it was inside a narrow canyon. All of the information on the transects, their faeces counts, and their landscape characteristics was examined, and the transects were grouped into datasets, as follows: (a) Entire landscape—included transects from the whole study site ($n = 128$); (b) Landscape barriers subset—included only transects from landscape barriers ($n = 54$); (c) Open landscape subset—included the remaining transects that were not from the landscape barriers ($n = 74$).

Evaluating the predicted least-cost pathways against empirical data

The number of faeces mounds per transect was used as an indication of wild ass pathway use along that transect. To compare wild ass pathway use in the different LCPs, we calculated the average of mounds per transect separately for each of the six LCP types, and performed a Kruskal–Wallis multiple comparison test (Breslow 1970). This test was used, since the distribution of faeces counts was not normal, and homogeneity of variances between LCPs was not a valid assumption (even after transformations).

Developing and evaluating alternative generalized linear models (GLMs)

Based on a literature survey and expert knowledge, a set of 40 alternative hypotheses (Appendix 3 in Supplementary material) was assembled a priori (before conducting the field survey), as a basis for exploring the effects of the five main landscape factors and the interactions between them on wild ass pathway use. According to the 40 hypotheses, a corresponding set of 40 alternative GLMs was developed, based on the empirical data (faeces field survey). We assumed that by evaluating the set of alternative GLMs against empirical data, we could quantify each factor's effect on—and relative contribution to—wild ass pathway use between the population's core areas.

The faeces counts along transects (the response variable) were related to the landscape factors characterizing the transects (the explanatory variables) using the alternative GLMs. The alternative GLMs were ranked according to their fit to the empirical data, using a model selection approach, whereby the maximum log-likelihoods of the models are compared simultaneously (Burnham and Anderson 2002). Given that the distribution of faeces counts along transects was not normal, a negative binomial distribution, which best fit the empirical data, was used, following Crawley (2007). The model selection approach was applied to the entire dataset (entire landscape), and to the two subsets (open landscape, and landscape barriers) in all models, except for those in the open landscape subset which included the (irrelevant) canyon parameter. The relative support for each model was evaluated using the Akaike information criterion (AIC; Burnham and Anderson 2002). The minimum corrected AIC (AICc) score represented the best fit to the observed data. This enabled us to rank and compare the models. In addition, the 'Akaike weight' of each model was used for estimating the probability that a given model was the best model within the given set of alternatives (Burnham and Anderson 2002). Thus, the models that had the highest rankings were indicative of the landscape factors with the greatest influence on wild ass pathway use. To quantify the relative importance of the different landscape factors, we used an 'evidence ratio' index, i.e. the ratio between the Akaike weights of two models (Anderson 2008). This index was used to compare any two models that differed from each other by a single landscape factor, while all the other components of the models were similar. To further quantify the relative importance of the predictor variables, all of the models in which a certain landscape factor appeared were selected, and the associated Akaike weights were summed up. The variable that had the highest total Akaike weight was considered the most important variable relative to the other predictor variables (Anderson 2008).

The model selection approach does not evaluate the goodness of fit of the models, yet this information is critical, especially for evaluating the prediction potential of the high ranking models. Therefore, the proportion of variance in the empirical data explained by the model (R^2) was calculated for each of the models (Faraway 2006). Due to the use of GLMs with a negative binomial distribution, an adjusted R^2 was used to fit the negative binomial GLMs, according to Faraway (2006).

The procedures—GLMs, R^2, model averaging, and model selection—were conducted using specific tools available in R statistical software (R Development Core Team 2005).

Results

The LCP models and their evaluation using empirical data

The complete outputs of the six LCP models, that predicted wild ass pathways between the population's core areas, are presented in Appendix 4 Supplementary material. Each of the LCPs predicted a different pathway, though there was some overlap between them. An example of the outputs of the LCP models that shows the magnified region between two population's core areas is presented in Fig. 2.

A total of 128 transects were surveyed from November 2010 through January 2011. All in all, in the entire landscape, 3,811 faeces mounds were counted, with an average of 29.77 ± 4.08 (mean and SE) mounds per transect. In 23 transects (17.9 %), there were no faeces mounds at all. In the open landscape, 2,580 faeces mounds were counted, with an average of 34.86 mounds per transect, and in the landscape barriers, 1,231 mounds were counted, with an average of 22.79 mounds per transect.

