On the move: Spatial ecology and habitat-use of red fox in the Trans-Himalayan cold desert (#69037)

First revision

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

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Red fox (*Vulpes vulpes*) is the most widespread wild carnivore globally, occupying diverse habitats. The species is known for their adaptability to survive in dynamic anthropogenic landscapes. Despite being one of the most extensively studied carnivores, there is a dearth of information on red fox from the Trans-Himalayan region. With the advancements in technology, studying animal movements has become crucial for understanding the basic ecology of a species. We studied the home range sizes using different estimation methods: minimum convex polygon (MCP), Kernel density estimator (KDE), localized convex hull (LoCoH) and Brownian-bridge movement model (BBMM). We also analyzed the daily movement and directionality of red foxes in the arid Trans-Himalayan cold desert. We then assess the habitat selection of red fox with respect to topographic factors- ruggedness, elevation, and slope; and anthropogenic factors- distance to road, water and human settlements. We captured and GPS-collared six red fox individuals (3 males and 3 females) from Chiktan and one female from the Hemis National Park, Ladakh, India. The collars were programmed to record GPS fixes every 15 minutes. The average Brownian bridge movement model home range estimate (95% contour) of red fox was 22.40 ± 4.94 SE km^2 and the average core area (50% contour) was 1.87 ± 0.35 SE km^2. The average daily movement of red fox was 13.28 ± 1.38 SE km/day. Red fox significantly selected lower elevations with lesser rugged terrains and was positively associated with water. The daily movements of red fox have been examined for the first time across its global distribution and help in understanding the species daily energetics and nutritional requirements. This study helps to understand 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

Red fox (*Vulpes vulpes*) is the most widespread wild carnivore globally, occupying diverse habitats. The species is known for their adaptability to survive in dynamic anthropogenic landscapes. Despite being one of the most extensively studied carnivores, there is a dearth of information on red fox from the Trans-Himalayan region. With the advancements in technology, studying animal movements has become crucial for understanding the basic ecology of a species. We studied the home range sizes using different estimation methods: minimum convex polygon (MCP), Kernel density estimator (KDE), localized convex hull (LoCoH) and Brownian-bridge movement model (BBMM). We also analyzed the daily movement and directionality of red foxes in the arid Trans-Himalayan cold desert. We then assess the habitat selection of red fox with respect to topographic factors- ruggedness, elevation, and slope, and anthropogenic factors- distance to road, water and human settlement. We captured and GPS-collared six red fox individuals (3 males and 3 females) from Chiktan and one female from the Hemis National Park, Ladakh, India. The collars were programmed to record GPS fixes every 15 minutes. The average Brownian bridge movement model home range estimate (95% contour) of red fox was 22.40 ± 4.94 SE km^2 and the average core area (50% contour) was 1.87 ± 0.35 SE km^2. The average daily movement of red fox was 13.28 ± 1.38 SE km/day. Red fox significantly selected lower elevations with lesser rugged terrains and was positively associated with water. The daily movements of red fox have been examined for the first time across its global distribution and help in understanding the species daily energetics and nutritional requirements. This study helps to understand 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.

Keywords Home range, Daily-movement, Directionality, Ladakh, Space-use, Step-selection function

Introduction

The basic fundamentals for understanding an animal's ecology is studying home range size, which is defined as an individual's area where movement occurs for normal activities like gathering food, mating and raising the young (Burt, 1943). The causes of these movements and their consequences are of great significance to understand several aspects of an animal's behaviour like dispersal (Small & Rusch, 1989), social interactions (Minta, 1993), space-use (Kenward et al., 2001) and population distributions (Turchin, 1991). Home ranges incorporate all individual's movements and depend upon species behavioural and physiological responses to the environment (Horne et al., 2007; Vanak & Gompper, 2010). Understanding the continuous movement of an animal is a powerful tool to quantify an animal's daily movement and home-range size (Turchin, 1998). However, in nature, it is impossible to visually monitor animals continuously, especially in rugged terrains with adverse climatic conditions such as that prevailing in the Trans-Himalayan cold desert (Mishra & Humbert-Droz, 1998). The advancement of GPS telemetry is now commonly used to understand fine-scale movement and space use of species in a varied landscape. It aids in continuous monitoring of animals spread over large distances and is particularly helpful for elusive, nocturnal, and present in areas that are otherwise not accessible by researchers.

