

On the move: spatial ecology and habitat-use of red fox in the trans-Himalayan cold desert

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An animal may move because of various reasons and the space-use depends upon its behaviour and responses to the environment. The causes of these movements, directionality and their consequences are of great significance to understand several aspects of an animal's ecology. A mosaic of different habitat types are required to fulfill different life stages of an individual. Red fox is the most widespread wild carnivore in the world occupying myriad habitats. They are also known for their adaptability to survive in the dynamic anthropogenic landscapes. Despite being one of the most extensively studied carnivore, there is a dearth of information on the red fox from the Trans-Himalayan region. In this study we explore the home ranges, daily movements, habitat-use and directionality of red fox in the arid Trans-Himalayan cold desert. We radio-collared seven red fox

individuals in Ladakh, India. The home range of red fox ranged from 3.81 to $49.22~\rm km^2$. Red fox significantly preferred lower elevations and lesser rugged terrains (P < 0.01). They were also positively associated with water. The daily average movement of red fox was $13.28 \pm 1.38~\rm km/day$. Downscaling of GPS fixes from 15 minutes to 2 hour interval fixes significantly reduced the daily average movement of red fox (P < 0.05). Red fox did not show any significant directional preference (P>0.01). The daily movements are crucial not only for understanding the individuals, but also for understanding species requirements at the population level. The daily movements further aids to comprehend the daily energetics and nutritional requirements of species. The daily movements of red fox have been examined for the first time across its global distribution. The study holds great significance as it helps in understanding the spatial ecology of an abundant and highly adaptable meso-carnivore which is important for managers to develop conservation strategies for red fox and its associated species.

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Abstract

An animal may move because of various reasons and the space-use depends upon its behaviour 23 24 and responses to the environment. The causes of these movements, directionality and their 25 consequences are of great significance to understand several aspects of an animal's ecology. A mosaic of different habitat types are required to fulfill different life stages of an individual. Red 26 fox is the most widespread wild carnivore in the world scupying myriad habitats. They are also 27 known for their adaptability to survive in the dynamic anthropogenic landscapes. Despite being 28 one of the most extensively studied carrivore, there is a dearth of information on the ed fox 29 from the Trans-Himalayan region. In this study we explore the home ranges, daily movements, 30 habitat — and directionality of red fox in the arid Trans-Himalayan cold desert. We radio-31 collared seven red fox individuals in Ladakh, India. The home range of red fox ranged from 5.01 32 to 49.22 km². Red fox significantly preferred lower elevations and lesser rugged terrains (33 0.01). They were also positively associated with water. The daily average movement of red fox 34 was 13.28 ± 1.38 km/day. Downscaling of GPS fixes from 15 minutes to 2 hour interval fixes 35 significantly reduced the daily average movement of red fox (P < 0.05). Red fox did not show 36 any significant directional preference (P>0.01). The dally movements are crucial not only for 37 38 understanding the individuals, but also for understanding species requirements at the population level. The daily movements further aids to comprehend the daily energetics and nutritional 39 requirements of species. The daily movements of red fox have been examined for the first time 40 across its global distribution. The study holds great significance as it helps in understanding the 41 spatial ecology of an abundant and highly adaptable meso-carnivore which is important for 42 managers to develop conservation strategies for red fox and its associated species. 43

Keywords

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Home range, Daily-movement, Directionality, Ladakh, space-use, step-selection function.

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Introduction

The space use of an animal depends upon its behavioural and physiological responses to the 48 environment (Horne et al., 2007; Vanak & Gompper, 2010). It is also influenced by ecological 49 50 and evolutionary factors (Cody, 1985). One of the most basic fundamental for understanding the 51 ecology of an animal is the study of home range size. Home range is generally defined as an area 52 that an individual utilizes for its normal activities like gathering food, mating and raising the young (Burt, 1943). An animal may move for several other reasons. The causes of these 53 movements and their consequences are of great significance to understand several aspects of an 54 animal's ecology like their dispersal (Small & Rusch, 1989), social interactions (Minta, 1993), 55 56 space-use (Kenward et al., 2001) and population distributions (Turchin, 1991). The continuous movements when directly monitored is the most powerful tool to quantify an animal's daily 57 movement and home-range size (Turchin, 1998). However, in nature it is impossible to monitor 58 animals continuously, especially in the rugged terrains with adverse climatic conditions such as 59 that prevailing in the Trans-Himalayan cold desert (Mishra & Humbert-Droz, 1998). GPS 60 telemetry is now commonly used for this purpose, as it aids in continuous monitoring of animals 61 spread over large distances and is particularly helpful for animals which are elusive, nocturnal 62 63 and present in areas that are otherwise not accessible by researchers. Red fox is the most widespread wild carnivore in the world (Hoffmann & Sillero-Zubiri, 2016) 64 and is known for its adaptability to survive in all sorts of environments (Geffen et al., 1996). The 65 generalist and opportunistic nature of red fox in terms of its diet, habitat and movement patterns 66



But on the other hand, mid-sized carnivores also face competition because of its wide spectrum 68 of diet which overlaps with the energetic needs of myriad other sympatric competitors (Caro & 69 Stoner, 2003). Small carnivores may often face the highest competitive pressure (Hunter & Caro, 70 2008) as they constantly survive in a landscape of fear (Laundre, Hernandez & Ripple, 2010). As 71 72 a result they may have to make tradeoffs either temporally or spatially (Schuette et al., 2013). In comparison to the large carnivores, there have been fewer studies pertaining to the meso-73 carnivores and there are knowledge gaps even in understanding their basic life-history traits like 74 75 home range size (de Satgé, Teichman & Cristescu, 2017). Although red fox is one of the most extensively studied carnivore in the world, there is a dearth 76 of information on the mountain red fox (Vulpes vulpes montana) found in the Trans-Himalayan 77 cold desert. Mountain red fox are unique and may be threatened like the Sierra Nevada red fox 78 (Aubry et al., 2009; Sacks et al., 2010). There have been only a handful of studies from India on 79 the mountain red fox, which are confined to the dietary habits (Ghoshal et al., 2016; 80 Maheshwari, 2018; Reshamwala et al., 2018). Despite having GPS telemetry technology, most 81 studies aim at obtaining home ranges where the GPS fixes are taken at large time intervals, 82 which are unsuitable for studying daily movements. The daily movement data is expensive at the 83 cost of battery life. However, it can provide important information such as the breeding and non-84 breeding individuals in a population (Jedrzejewski et al., 2001; Alfredéen, 2006), human activity 85 86 and disturbances (Theuerkauf et al., 2007) and can also act as an indicator for the health of an ecosystem by identifying food deticient habitats (Owen-smith, 2013). 87 88 A mosaic of different habitat types are required to fulfill different life stages and these are 89 reflected in the animal's movement at larger spatial scales (Ims, 1995; Benson & Chamberlain,

has contributed to its success (Geffen et al., 1996; Walton et al., 2017; Reshamwala et al., 2018).