There were clear differences in the mean number of faeces counts between the LCP types in the entire landscape [Kruskal–Wallis test, H $(5) = 13.29$, $P = 0.02$], indicating that the distribution of faeces was not random, and that differences in wild ass pathway use were a function of the terrain (Fig. 3a). The vegetation LCP was, by far, the most frequently used in the entire landscape, with an average of 49.52 mounds per transect (Fig. 3a). All landscape-related LCPs, except water, were used more frequently than the shortest distance routes (Fig. 3a), supporting the assumption regarding the effect these landscape factors have on wild ass pathway use. Within the landscape barriers, the slopes LCP was the most frequently used, with an average of 48.54 mounds per transect, followed by the LCP which considered the combined cost of narrow canyons and slope; by contrast, the vegetation pathway was rarely used within the landscape barriers (Fig. 3b). All LCPs were used more frequently than the shortest distance route. Within the open landscape subset, the vegetation LCP was the most frequently used pathway (with a mean number of 58.72 faeces mounds per transect), a outcome similar to that found in the entire landscape subset, whereas the use of slope pathways in the open landscape was lower than in the entire dataset (30.0 and 35.9 mounds per transect, respectively).

The GLMs and their evaluation against empirical data

The best GLM for the effect of landscape factors on wild ass pathway use for the entire landscape dataset, with an Akaike weight of 0.33, consisted of the following main landscape factors: vegetation, water and slope, and an interaction between water and slope (Table 1). The model ranked second consisted of vegetation and water, and had an Akaike weight of 0.20; together, these two models accounted for 0.54 of the Akaike weight. The four top-ranked models accounted for 0.7 of the Akaike weight (Table 1).

The vegetation was found to be the most important predictor affecting pathway use in the entire landscape, with a total Akaike weight of 1. The second most important variable was water (0.86), followed by slope (0.59), canyons (0.18), and 4WD routes (0.05). An evidence ratio of 6,002 between the best model, which included vegetation (rank 1, Table 1), and the same model without vegetation (rank 12, Appendix 5.1 in Supplementary material) indicates the importance of the vegetation variable. Similarly, an evidence ratio of 4,447 between the best model, which included water (rank 2, Table 1), and the model without it (rank 13, Appendix 5.1 in Supplementary material) indicates the importance of water for wild ass movements. In contrast, an evidence ratio of 1.5 between the best model with slope (rank 4, Table 1) and without slope