Red fox (*Vulpes vulpes*) is the most widespread wild carnivore in the world (Hoffmann & Sillero-Zubiri, 2016) and is known for its adaptability to survive in all sorts of environments (Geffen et al., 1996). The generalist and opportunistic nature of red fox in terms of their diet, habitat and movement patterns have contributed to its success (Geffen et al., 1996; Walton et al., 2017; Reshamwala et al., 2018). However, such mid-sized carnivores are also facing competition because of their broad spectrum of diet, which overlaps with the energetic needs of myriad other sympatric competitors (Caro & Stoner, 2003). For example, a previous study reports a high diet-overlap of red fox with wolves and dogs from the Trans-Himalayan region (Reshamwala et al., 2021). As a result, they may have to make trade-offs either temporally or spatially (Schuette et al., 2013). Also, compared to the large carnivores, there have been fewer studies pertaining to meso-carnivores.

Globally, the red fox is one of the most extensively studied carnivores; however, there is a dearth of information on the mountain red fox (*Vulpes vulpes montana*) found in the Trans-Himalayan cold desert. Mountain red fox is unique and maybe threatened like the Sierra Nevada red fox (Aubry et al., 2009; Sacks et al., 2010). There have been only a handful of studies from India on the mountain red fox, which are confined to dietary habits (Ghoshal et al., 2016; Maheshwari, 2018; Reshamwala et al., 2018).

Despite having GPS telemetry technology, most studies aim at obtaining home ranges where the GPS fixes are taken at large time intervals, which are unsuitable for studying daily movements. Understanding the the daily movement of species is expensive at the cost of battery life. However, it can provide important information such as the breeding and non-breeding individuals in a population (Jedrzejewski et al., 2001; Alfredéen, 2006), human activity and disturbances (Theuerkauf et al., 2007) and can also act as an indicator for the health of an ecosystem by identifying food-deficient habitats (Owen-Smith, 2013).

A mosaic of different habitat types is required to fulfil various life requisites, and these are reflected in the animal's movement at larger spatial scales (Ims, 1995; Benson & Chamberlain, 2007). Intra and inter-specific interactions in terms of competition, predation or facilitation also determine animal spatial distributions. In some cases, the directionality of movements may also have a great biological significance (Freake, Muheim & Philips 2006). The magnetic alignment of animals may have 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 red foxes, it has been observed that their directional preference enhances the accuracy of catching prey (Cerveny et al., 2011). Ecologists are often interested in understanding these spatial distribution patterns to know about an animal's requirements and how these requirements are fulfilled (Johnson, 1980; Manly et al., 2007).

In this study, we first explore the home range sizes of red fox by different methods. We then estimate the average daily movement and assess the habitat-use in the arid Trans-Himalayan cold desert. We also hypothesize the movement of red fox would have directionality with more persistence towards the north-east direction, as this would enhance their prey catching efficiency (Cerveny et al., 2011). This is the first study that aims to understand the red fox's daily movements to the best of our knowledge. The movement of an individual gives an insight into the population distribution of a species and thereby aids in understanding population-level processes (Wiens et al., 1993; Ims, 1995). Therefore, understanding the spatial ecology of an abundant and highly adaptable meso-carnivore is important for managers to develop conservation strategies in the Trans-Himalayan region.

Materials and methods

Study area

The study was conducted in Ladakh, which belongs to the North-western Trans-Himalayan region of India (Fig. 1). The area is characterized by dry rugged terrain with very little precipitation of 100 mm/year (Bharti et al., 2016). The cold desert has an elevation of 3000 to 7000 m above sea level and harsh winter temperatures, which go down to - 30 °C in winters. The vegetation is very sparse and patchy, with alpine meadows in certain areas (Kachroo & Dhar, 1977). The place is also scarcely populated and has a human density of 4.9 individuals/km^2 (Chandramouli, 2013). Six foxes were GPS-collared in the village of Chiktan, which is a small hamlet 80 km from the city of Kargil. The people comprise the Muslim community, and there is a high amount of anthropogenic food subsidy and fox abundance in this area (Reshamwala et al., 2018). One vixen (F3) was GPS-collared in Hemis National Park at Rumbuck. People are primarily associated with agriculture or agro-pastoralism and are sometimes involved with tourism, especially in Hemis National Park (Reshamwala et al., 2021). Besides red fox, snow leopard (*Panthera uncia*), wolf (*Canis lupus*), Ladakh urial (*Ovis vignei*), bluesheep (*Pseudois nayaur*), ibex (*Capra ibex*), weasel (*Mustela altaica*), and stone marten (*Martes foina*) are other animals found in this landscape.