90	2007). Intra and inter-specific interactions in terms of competition, predation or facilitation also
91	determines animal spatial distributions. In some cases, the directionality of movements may also
92	have a great biological significance (Michael J. Freake, 2019). Ecologists are often interested in
93	understanding these spatial distribution patterns to know about an animal's requirements and
94	how these requirements are fulfilled (Johnson, 1980; Manly, McDonald, Thomas, McDonald, &
95	Erickson, 2007). The resource selection function and resource selection probability functions
96	have been widely used to identify the habitats used by radio-collared individuals (Manly et al.,
97	2007; Lele, 2009). A more advanced and robust method that is now adopted is the use of step
98	selection function (Thurfjell, Ciuti & Boyce, 2014). In step selection function, the consecutive
99	time locations taken at regular intervals are defined as steps and compared with the random steps
100	that are available for an animal to choose (Thurfjell, Ciuti & Boyce, 2014). Step selection
101	function provides the advantage of incorporating the actual movement data of an animal as
102	opposed to comparing with just random points used in resource selection function (Johnson et
103	al., 2008).
104	The movement of an individual gives an insight on the population distribution of a species and
105	thereby, aids in understanding population level processes (John A. Wiens, Nils Chr. Stenseth,
106	1993; Ims, 1995). To the best of our knowledge, this is the first study that aims at understanding
107	the daily movements of the red-fox. Besides this, our study also holds great significance as it
108	helps in understanding the spatial ecology of an abundant and highly adaptable meso-carnivore
109	which is often important for managers to develop conservation strategies not only for this species
110	but also other associated species.

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Materials and methods



Study area

The study was conducted in Ladakh which belongs to the North-western Trans-Himalayan 114 115 region of India (Fig. 1). The area is characterized by dry rugged terrain with very little precipitation of about 100 mm (Bharti et al., 2016). The cold desert has an elevation of 3000 to 116 7000 m above sea level and harsh winter temperatures which go up to - 30 °C in winters. The 117 118 vegetation is very sparse and patchy with alpine meadows in certain areas (Kachroo P, Dhar U, 1977). The area is also very scarcely populated in terms of human density i.e. 4.9 119 individuals/km² (Chandramouli, 2013). Six foxes were radio-collared in the village of Chiktan, 120 which is a small hamlet 80 km from the city of Kargil. The people comprise of the Muslim 121 community and there is high amount of anthropogenic food subsidy and fox abundance in this 122 area (Reshamwala et al., 2018). One vixen (F3) was collared in Hemis National Park at 123 Rumbuck. People are majorly associated with agriculture or agro-pastoralism and sometimes 124 involved with tourism, especially in Hemis National Park (Reshamwala et al., 2021). Besides red 125 126 fox; snow leopard, wolves, Ladakh urial, bluesheep, ibex, weasel and stone marten are other animals found in this landscape. 127 128 Fox capture

We captured seven red fox from November 2018 to January 2019 using five Victor soft catch #3
leg hold traps. The animals were immediately collared with Sirtrack (Litetrack 150 iridium,
weighing ~ 200 grams) collars and released within 20 - 30 minutes at the place of capture.
Animal handling, capture and release were approved by the Department of Wildlife Protection
Department Jammu and Kashmir (CCFWL\Permission\2016\575-76). No drugs were
administered to the animals and the methodology was refined to ensure minimum stress,
handling time, and injury to the captured individual, approved by Wildlife Institute of India,



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Animal Ethics Committee. The foxes were measured, weighed and sexed before release. The collars were programmed to record GPS fixes for every 15 minutes intervals and transmit the same at every 3 hours. We chose 15 minutes time interval as it gives robust results for the actual daily distance travelled by animals (Musiani, Okarma & Jędrzejewski, 1998). The collars also had an auto drop-off scheduled for 364 days. For individuals M3 and M4 the collars were reprogrammed to take GPS fixes every 2 hours and 10 minutes after one month to increase the battery life.

Data analysis

The data constituted from seven red foxes of 32,711 GPS fixes was filtered in ArcGis 9.2.1 with 144 the ArcMet tool (Wall, 2014). The filtered data excluded fox locations that exceeded > 48 km/hr 145 as this is the highest speed of the fox (Haltenorth, T., & Roth, 1968). Home-ranges were 146 estimated using minimum convex polygon (MCP), Kernels, localized convex hull (LoCoH) and 147 Brownian-bridge movement model (BBMM). Displacement was calculated with the help of the 148 net square displacement obtained from the trajectory details from the ArcMet tool in ArcGIS. 149 Angular data was analyzed in the R package circstat, spatstat and circular (Agostinelli & Lund, 150 2011). 151 To calculate the daily movements of the red fox we encountered two false positive errors. Type 1 152 error - when the foxes were in the den and the GPS fix was at a place well within the home range 153 154 with speeds less than 48km/hr. Type 2 error - when the fox was travelling far at the boundary of its home range but the GPS fix was near its den or at the other end of its territory. To eliminate 155 these errors we utilized the speed data to identify erroneous spikes and restricted the data 156 containing speeds to \leq 9.35 km/hr (Fig. S.1). The daily movements of the red fox were then 157 plotted using the violin plots in R. 158



Habitat-selection analysis for red fox was done using step selection function in the animal movement tool package of R (Signer, Fieberg & Avgar, 2019). We used conditional logistic regression with 10 random steps available for each true step of red fox for the variables: - distance to road, distance to water, distance to human settlements, ruggedness, elevation and slope. We used the Biodiversity Information System portal of the Indian Institute of Remote Sensing (http://bis.iirs. gov.in) land-use land-cover map and classified our field area into agriculture, vegetation, barren, snow and others (Roy et al., 2015).