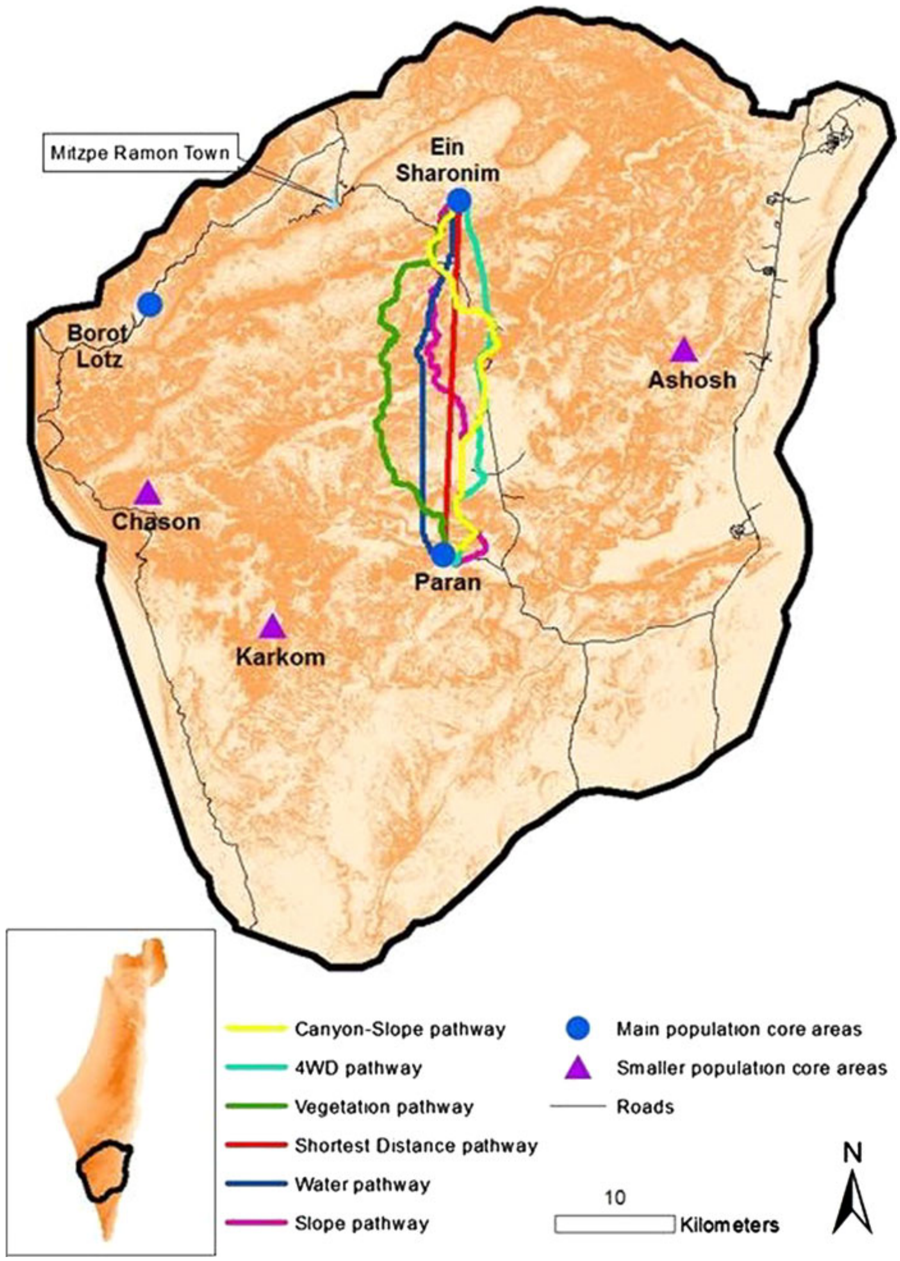

Fig. 2 An example of the outputs of the least-cost pathways that connect the Ein Sharonim with the Paran population's core area

(rank 6, Appendix 5.1 in Supplementary material) suggests that slope is of low importance in the entire landscape dataset.

The top-ranked model had the highest R^2 (0.3), revealing a relatively good fit to the empirical data (Table 1), while the 'null' model (i.e. a model with no landscape factors—only an intercept) had the lowest R^2 (2.2×10^{-15}). The null model was ranked 30th and had a negligible Akaike weight of 10^{-15} (Table 1).

The best model for the landscape barriers subset included the main landscape factors of water, canyons and 4WD, and interactions between 4WD × water and 4WD × canyons. It received the highest support, with an Akaike weight of 0.41. The two top-ranked models accounted together for 0.62 of the Akaike weight (Table 2).

The canyons and the 4WD routes were the two most important predictors of wild ass faeces in