166 Results



Spatial distribution of the red fox

We used different methods to evaluate the home ranges (95% contour) and core areas (50% contour) of each individual of the red fox. The red fox showed high variation in the size of their home ranges and core area utilization (Table 1). We found the highest home range using BBMM of the individual F3 from Hemis National Park (49.23 km²). The smallest home range was for the individual F1 (3.81 km²). The highest core area using BBMM was for M3 (2.69 km²) and the smallest was found for F1 (0.55 km²). The results showed that the M1, M2 and F3 individuals utilise multiple core zones.

Identification of dispersing animal

The individual F3 collared in Hemis National Park was a dispersing individual as it showed displacement from its collared area and shifted from its original place of collaring (trend line of F3, Fig. S.2).

Directionality in red fox





180	The red fox moved in all directions across different areas of its home range with dens at the
181	center. We conducted a Rayleigh test to find out if the red fox prefers to orient themselves in a
182	particular direction. The Rayleigh test results showed no significant directionality for the

movement of red fox (P > 0.01) for all individuals, Table S.1).



184	The daily movement of red fox
185	The individual F2 showed the highest daily average movement of 20.88 km/day and the least
186	movement was shown by M4 of 6.50 km/day (Fig. 2). The daily average movement of red fox
187	was $13.28 \pm 1.38 \text{km/day}$.
188	The downscaling of data from 15 minutes GPS fixes to 2 hour interval fixes significantly (P <
189	0.05 one tail T test) reduced the average distances walked by red fox (S.4). Since for M3 and M4
190	individuals 15 minute GPS locations were obtained for the first 30 days, only these were used to
191	examine the effect of down-sampling.
192	Habitat selection by red fox
193	F1 preferred agricultural land as compared to other land-use categories, while F2 was mainly
194	found in barren land (Fig. 3). F3 vixen in Hemis National Park preferred barren land and alpine
195	vegetation. Both M1 and M2 utilized agriculture and barren land. M3 and M4 were found in
196	barren and agricultural land; but they utilized the snow in higher proportions.
197	The red fox preferred lower elevations and lesser rugged terrains ($P < .001$, Fig. 4). With respect
198	to human settlements only F1 showed significant negative association (P<0.001), while F3, M2,
199	M3 and M4 were positively associated with human settlements (P< 0.01). Individuals F2 and M1
200	did not have any significant association with human settlements (P>0.01). The red fox showed
201	preference for water bodies, however for M3 and M4 individuals it was non-significant (P>0.01)
202	Except for F2 and F1 all individuals had a significant negative association with roads and slope
203	(P < 0.001).
204	Discussion
205	Spatial distribution of red fox



206	Rugged terrains often have cliffs and hard boundaries that force animals to follow a fixed path.
207	In such areas, Localised convex hull (LoCoH) gives a reliable home range of animals as this
208	method can identify hard boundaries such as rivers, lakes and even inhospitable terrain (Getz et
209	al., 2007). Although, most studies pertaining to home ranges refer to the traditional use of
210	minimum convex polygon (MCP) or the Kernels method, in our study we found LoCoH and
211	BBMM were the best suitable methods for estimation of home range (LoCoH 1.17 - 78.43 Km ²)
212	and BBMM 3.81 - 49.23 Km ²). Estimates from MCP and Kernal were large and overestimated
213	the home range utilization distribution (MCP 1.95 - 672.19 Km ² and Kernals 1.62 - 269.15 Km ²)
214	.The BBMM method takes into consideration the time and probability of movements, thereby
215	models the animal movements and helps to determine animal home ranges more robustly (Horne
216	et al., 2007). Studies also caution to consider nomadic foxes while calculating home ranges
217	(Jean-Steve Meia, 1995). Similarly, the vixen F3 collared in Hemis National Park was either
218	nomadic or dispersing vixen as it showed large displacement from its initial place of collaring
219	(Fig. S.2) and hence the large estimate of home range (49.22 km², BBMM). The home range
220	sizes of red fox are known to have great variations ranging from as small as 0.40 km² in urban
221	areas of Oxford to as large as 40 km² in Arctic or even larger and is determined majorly by the
222	type of habitat (Sillero-Zubiri, C., Hoffmann, M., & Macdonald, 2004). At higher latitude and
223	altitude animals tend to have bigger home ranges (Mattisson et al., 2013; Morellet et al., 2013).
224	Foxes living at higher elevations are reported to have four times larger home ranges as compared
225	to lower elevations (Walton et al., 2017). In Australia, larger home ranges of red fox were
226	reported in the arid Simpson Desert (Newsome, Spencer & Dickman, 2017). But on the other
227	hand, the use of smaller home ranges by medium sized canids near human settlements are also
228	reported (Coman, Robinson & Beaumont, 1991; Saeki, Johnson & Macdonald, 2007; Rotem et





al., 2011). In cities where food is available in abundance the home ranges of red fox tend to be smaller (Newdick, 1983). Our study site is a high altitude cold desert with the presence of anthropogenic food subsidies [13] and hence, we speculate a mix effect of both; the high elevation cold desert and the presence of anthropogenic food subsidies. The home ranges of fox were highly variable ranging from 3.81 to 49.22 km² (BBMM). Such results are not uncommon and the home ranges of fox within the same area may often show wide variations; for example, in Illinois it was observed to vary from less than 1 to > 35 km² (Gosselink et al., 2003).

Directionality of red fox

The magnetic alignment of animals may have a significant biological reasoning (Cerveny et al., 2011). Recent studies show that resting cattle and deer have a typical north-south alignment along the geomagnetic field (Begall et al., 2008). To maintain these alignments, animals may often have a directional spatial orientation (Schlegel, 2008). In, fox it has been observed that their directional preference enhances the accuracy of catching prey (Cerveny et al., 2011). Since our data was not confined to just the hunting activity and comprised of the overall movement of red fox, we could not find any significant directional preference (P > 0.01, Table S.2). The higher movements in the north-west and south-east directions were moreover because of the orientation of the valley (Fig. S.3).

Daily movement of red fox

The daily average movement ability of fox could be a key factor to understand their home range and defending territory systems. Foxes with smaller home ranges may not necessarily travel less. It is observed that the daily distance travelled by individuals having a smaller home-range may



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be same as compared to that of an individual having larger home range and the difference may only reflect the different foraging sites used by the individuals (Carter, Luck & McDonald, 2012). Similarly, the individual F1 had a very small home range (3.81 km², BBMM), but its daily average movement was 11.10 km/day. It is also very essential to have the GPS fixes at fine scale time interval for calculating the daily average distance travelled by red fox. Our data suggests that increasing the time interval of GPS fixes decreases the daily movement of red fox significantly (P < 0.01, Fig. S.4). Fixes at a very small time interval on the other hand may overestimate the daily average distance travelled due to location error (Poulin, Clermont & Berteaux, 2021). Although the actual distance travelled by an animal as compared to the straight line distances obtained from the GPS fixes may be an under-estimate, we also assume that additional errors pertaining to the accuracy of GPS fixes in the short 15 minute time interval may nullify this effect. For example, despite being inside the den the GPS fixes may vary and show a continuous movement. We found the daily average movement of red fox was 13.28 ± 1.38 km/day. We found only one study pertaining to the daily average movement of red fox which reported 4.8 to 16 km/day. However, the study used VHF telemetry which has its limitations (Carter, Luck & McDonald, 2012). Long distance dispersal events are reported in red fox where foxes have travelled over a distance of 132-1036 km over a short period of time(Walton et al., 2018). The daily average movement travelled by arctic fox is comparatively well studied and is reported to be 51.9 ± 11.7 km/day (Poulin, Clermont & Berteaux, 2021). Habitat selection by red fox Red fox are known for their highly adaptive behavior and often show large variations in their space-use depending upon various factors (Walton et al., 2017; Walton, 2020). We found that the dominant larger foxes i.e. F1, M1 and M2 preferred agricultural land, while F2, M3 and M4 were



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smaller individuals and found in barren and snow land categories. F3 in Hemis National Park was found in both; barren and alpine vegetation. To understand these variations, analyzing step selection modelling at an individual level proves to be more advantageous over population level (Thurfiell, Ciuti & Boyce, 2014). Further, our sample size of seven individuals also advocates for individual modelling. Red fox in the trans-Himalayan landscape have been reported to be at higher densities and often den near human settlements due to the presence of anthropogenic food subsidies (Reshamwala et al., 2018, 2021). In our study with the exception of F1 and F2 all the other individuals were positively associated with human settlements. The presence of water bodies is also known to have a positive influence because of the presence of rodents and has been reported from previous studies (Szor, Berteaux & Gauthier, 2008; Reshamwala et al., 2021). We found that all individuals were positively associated with water. Animals are known to avoid higher elevations, steep slopes and rugged terrains which are known to be energetically costly (Filla et al., 2017; Fullman, Joly & Ackerman, 2017). Similarly, we found red fox significantly preferred lower elevations and lesser rugged terrains (P < 0.01). Except for F1 and F2, all other individuals significantly avoided slopes. From our field observations we found both F1 and F2 to be breeding vixens and hence presume that they avoided human settlements and preferred slopes in comparison to others. Limitations of study Data on average speeds travelled by red fox is completely lacking, but the average speed with which wolves travel ranges from 0.8 to 1.1 km/hr (Burkholder, 1959; Bibikov, Kudaktin, & Filimonov, 1985; Ciucci et al., 1997; Jedrzejewski et al., 2001). Mech et al. (Mech, 1994) reported that the wolves travelled at speeds of 9.6 to 13 km/hr which had 15 minutes time

interval for location of animals. Hence, our method of restraining the maximum speed limit of



298	9.35 km/hr for red fox may be a fair estimate. The use of speeds to identify GPS errors especially
299	for calculating daily movements has been reported in other studies as well (Bjørneraas et al.,
300	2010; Wysong et al., 2020). However, further studies with greater sample size are warranted to
301	enhance our knowledge on maximum speeds with which red fox can travel.
302	Although we found the daily average movement for F2 to be as high as 20.92 km/day and as low
303	as 7.46 km/day and 6.50 km/day for M3 and M4 individuals respectively, this could be an effect
304	of sampling bias. The radio-collar for F2 individual worked for lower number of days (56 days).
305	In addition, for the individuals M3 and M4, the collars were reprogrammed for a longer battery
306	life from 15 minutes time interval for the first month to 2 hour time interval which further
307	decreased their daily movements (199 and 212 days respectively). However, based on our field
308	observations, we could confirm that F2 showed greater movements in comparison to other
309	individuals and could be an exception. We also presume the movements for F2 to have reduced
310	after the short collaring period, however we lack the GPS data to prove so. Further, when we
311	compare the daily average movement of F2 with 30 days data of M3, M3 showed higher daily
312	average movement (34.22 km/day, Fig. S.4). This is also due to the fact that M3 made many
313	forays outside its normal home range during this period. At four instances the individual M3 has
314	moved about 60 kilometers or more in one single day. Such long distances are not uncommon
315	and in case of arctic fox the maximum distance travelled in a day is reported to be 154 kilometers
316	(Fuglei & Tarroux, 2019).
317	The daily average movement in case of wolves showed a great variation, ranging from 17 to 38
318	km/day (Ciucci et al., 1997). It is reported that the daily average movement travelled during the
319	mating season for wolves may go as high as 34 km/day (Jedrzejewski et al., 2001). During the
320	breeding season, it is observed that males in Lynx frequently move at longer distances and at



greater speeds to increase their chances of mating with females (Schmidt, 1999). Since our collaring sessions coincides with the breeding time of red fox, we suspect M3 and M4 to have made these long forays.

This study explores the spatial ecology of red fox in the Trans-Himalayan cold desert. In addition to home-ranges we provide insights on the daily movements and directionality in red fox. The red fox avoided higher elevations and rugged terrains. Although, we did not find any significant directionality in the movement of red fox this is the first study that explores this possibility. The daily movements are crucial not only for understanding the individuals, but also for understanding species requirements at the population level. The daily movements further aids to comprehend the daily energetics and nutritional requirements of species (Miller et al., 2014).

Despite the red fox being one of the most extensively studied carnivore, there is no literature available for the daily movement of red fox. Further studies regarding movements of the red fox are warranted to understand the impact of dynamic anthropogenic landscapes coupled with climate change and how these animals adapt their behaviour and movement for survival.