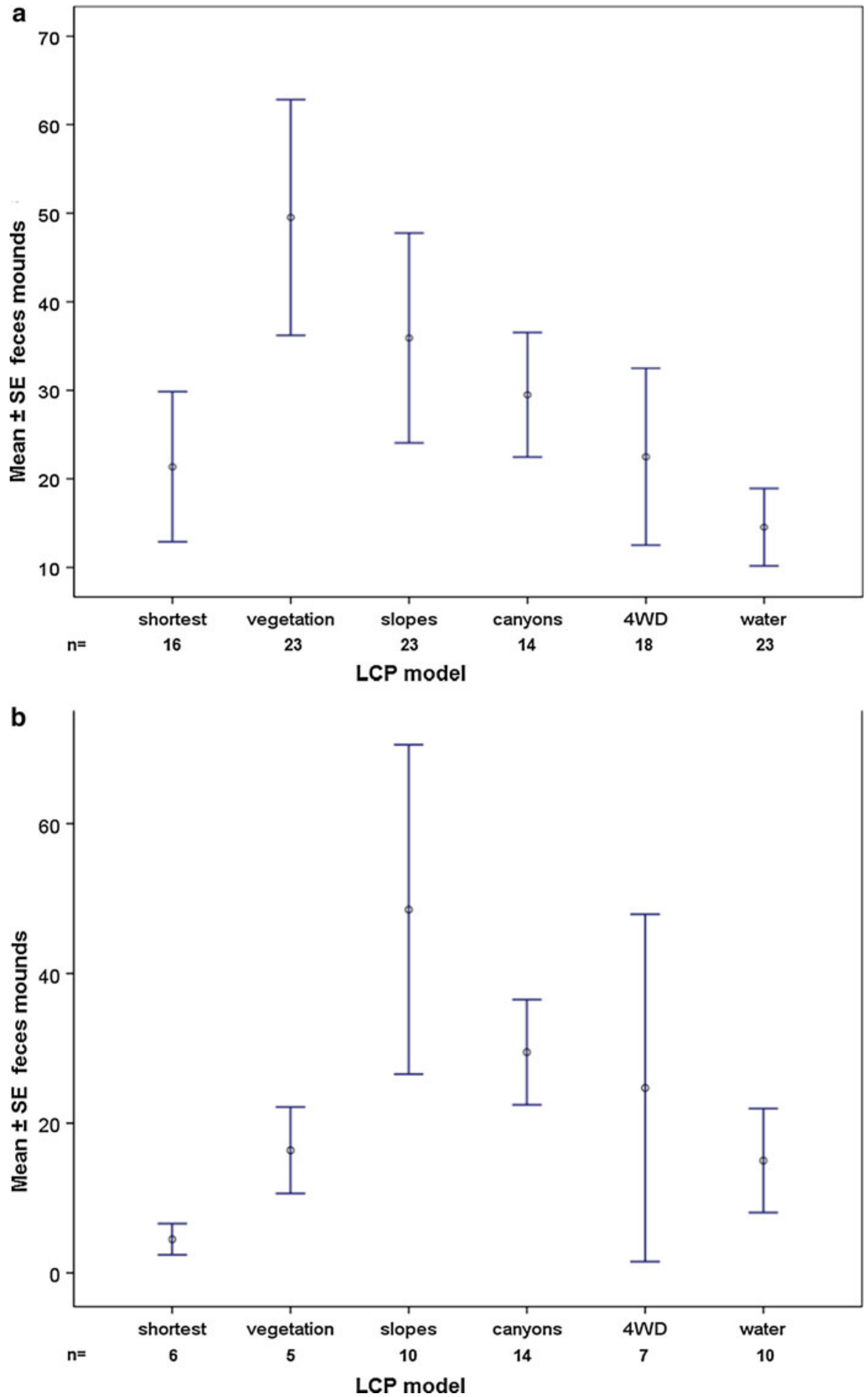

Fig. 3 Faeces mounds along the predicted least-cost pathways, using **a** the entire landscape, and **b** the landscape barriers transects only. 'Shortest' is the straight line connecting two population's core areas

pathways within the landscape barriers subset, with a sum of Akaike weights of 0.84, and 0.82, respectively, followed by water (0.6), vegetation (0.27), and slope (0.11). The canyon and 4WD route variables and the interaction between them appeared in the top ranking models, supporting their influential roles in

Table 1 Model selection statistics for models of the effect of landscape factors on wild ass pathways: the entire landscape dataset

Rank	Model structure	K	AICc	ΔAICc	Weight	R^2
1	Vegetation + water+slope+water:slope	6	1035.2	0	0.338	0.3
2	Vegetation + water	4	1036.2	1	0.205	0.24
3	Canyon + vegetation + water	5	1037.1	1.9	0.131	0.26
4	Slope + vegetation + water + water:vegetation	6	1037.6	2.4	0.102	0.25
30	Intercept only	1	1071.4	36.2	4.6×10^{-9}	2.2×10^{-15}

Alternative models were sorted by AICc and model weight. Interactions are indicated with a colon (:). K is the number of model parameters. The complete table is presented in Appendix 5.1 Supplementary material

Table 2 Model selection statistics for models of the effect of landscape factors on wild ass pathways: the landscape barriers subset

Rank	Model structure	K	AICc	ΔAICc	Weight	R^2
1	Water + canyon + 4WD + water:4WD + 4WD:canyon	7	410.1	0	0.418	0.43
2	Vegetation + canyon + 4WD + 4WD:canyon + vegetation:4WD	7	411.6	1.5	0.197	0.39
3	Slope + 4WD + canyon + slope:4WD	6	414.8	4.7	0.040	0.28
4	Water	3	414.9	414.5	0.038	0.11
14	Intercept only	1	417.2	7.1	0.012	0.00

Alternative models sorted by AICc and model weight. Interactions are indicated with a colon (:). K is the number of model parameters. The complete table is presented in Appendix 5.2 Supplementary material

determining pathway use in landscape barriers (Table 2).

The average number of faeces mounds for transects located in canyons with 4WD routes was significantly smaller than the average number in canyons with no 4WD routes (3.2 vs. 65, respectively, Mann–Whitney *U* test, $U_{5,6} = 2, P = 0.015$). The best model had the highest R^2 value (0.43), which implies a good fit to the empirical data (Table 2), while the null model was ranked 14th and had a low Akaike weight of 0.01 (Table 2).

The top-ranked models for the open landscape dataset were similar to those of the entire landscape data set (Table 3). The best model included the following landscape factors: vegetation, water, and slope, with an Akaike weight of 0.36 (Table 3).

Discussion

Our non-invasive approach for predicting pathways yielded insights into landscape factors affecting the pathway use by *E. hemionus* throughout the Negev. Movement among sites is not random, and the wild ass prefers certain path types over others, as a function of landscape features. The main landscape factors which we hypothesized would demonstrate considerable effects on wild ass pathway use—steep slopes; narrow canyons; vegetation cover; water sources, and 4WD routes, and their interactions—were found indeed to affect pathway routes. These landscape factors have been previously shown to affect the space use patterns of mammals (e.g. Johnson et al. 2008). Thus, they

Table 3 Model selection statistics for models of the effect of landscape factors on wild ass pathways: the open landscape subset

Rank	Model structure	K	AICc	ΔAICc	Weight	R^2
1	Vegetation + slope + water	5	631.2	1	0.360	0.46
2	Vegetation + water	4	632.4	1.2	0.198	0.41
3	Vegetation + water + slope + water:vegetation	6	633.2	2	0.133	0.46
4	Water + vegetation + slope + vegetation:slope	6	633.3	2.1	0.126	0.46
16	Intercept only	1	665.3	34.1	1.4×10^{-8}	5.8×10^{-12}

Alternative models sorted by AICc and model weight. Interactions are indicated with a colon (:). K is the number of model parameters. The complete table is presented in Appendix 5.3 Supplementary material should be considered in future studies which aim to characterize landscape factors that determine pathway use by other species, in particular large herbivores. Addressing these factors is especially pertinent when using an a priori approach, as in this study.

We further found that the factors affecting *E. hemionus* pathway use varied largely between two major terrain types: open landscape vs. landscape barriers. Vegetation was the most important factor affecting pathway use in open landscapes, suggesting that the travel patterns of the wild ass in its range are largely defined by the presence of vegetation. Similarly, Nezer (2011) found that vegetation was the most significant predictor explaining the spatial distribution of *E. hemionus* in the Negev Desert, and Kaczensky et al. (2008) found that the movement of Mongolian wild asses (*E. h. hemionus*) was affected primarily by the availability of vegetation in open landscapes. Also patterns of pathway use of other large herbivores were found to be considerably affected by vegetation: for example, the forest dwelling woodland caribou (*Rangifer tarandus caribou* Gmelin) used conifer forests in their migration corridors (Ferguson and Elkie 2004).

Topography played a critical role in determining wild ass pathway use in the landscape barriers terrain. Wild asses tended to cross the mountain ridges through pathways with the lowest slope, preferably through canyons (unless there were 4WD routes in them). In agreement with our results, Sharma et al. (2004) found that the Tibetan wild ass (*E. kiang*) avoided traveling on steep slopes; Nezer (2011) found that steep slopes had a negative effect on the spatial distribution of *E. hemionus* in the Negev Desert; and Henley et al. (2007) suggested that *E. hemionus* in the Negev tends to avoid areas of steep slopes and prefers to move on flatter terrains. Slope has a negative effect on the movement of other herbivores, such as the American bison (*Bison bison*) (Bruggeman et al. 2007) and Elk (*Cervus elaphus*) (Fortin et al. 2005). Our results further suggest that wild ass movement through landscape barriers is often directed to canyons, which offer the most direct routes when crossing mountain ridges (Sharma et al. 2004; Bruggeman et al. 2007; Kaczensky et al. 2008). Thus, canyons in mountain ridges may serve as corridors, facilitating the long distance movements of the wild ass, as in the case of other mammals (Dickson and Beier 2007; Bruggeman et al. 2007; Long et al. 2010).

Distance from temporary water sources was found to be the second most important factor affecting wild ass pathway use in the open landscape and the third most important factor in the landscape barriers. It is the only landscape factor that was relatively important in both types of terrain, emphasizing the key role of water sources in the wild ass's space-use patterns. These results are consistent with the findings of Saltz and Rubenstein (1995), Saltz et al. (2000), and Kaczensky et al. (2008), which demonstrated that the availability of water is important in determining the movement of the Asiatic wild ass, as well as with those of Nezer (2011), who found that permanent water sources in the Negev affect their spatial distribution of the Asiatic wild ass. Water availability drives space use patterns of other large herbivores, such as the African savannah elephant (*Loxodonta africana*) (Loarie et al. 2009) and African buffalo (*Syncerus caffer*) (Redfern et al. 2003). In contrast, pathways in LCPs that minimized the distance to water sources revealed little wild ass activity. The LCP method clearly detected the two prominent factors affecting wild ass pathways use, namely, vegetation and topography, but it did not detect the less pronounced effects of the other landscape factors, which were revealed using the alternative GLMs. Apparently, the LCP models, which were developed based on a single landscape factor have some value for predicting specific pathways, but are likely to be crude, since there are multiple factors that contribute to path selection. Hence, use of LCPs in this approach should be restricted either to direct sampling efforts, or to the identification of major factors which affect space use patterns.