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349	The authors declare that they have no competing interests.
350	Author Contributions
351	HSR did the fieldwork, procured data, analyzed, and wrote the first draft. SK, ZH and PR helped
352	in the analysis and writing of the manuscript. BH and PR procured the funding. BH
353	conceptuslised the study. BH and RD supervised the project and discussed the results to
354	improvise and produce the final manuscript.
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356	All red foxes were captured following standard and approved protocols after due permission
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361	References
362	Agostinelli C, Lund U. 2011. Circular: Circular statistics. URL http://cran. r-project.
363	org/src/contrib/Descriptions/CircStats. html.
364	Alfredéen A. 2006. Denning behaviour and movement pattern during summer of wolves Canis
365	lupus on the Scandinavian Peninsula. :35.
366	Aubry KB, Statham MJ, Sacks BN, Perrine JD, Wisely SM. 2009. Phylogeography of the North
367	American red fox: Vicariance in Pleistocene forest refugia. Molecular Ecology 18:2668-
368	2686. DOI: 10.1111/j.1365-294X.2009.04222.x.
369	Begall S, Červený J, Neef J, Vojtěch O, Burda H. 2008. Magnetic alignment in grazing and
370	resting cattle and deer. Proceedings of the National Academy of Sciences of the United
371	States of America 105:13451–13455. DOI: 10.1073/pnas.0803650105.
372	Benson JF, Chamberlain MJ. 2007. Space Use and Habitat Selection by Female Louisiana Black
373	Bears in the Tensas River Basin of Louisiana. <i>Journal of Wildlife Management</i> 71:117–126.
374	DOI: 10.2193/2005-580.
375	Bharti V, Singh C, Ettema J, Turkington TAR. 2016. Spatiotemporal characteristics of extreme
376	rainfall events over the Northwest Himalaya using satellite data. International Journal of
377	Climatology 36:3949–3962. DOI: 10.1002/joc.4605.
378	Bibikov, D. I., Kudaktin, A. N., & Filimonov AN. 1985. The wolf: history, systematics,
379	morphology, ecology. Nauka, Moscow.
380	Bjørneraas K, Van Moorter B, Rolandsen CM, Herfindal I. 2010. Screening Global Positioning
381	System Location Data for Errors Using Animal Movement Characteristics. Journal of
382	Wildlife Management 74:1361–1366. DOI: 10.2193/2009-405.
383	Burkholder. 1959. MOVEMENTS AND BEHAVIOR OF A WOLF PACK IN ALASKA. THE

JOURNAL OF WILDLIFE MANAGEMENT 23:1–11. 384 Burt HW. 1943. American Society of Mammalogists Territoriality and Home Range Concepts as 385 Applied to Mammals. *Journal of Mammalogy* 24:346–352. 386 Caro TM, Stoner CJ. 2003. The potential for interspecific competition among African carnivores. 387 Biological Conservation 110:67–75. DOI: 10.1016/S0006-3207(02)00177-5. 388 389 Carter A, Luck GW, McDonald SP. 2012. Ecology of the red fox (Vulpes vulpes) in an agricultural landscape. 2. Home range and movements. Australian Mammalogy 34:175– 390 187. DOI: 10.1071/AM11041. 391 Cerveny J, Begall S, Koubek P, Nováková P, Burda H. 2011. Directional preference may 392 enhance hunting accuracy in foraging foxes. *Biology Letters* 7:355–357. DOI: 393 10.1098/rsbl.2010.1145. 394 Chandramouli C. 2013. Census of India 2011: Primary Census Abstract. New Delhi, India: 395 Office of the Registrar General & Census Commissioner, India. 396 Ciucci P, Boitani L, Francisci F, Andreoli G. 1997. Home range, activity and movements of a 397 wolf pack in central Italy. Journal of Zoology 243:803–819. DOI: 10.1111/j.1469-398 7998.1997.tb01977.x. 399 Cody ML. 1985. Habitat selection in birds. Academic Press. 400 Coman BJ, Robinson J, Beaumont C. 1991. Home range, dispersal and density of red foxes 401 402 (Vulpes vulpes 1.) in central Victoria. Wildlife Research 18:215–223. DOI: 403 10.1071/WR9910215. Filla M, Premier J, Magg N, Dupke C, Khorozyan I, Waltert M, Bufka L, Heurich M. 2017. 404 Habitat selection by Eurasian lynx (Lynx lynx) is primarily driven by avoidance of human 405 406 activity during day and prey availability during night. Ecology and Evolution 7:6367–6381.



420

DOI: 10.1002/ece3.3204.

408	Fuglei E, Tarroux A. 2019. Arctic fox dispersal from Svalbard to Canada: One female's long run
409	across sea ice. Polar Research 38:1-7. DOI: 10.33265/polar.v38.3512.
410	Fullman TJ, Joly K, Ackerman A. 2017. Effects of environmental features and sport hunting on
411	caribou migration in northwestern Alaska. Movement Ecology 5:1-11. DOI:
412	10.1186/s40462-017-0095-z.
413	Geffen E, Gompper ME, Gittleman JL, Luh H, David W, Wayne RK, Geffen ELI, Macdonald
414	DW. 1996. Size , Life-History Traits , and Social Organization in the Canidae : A
415	Reevaluation Published by : The University of Chicago Press for The American Society of
416	Naturalists Stable URL: http://www.jstor.org/stable/2463228. The University of Chicago
417	Press. <i>Organization</i> 147:140–160.
418	Getz WM, Fortmann-Roe S, Cross PC, Lyons AJ, Ryan SJ, Wilmers CC. 2007. LoCoH:
419	Nonparameteric Kernel methods for constructing home ranges and utilization distributions.

- 421 Ghoshal A, Bhatnagar YV, Mishra C, Suryawanshi K. 2016. Response of the red fox to
- expansion of human habitation in the Trans-Himalayan mountains. European Journal of
- *Wildlife Research* 62:131–136. DOI: 10.1007/s10344-015-0967-8.

PLoS ONE 2. DOI: 10.1371/journal.pone.0000207.