The presence of 4WD routes was also found to be an important factor in landscape barriers, but their effect was a function of the topography: 4WD routes had a positive effect on pathways use when they followed a mountain ridge along relatively steep slopes, and a pronounced negative effect when these routes extended along narrow canyons. 4WD routes in the Negev usually follow ancient pathways which, when crossing mountain ridges, may facilitate the spatial movement of animals (Bruggeman et al. 2007). In contrast, in areas where 4WD routes go through narrow canyons, the probability of encountering vehicles may pose a high risk. This may explain the wild ass's avoidance of 4WD routes in narrow canyons. Kaczensky et al. (2008) found that

Mongolian wild asses fleeing from an encounter with 4WD vehicles traversed a distance ranging between 0.5 and 2 km. Thus, we concluded that canyons with 4WD routes may be eliminated as corridors for wild ass movement.

This important finding would have been overlooked had we conducted solely the analysis pertaining to the entire landscape data. However, drawing a distinction between the landscape types—barriers and open landscape terrains—in the analysis of the subsets of the entire landscape enabled us to identify this phenomenon that was restricted to landscape barriers and was masked when analysing the entire dataset. These results also indicate that wild asses view treat landscape barriers and open landscapes as different elements within the landscape. This demonstrates the importance of studying space use patterns by analysing subsets of the entire landscape. Hence, it may be assumed that research that examines different landscape types is likely to provide additional insights into the movement dynamics of species in heterogeneous landscapes.

Research implications

The insights gained from this research can be used to predict wild ass pathway use as a basis for landscape planning and management approaches intended for the protection of this species. Wild ass may use pathways when moving relatively short distances between foraging/resting sites, and they may also move relatively long distances (20 km) for the purpose of drinking (Saltz et al. 2000) and mating. Long distance movement between the population's core areas, where water and mating are available, is important for maintaining landscape connectivity and 'gene flow' within the population. Long distance movements may lead to the occupancy of new sites, thus expanding the wild ass's range of distribution, which is an important component in the establishment process of reintroduced species (Dunham 1998; Dolev et al. 2002; Bar-David et al. 2005). Furthermore, given that wild asses serve as an important vector for the seed dispersal of a great variety of plant species in the Negev Desert (Peled 2010), long distance movement may facilitate seed dispersal. Therefore, identifying and protecting long-distance pathways of the wild ass is important for the species' persistence, as well as for the continuous functioning of the ecosystem.

Our results suggest that the mountain ridges have a considerable effect on the location of pathways. The ridges act as topographical bottlenecks, which direct the pathways into a few narrow canyons. A main finding of this study was the negative effect that 4WD routes in canyons have on wild ass's patterns of movements when crossing mountain ridges. Therefore, creating new 4WD routes in major passages within canyons might have a detrimental effect on the wild ass's long distance movements and should not be permitted. Similarly, preventing 4WD traffic routes from entering or crossing canyons which may serve as critical routes for wild ass should be part of a management regime for maintaining the species' free movement along its major pathways.

Our innovative non-invasive research approach is based on constructing least-cost pathway models, mapping the predicted pathways to efficiently direct a faeces survey, which in turn provides an empirical basis for the evaluation of the predicted pathways and a set of alternative GLMs, using model-selection strategies. This approach, conducted at two landscape types, enabled the identification and assessment of landscape factors that affect the movement of wild ass along pathways. This approach may serve as a non-invasive framework for studying the movement dynamics of various animal species in heterogeneous landscapes. The principal limitation in the use of faeces surveys for studying movement dynamics is probably the fact that the method provides only a general outline of the movement patterns of the population, and cannot identify temporal, individual, or behavioural attributes. Nevertheless, it is a cheap and non-invasive method that provides direct insights, at a population level, and is particularly suited for tracking the movement of elusive animals. The information gathered in these studies could be implemented in landscape planning approaches which consider the protection of the species and their habitat.

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References

Anderson D (2008) Model based inference in the life sciences: a primer on evidence. Springer, New York

Bar-David S, Saltz D, Dayan T, Perelberg A, Dolev A (2005) Demographic models and reality in reintroductions: Persian fallow deer in Israel. Conserv Biol 19:131–138

Beier P, Penrod KL, Luke C, Spencer W, Cabañero C (2005) South Coast Missing Linkages: restoring connectivity to wild lands in the largest metropolitan area in the United States. In: Crooks KR, Sanjayan MA (eds) Connectivity and conservation. Cambridge University Press, London, pp 555–586

Breslow N (1970) A generalized Kruskal–Wallis test for comparing K samples subject to unequal patterns of censorship. Biometrika 57:579

Brown JH, Kodric-Brown A (1977) Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58:445–449

Bruggeman JE, Garrott RA, White PJ, Watson FG, Wallen R (2007) Covariates affecting spatial variability in bison travel behavior in Yellowstone National Park. Ecol Appl 17:1411–1423

Buchmann CM, Schurr FM, Nathan R, Jeltsch F (2012) Movement upscaled—the importance of individual foraging movement for community response to habitat loss. Ecography 35:436–445

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York

Chetkiewicz C-LB, Boyce MS (2009) Use of resource selection functions to identify conservation corridors. J Appl Ecol 46:1036–1047

Clobert J, Danchin E, Dhondt AA, Nichols JD (2001) Dispersal. Oxford University Press, New York

Crawley MJ (2007) The R book. Wiley, London

Dickson BG, Beier P (2007) Quantifying the influence of topographic position on cougar (*Puma concolor*) movement in southern California, USA. J Zool 271:270–277

Dobson FS, Jones WT (1985) Multiple causes of dispersal. Am Nat 126:855–858

Dolev A, Saltz D, Bar-David S, Yom-Tov Y (2002) Impact of repeated releases on space-use patterns of Persian fallow deer. J Wildl Manag 66:737–746

Dunham KM (1998) Spatial organization of mountain gazelles *Gazella gazella* reintroduced to central Arabia. J Zool 245:371–384

Faraway JJ (2006) Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models. CRC Press, Boca Raton

Ferguson SH, Elkie PC (2004) Habitat requirements of boreal forest caribou during the travel seasons. Basic Appl Ecol 5:465–474

Fortin D, Beyer HL, Boyce MS, Smith DW, Duchesne T, Mao JS (2005) Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320–1330

Ganskopp D, Cruz R, Johnson DE (2000) Least-effort pathways?: a GIS analysis of livestock trails in rugged terrain. Appl Anim Behav Sci 68:179–190

Groves CP (1986) The taxonomy, distribution and adaptations of recent equids. In: Meadows RH, Uerpmann HP (eds) Equids in the ancient world. Dr Ludwig Reichert Verlag, Wiesbaden, pp 11–65

Henley SR, Ward D, Schmidt I (2007) Habitat selection by two desert-adapted ungulates. J Arid Environ 70:39–48

Holyoak M, Casagrandi R, Nathan R, Revilla E, Spiegel O (2008) Trends and missing parts in the study of movement ecology. PNAS 105:19060–19065

IUCN (2001) IUCN Red List Categories and Criteria, Version 3.1. http://www.iucnredlist.org/technical-documents/categories-and-criteria/2001-categories-criteria. Accessed June 2013

Johnson CJ, Parker KL, Heard DC, Gillingham MP (2008) A multiscale behavioral approach to understanding the movements of woodland caribou. Ecol Appl 12:1840–1860

Kaczensky P, Ganbaatar O, von Wehrden H, Walzer C (2008) Resource selection by sympatric wild equids in the Mongolian Gobi. J Appl Ecol 45:1762–1769

Koenig WD, Van Vuren D, Hooge PN (1996) Detectability, philopatry, and the distribution of dispersal distances in vertebrates. Trends Ecol Evol 11:514–517

Laing SE, Buckland ST, Burn RW, Lambie D, Amphlett A (2003) Dung and nest surveys: estimating decay rates. J Appl Ecol 40:1102–1111

Loarie SR, Van Aarde RJ, Pimm SL (2009) Fences and artificial water affect African savannah elephant movement patterns. Biol Conserv 142:3086–3098

Long ES, Diefenbach DR, Wallingford BD, Rosenberry CS (2010) Influence of roads, rivers, and mountains on natal dispersal of white-tailed deer. J Wildl Manag 74:1242–1249

Lozano J, Virgós E, Malo AF, Huertas DL, Casanovas JG (2003) Importance of scrub–pastureland mosaics for wild-living cats occurrence in a Mediterranean area: implications for the conservation of the wildcat (*Felis silvestris*). Biodivers Conserv 12:921–935