- Gosselink TE, Deelen TR Van, Warner RE, Joselyn MG. 2003. Temporal Habitat Partitioning
- and Spatial Use of Coyotes and Red Foxes in East-Central Illinois. *The Journal of Wildlife*
- 426 *Management* 67:90. DOI: 10.2307/3803065.
- Haltenorth, T., & Roth HH. 1968. Short review of the biology and ecology of the red fox.
- 428 Saugetierkunde Mitteilungen 16:339–352.
- Hoffmann M, Sillero-Zubiri C. 2016. Vulpes vulpes. The IUCN Red List of Threatened Species



130	2016: e.T23062A46190249. http://dx.doi.org/10.2305/IUCN.UK.2016-
131	1.RLTS.T23062A46190249.en. The IUCN Red List of Threatened Species 2016
132	8235:e.T23062A4. DOI: 10.2305/IUCN.UK.2016-1.RLTS.T23062A46190249.en.
133	Horne JS, Garton EO, Krone SM, Lewis JS. 2007. Analyzing animal movements using Brownian
134	bridges. <i>Ecology</i> 88:2354–63.
135	Hunter J, Caro T. 2008. Interspecific competition and predation in American carnivore families.
136	Ethology Ecology and Evolution 20:295–324. DOI: 10.1080/08927014.2008.9522514.
137	Ims RA. 1995. Movement patterns related to spatial structures. Mosaic landscapes and
138	ecological processes, Springer, Dordrecht.
139	Jean-Steve Meia J-MW. 1995. Home ranges and movements of red foxes in central Europe:
140	stability despite environment changes. Canadian Journal of Zoology 73:1960–1966.
141	Jedrzejewski W, Schmidt K, Theuerkauf J, Jedrzejewska B, Okarma H. 2001. Daily movements
142	and territory use by radio-collared wolves (Canis lupus) in Bialowieza Primeval Forest in
143	Poland. Canadian Journal of Zoology 79:1993–2004. DOI: 10.1139/cjz-79-11-1993.
144	John A. Wiens, Nils Chr. Stenseth BVH and RAI. 1993. Ecological Mechanisms and Landscape
145	Ecology Author(s): Oikos 66:369–380.
146	Johnson DH. 1980. The Comparison of Usage and Availability Measurements for Evaluating
147	Resource Preference. <i>Ecology</i> 61:65–71. DOI: 10.1088/1751-8113/44/8/085201.
148	Johnson DS, Thomas DL, Ver Hoef JM, Christ A. 2008. A general framework for the analysis of
149	animal resource selection from telemetry data. <i>Biometrics</i> 64:968–976. DOI:
150	10.1111/j.1541-0420.2007.00943.x.
151	Kachroo P, Dhar U SB. 1977. Flora of Ladakh.
152	Kenward RE, Clarke RT, Hodder KH, Walls SS. 2001. Density and linkage estimators of home



- range: Nearest-neighbor clustering defines multinuclear cores. *Ecology* 82:1905–1920.
- 454 DOI: 10.1890/0012-9658(2001)082[1905:DALEOH]2.0.CO;2.
- Laundre JW, Hernandez L, Ripple WJ. 2010. The Landscape of Fear: Ecological Implications of
- 456 Being Afraid~!2009-09-09~!2009-11-16~!2010-02-02~! *The Open Ecology Journal* 3:1–7.
- 457 DOI: 10.2174/1874213001003030001.
- Lele SR. 2009. A New Method for Estimation of Resource Selection Probability Function.
- *Journal of Wildlife Management* 73:122–127. DOI: 10.2193/2007-535.
- 460 Maheshwari A. 2018. Journal of Threatened Taxa Article. Journal of Threatened Taxa
- 461 10:11391–11398.
- 462 Manly, B. F. L., McDonald, L., Thomas, D. L., McDonald, T. L., & Erickson WP. 2007.
- 463 Resource Selection by Animals Statistical Design and Analysis for Field Studies Second
- 464 Edition. Springer Sci. Bus. Media. DOI: 10.1088/1751-8113/44/8/085201.
- 465 Mattisson J, Sand H, Wabakken P, Gervasi V, Liberg O, Linnell JDC, Rauset GR, Pedersen HC.
- 466 2013. Home range size variation in a recovering wolf population: Evaluating the effect of
- environmental, demographic, and social factors. *Oecologia* 173:813–825. DOI:
- 468 10.1007/s00442-013-2668-x.
- 469 Mech D. 1994. Regular and Homeward Travel Speeds of Arctic Wolves. *Journal of Mammalogy*
- 470 75:741–742.
- 471 Michael J. Freake RM and JBPS. 2019. The quarterly review of biology. *Quarterly Review of*
- 472 *Biology* 94:124–147. DOI: 10.1086/703580.
- 473 Miller CS, Hebblewhite M, Petrunenko YK, Seryodkin IV, Goodrich JM, Miquelle DG. 2014.
- Amur tiger (Panthera tigris altaica) energetic requirements : Implications for conserving
- 475 wild tigers. 170:120–129.



476	Minta SC. 1993. Sexual differences in spatio-temporal interaction among badgers. <i>Oecologia</i>
477	96:402–409. DOI: 10.1007/BF00317511.
478	Mishra C, Humbert-Droz B. 1998. Avifaunal survey of Tsomoriri Lake and adjoining Nuro
479	Sumdo Wetland in Ladakh, Indian trans-Himalaya. Forktail 14:67–70.
480	Morellet N, Bonenfant C, Börger L, Ossi F, Cagnacci F, Heurich M, Kjellander P, Linnell JDC,
481	Nicoloso S, Sustr P, Urbano F, Mysterud A. 2013. Seasonality, weather and climate affect
482	home range size in roe deer across a wide latitudinal gradient within Europe. Journal of
483	Animal Ecology 82:1326–1339. DOI: 10.1111/1365-2656.12105.
484	Musiani M, Okarma H, Jędrzejewski W. 1998. Speed and actual distances travelled by
485	radiocollared wolves in Bialowieza Primeval Forest (Poland). Acta Theriologica 43:409–
486	416. DOI: 10.4098/AT.arch.98-51.
487	Newdick MT. 1983. The behavioural ecology of urban foxes, Vulpes vulpes, in Oxford.
488	University of Oxford.
489	Newsome TM, Spencer EE, Dickman CR. 2017. Short-term tracking of three red foxes in the
490	Simpson Desert reveals large home-range sizes. <i>Australian Mammalogy</i> 39:238–242. DOI:
491	10.1071/AM16037.
492	Owen-smith N. 2013. Daily movement responses by African savanna ungulates as an indicator
493	of seasonal and annual food stress. Wildlife Research 40:232–240. DOI: 10.1071/WR13024
494	Poulin M-PP, Clermont J, Berteaux D. 2021. Extensive daily movement rates measured in
495	territorial arctic foxes. <i>Ecology and Evolution</i> In press:2503–2514. DOI:
496	10.1002/ece3.7165.
497	Reshamwala HS, Mahar N, Dirzo R, Habib B. 2021. Successful neighbour: Interactions of the
498	generalist carnivore red fox with dogs, wolves and humans for continued survival in