Lunney D, Phillips S, Callaghan J (1998) Determining the distribution of koala habitat across a shire as a basis for conservation: a case study from Port Stephens, New South Wales. Pac Conserv Biol 4:186–196

McCoy J, Johnston K (2001) Using ArcGIS spatial analyst. ESRI Press, New York

Murtskhvaladze M, Gavashelishvili A, Tarkhnishvili D (2010) Geographic and genetic boundaries of brown bear (*Ursus arctos*) population in the Caucasus. Mol Ecol 19:1829–1841

Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE (2008) A movement ecology paradigm for unifying organismal movement research. Proc Natl Acad Sci USA 105:19052–19059

Nezer O (2011) The use of predicted distribution model of the Asiatic wild ass (*Equus hemionus*) for sustainable management of the Negev and the Arava. Thesis, Technion, Institute of Technology

Peled T (2010) Reintroductions as an ecosystem restoration tool: a case study of reintroduced ungulates as vectors for seed-dispersal. Thesis, Ben-Gurion University of the Negev

Perelberg A, Saltz D, Bar-David S, Dolev A, Yom-Tov Y (2003) Seasonal and circadian changes in the home ranges of reintroduced Persian fallow deer. J Wildl Manag 67:485–492

R Development Core Team (2005) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org. Accessed June 2013

Redfern JV, Grant R, Biggs H, Getz WM (2003) Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. Ecology 84:2092–2107

Riley SPD, Pollinger JP, Sauvajot RM, York EC, Bromley C, Fuller TK, Wayne RK (2006) A southern California freeway is a physical and social barrier to gene flow in carnivores. Mol Ecol 15:1733–1741

Rueness EK, Stenseth NC, O'Donoghue M, Boutin S, Ellegren H, Jakobsen KS (2003) Ecological and genetic spatial structuring in the Canadian lynx. Nature 425:69–72

Saccheri I, Kuussaari M, Kankare M, Vikman P, Fortelius W, Hanski I (1998) Inbreeding and extinction in a butterfly metapopulation. Nature 392:491–494

Saltz D, Rubenstein DI (1995) Population dynamics of a reintroduced Asiatic wild ass (*Equus hemionus*) herd. Ecol Appl 5:327–335

Saltz D, Rowen M, Rubenstein DI (2000) The effect of space-use patterns of reintroduced Asiatic wild ass on effective population size. Conserv Biol 14:1852–1861

Sarrazin F, Barbault R (1996) Reintroduction: challenges and lessons for basic ecology. Trends Ecol Evol 11:474–478

Sharma BD, Clevers J, De Graaf R, Chapagain NR (2004) Mapping *Equus kiang* (Tibetan Wild Ass) Habitat in Surkhang, Upper Mustang, Nepal. Mt Res Dev 24:149–156

Sharp A, Norton M, Marks Holmes K A, Holmes K (2001) An evaluation of two indices of red fox (*Vulpes vulpes*) abundance in an arid environment. Wildl Res 28:419–424

Stern E, Gradus Y, Meir A, Krakover S, Tsoar H (1986) Atlas of the Negev. Keter Publishing House, Jerusalem

Tallmon DA, Luikart G, Waples RS (2004) The alluring simplicity and complex reality of genetic rescue. Trends Ecol Evol 19:489–496

Taylor LR, Taylor RA (1977) Aggregation, migration and population mechanics. Nature 265:415–421

Trakhtenbrot A, Nathan R, Perry G, Richardson DM (2005) The importance of long-distance dispersal in biodiversity conservation. Divers Distrib 11:173–181

Trombulak SC, Frissell CA (2000) Review of ecological effects of roads on terrestrial and aquatic communities. Conserv Biol 14:18–30

Turchin P (1996) Fractal analyses of animal movement: a critique. Ecology 77:2086–2090

Wennergren U, Ruckelshaus M, Kareiva P (1995) The promise and limitations of spatial models in conservation biology. Oikos 74:349–356

Wiens JA, Chr N, Van Horne B, Ims RA (1993) Ecological mechanisms and landscape ecology. Oikos 66:369–380

Yott A, Rosatte R, Schaefer JA, Hamr J, Fryxell J (2011) Movement and spread of a founding population of reintroduced elk (*Cervus elaphus*) in Ontario, Canada. Restor Ecol 19:70–77

Yousef MK, Dill DB, Freeland DV (1972) Energetic cost of grade walking in man and burro, *Equus asinus*: desert and mountain. J Appl Physiol 33:337–340