499	dynamic anthropogenic landscapes. Global Ecology and Conservation 25:e01446. DOI:
500	10.1016/j.gecco.2020.e01446.
501	Reshamwala HS, Shrotriya S, Bora B, Lyngdoh S, Dirzo R, Habib B. 2018. Anthropogenic food
502	subsidies change the pattern of red fox diet and occurrence across Trans-Himalayas, India.
503	Journal of Arid Environments 150:15-20. DOI: 10.1016/j.jaridenv.2017.12.011.
504	Rotem G, Berger H, King R, Bar P, Saltz D. 2011. The effect of anthropogenic resources on the
505	space-use patterns of golden jackals. <i>Journal of Wildlife Management</i> 75:132–136. DOI:
506	10.1002/jwmg.9.
507	Roy PS, Behera MD, Murthy MSR, Roy A, Singh S, Kushwaha SPS, Jha CS, Sudhakar S, Joshi
508	PK, Reddy CS, Gupta S, Pujar G, Dutt CBS, Srivastava VK, Porwal MC, Tripathi P, Singh
509	JS, Chitale V, Skidmore AK, Rajshekhar G, Kushwaha D, Karnatak H, Saran S, Giriraj A,
510	Padalia H, Kale M, Nandy S, Jeganathan C, Singh CP, Biradar CM, Pattanaik C, Singh DK,
511	Devagiri GM, Talukdar G, Panigrahy RK, Singh H, Sharma JR, Haridasan K, Trivedi S,
512	Singh KP, Kannan L, Daniel M, Misra MK, Niphadkar M, Nagabhatla N, Prasad N,
513	Tripathi OP, Rama Chandra Prasad P, Dash P, Qureshi Q, Tripathi SK, Ramesh BR, Gowda
514	B, Tomar S, Romshoo S, Giriraj S, Ravan SA, Behera SK, Paul S, Das AK, Ranganath BK,
515	Singh TP, Sahu TR, Shankar U, Menon ARR, Srivastava G, Neeti, Sharma S, Mohapatra
516	UB, Peddi A, Rashid H, Salroo I, Hari Krishna P, Hajra PK, Vergheese AO, Matin S,
517	Chaudhary SA, Ghosh S, Lakshmi U, Rawat D, Ambastha K, Malik AH, Devi BSS, Sharma
518	KC, Mukharjee P, Sharma A, Davidar P, Raju RRV, Katewa SS, Kant S, Raju VS, Uniyal
519	BP, Debnath B, Rout DK, Thapa R, Joseph S, Chhetri P, Ramachandran RM. 2015. New
520	vegetation type map of India prepared using satellite remote sensing: Comparison with
521	global vegetation maps and utilities. International Journal of Applied Earth Observation



22	and Geoinformation 39:142–159. DOI: 10.1016/j.jag.2015.03.003.
523	Sacks BN, Statham MJ, Perrine JD, Wisely SM, Aubry KB. 2010. North American montane red
524	foxes: Expansion, fragmentation, and the origin of the Sacramento Valley red fox.
525	Conservation Genetics 11:1523–1539. DOI: 10.1007/s10592-010-0053-4.
26	Saeki M, Johnson PJ, Macdonald DW. 2007. Movements and habitat selection of raccoon dogs
527	(Nyctereutes procyonoides) in a mosaic landscape. <i>Journal of Mammalogy</i> 88:1098–1111.
528	DOI: 10.1644/06-MAMM-A-208R1.1.
529	de Satgé J, Teichman K, Cristescu B. 2017. Competition and coexistence in a small carnivore
30	guild. Oecologia 184:873–884. DOI: 10.1007/s00442-017-3916-2.
31	Schlegel PA. 2008. Magnetic and other non-visual orientation mechanisms in some cave and
32	surface urodeles. <i>Journal of Ethology</i> 26:347–359. DOI: 10.1007/s10164-007-0071-y.
33	Schmidt K. 1999. Variation in daily activity of the free-living Eurasian lynx (Lynx lynx) in
34	Bialowieza Primeval Forest, Poland. Journal of Zoology 249:417–425. DOI:
35	10.1017/S0952836999009851.
36	Schuette P, Wagner AP, Wagner ME, Creel S. 2013. Occupancy patterns and niche partitioning
37	within a diverse carnivore community exposed to anthropogenic pressures. Biological
38	Conservation 158:301-312. DOI: 10.1016/j.biocon.2012.08.008.
39	Signer J, Fieberg J, Avgar T. 2019. Animal movement tools (amt): R package for managing
540	tracking data and conducting habitat selection analyses. <i>Ecology and Evolution</i> 9:880–890.
541	DOI: 10.1002/ece3.4823.
542	Sillero-Zubiri, C., Hoffmann, M., & Macdonald DW. 2004. Canids: foxes, wolves, jackals, and
543	dogs: status survey and conservation action plan. Gland, Switzerland: IUCN.
544	Small RT. Rusch DH. 1989. The Natal Dispersal of Ruffed Grouse Author (s): Robert J. Small



and Donald H. Rusch Published by: Oxford University Press Stable URL: 545 https://www.jstor.org/stable/4087758 REFERENCES Linked references are available on 546 JSTOR for this article: refere. 106:72–79. 547 Szor G, Berteaux D, Gauthier G. 2008. Finding the right home: Distribution of food resources 548 and terrain characteristics influence selection of denning sites and reproductive dens in 549 550 arctic foxes. *Polar Biology* 31:351–362. DOI: 10.1007/s00300-007-0364-1. Theuerkauf J, Gula R, Pirga B, Tsunoda H, Eggermann J, Brzezowska B, Rouys S, Radler S. 551 2007. Human impact on wolf activity in the Bieszczady Mountains, SE Poland. Annales 552 Zoologici Fennici 44:225–231. 553 Thurfiell H, Ciuti S, Boyce MS. 2014. Applications of step-selection functions in ecology and 554 conservation. :1–12. 555 Turchin P. 1991. Reconstructing Endogenous Dynamics of a Laboratory Drosophila Population 556 Author (s): P. Turchin Source: Journal of Animal Ecology, Oct., 1991, Vol. 60, No. 3 557 (Oct., 1991), pp. 1091-1098 Published by: British Ecological Society Stable URL: 558 60:1091-1098. 559 Turchin P. 1998. *Quantitative analysis of movement*. Sunderland (mass): Sinauer assoc. 560 Vanak AT, Gompper ME. 2010. Multi-scale resource selection and spatial ecology of the Indian 561 fox in a human-dominated dry grassland ecosystem. *Journal of Zoology* 281:140–148. DOI: 562 10.1111/j.1469-7998.2010.00690.x. 563 564 Wall J. 2014. Movement ecology tools for ArcGIS (arcmet) Version, 10(2), V3. Walton Z. 2020. Zea Walton Movement across scales: red fox spatial ecology. 565 Walton Z, Samelius G, Odden M, Willebrand T. 2017. Variation in home range size of red foxes 566 567 Vulpes vulpes along a gradient of productivity and human landscape alteration. PLoS ONE





568	12:1–14. DOI: 10.1371/journal.pone.0175291.
569	Walton Z, Samelius G, Odden M, Willebrand T. 2018. Long-distance dispersal in red foxes
570	Vulpes vulpes revealed by GPS tracking. European Journal of Wildlife Research 64. DOI:
571	10.1007/s10344-018-1223-9.
572	Wysong ML, Hradsky BA, Iacona GD, Valentine LE, Morris K, Ritchie EG. 2020. Space use
573	and habitat selection of an invasive mesopredator and sympatric, native apex predator.
574	Movement Ecology 8:1–14. DOI: 10.1186/s40462-020-00203-z.
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576	List of Figures and Tables
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578	desert, Ladakh, India
579	Figure. 2 Average daily movement of red fox in the trans-Himalayan cold desert, Ladakh, India
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581	Himalayan cold desert, Ladakh, India (case; True = true steps, False = random steps)
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Table 1(on next page)

Home range of red fox calculated by different methods



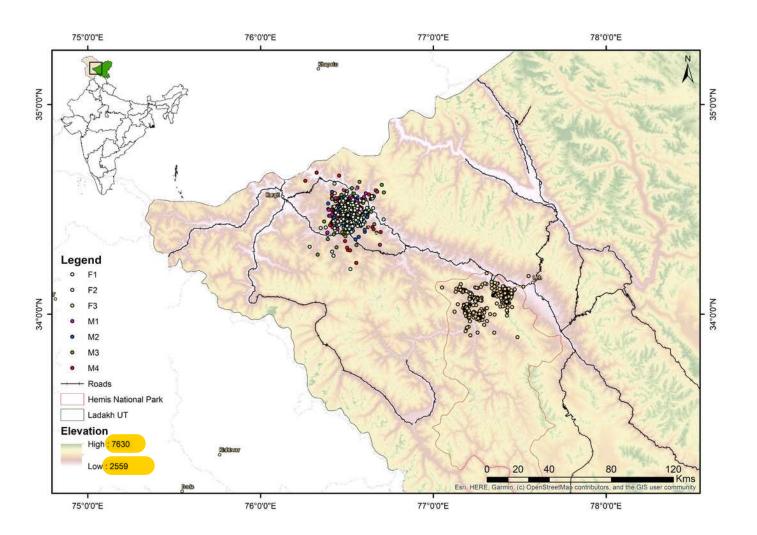
1 Table. 1 Home range of red fox calculated by different methods



HR Method	МСР	Kernel	LoCoH	BBMM	МСР	Kernel	LoCoH	BBMM	
Methou									
	Percent Contour								
Individual	50	50	50	50	95	95	95	95	
F1	0.14	0.22	0.05	0.55	1.95	1.62	1.17	3.81	
F2	0.36	1.27	0.32	2.33	45.99	41.59	37.57	29.75	
F3	18.86	16.84	0.59	2.31	672.19	269.15	78.42	49.23	
M1	1.74	1.50	0.18	1.93	118.77	18.49	8.97	31.02	
M2	24.47	4.02	0.26	2.62	39.36	26.65	10.63	26.19	
M3	1.15	1.57	0.43	2.69	39.99	38.83	35.57	32.93	
M4	0.44	0.77	0.36	1.15	11.00	12.07	10.11	10.75	



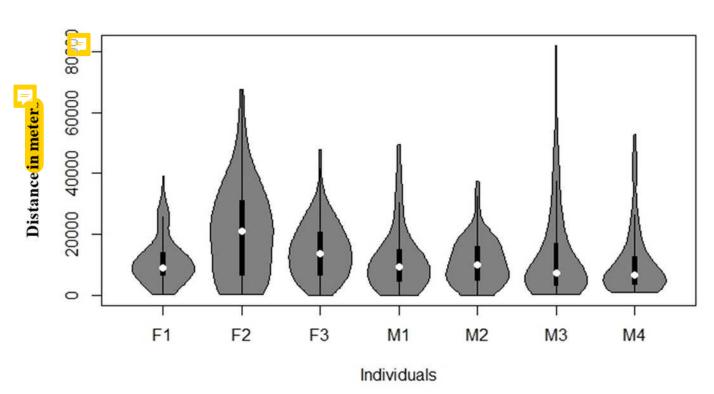
Study area and GPS fixes of radio-collared red foxes in the Trans-Himalayan cold desert, Ladakh, India





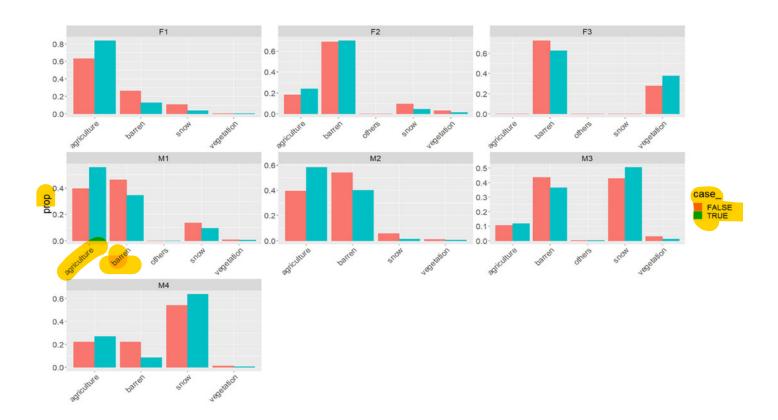
Average daily movement of red fox in the trans-Himalayan cold desert, Ladakh, India







Land-use land cover categories utilized by different red fox μ dividuals in the trans-Himalayan cold desert, Ladakh, India (case; True = true steps, False = random steps)





Step-Selection function beta coefficients of different red fox individuals