Fox capture

We captured seven red foxes from October 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, Animal Ethics Committee. The foxes were measured, weighed, and sexed before release (Table. 1). The fox weight was taken by holding them on a weighing scale and subtracting the observer's weight subsequently. The collars were programmed to record GPS fixes every 15 minutes interval and transmit the same every 3 hours. We chose 15 minutes time interval as previous studies advocate this time for calculating the 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 130 minutes after one month to increase the battery life.

Data analysis

The data from seven red foxes included 31,261 GPS fixes and filtered in ArcGis 9.2.1 with the ArcMET filter tools (Wall, 2014). The filtered data excluded fox locations that exceeded > 48 km/h as this is the highest speed of the red fox (Haltenorth, & Roth, 1968). Home ranges were estimated using minimum convex polygon (MCP), Kernel density estimator (KDE), localized convex hull (LoCoH) and Brownian-bridge movement model (BBMM) from the ArcMET utilization distribution and range tools (Wall, 2014). We used different methods to evaluate the home ranges (95% contour) and core areas (50% contour) of each individual of the red fox.

We calculated the daily movement of red fox, i.e., the sum of displacement in one day, with the help of trajectory details from the ArcMET path statistics tool in ArcGIS. We considered the daily movement as the sum of linear distances obtained from each consecutive GPS fix from the first location of midnight and the last location of the same day. We then estimated the average distance walked in a day by obtaining the mean and median for every individual. However, to estimate the daily movements, we encountered two false-positive errors. Error 1 - when the foxes were in the den, and the GPS fix was at a place well within the home range with speeds less than 48 km/h. Error 2 - 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. We used speed data to identify erroneous spikes to resolve these false-positive errors and restricted the data containing speeds to ≤ 9.35 km/h (Fig. S.1). To evaluate the effect of down-sampling on the GPS fixes and movement, we resample our 15 minutes GPS fixes to 30, 60 and 120 minutes time intervals. We did a one-sample T-test for evaluating the differences.

To understand the directionality or orientation of the animal, we compared turning angles. We estimated κ, the concentration parameter of a von Mises distribution (Mardia & Jupp, 1999), which defines the degree of linearity in an animal movement given a set of angular measurements. To check for directionality in the movements of red fox, the angular data were analyzed in the R package circstat, spatstat and circular (Agostinelli & Lund, 2011). We then conducted a Rayleigh test (Lund et al., 2017) to find a significant difference in the directionality of red fox.

To assess the habitat selection with variation in topography (ruggedness, elevation, and slope) and anthropogenic disturbance (distance to road, water and human settlements), we used Integrated Step-Selection Functions (iSSF) from the amt package in R (Signer, Fieberg & Avgar, 2019). Resource selection and resource selection probability functions have been widely used to identify the habitats used by radio-collared individuals (Manly *et al.*, 2007; Lele, 2009). A more advanced and robust method is the step selection function (Thurfjell, Ciuti & Boyce, 2014). Step selection functions provides the advantage of incorporating actual movement data of an animal as opposed to comparing it with random points used in the resource selection function (Johnson et al., 2008). iSSA jointly estimates resource selection and animal movement parameters (e.g. step length and turn angle) by relaxing the implicit assumption that these are independent (Signer, Fieberg & Avgar, 2019). Step-Selection Functions are a method of assessing habitat preference in animals by comparing each used step (i.e., movement between two consecutive GPS fixes) to those of randomly placed steps (i.e., that animal could have taken) within the movement path. The random steps are generated using distances sampled from a gamma distribution fitted to the empirical step length distribution and random turning angles by von-misses distribution. We generated both true and random steps for 15 minutes intervals for all the individuals. We produced 10 random steps per used step, based on the recommendations of Thurfjell et al. (2014). 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). At the end of each step, we extracted environmental covariates. All variables were scaled and centred and screened for collinearity using Pearson's correlation coefficient with a threshold of $|r| > 0.7$. We performed an iSSA using 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.

Results

Home range

The red fox showed high variation in the size of their home ranges and core area utilization (Table. 2). The average BBMM home range (95% contour) of red fox was 22.40 ± 4.94 SE km^2 and the average core area (50% contour) was 1.87 ± 0.35 SE km^2. The smallest home range was for the individual F1 (3.81 km^2). The highest core area was estimated for M3 (2.69 km^2), and the smallest was found for F1 (0.55 km^2). The results showed that the M1, M2, and F3 individuals utilize multiple core zones (Fig. S.2). The vixen F3 collared from the Hemis National Park was excluded from estimating the home range size as it was identified as a dispersing individual from its movement. The individual displacement from its collared area is shown in the trend line of F3 (Fig S.3).

Daily movement

The average daily movement of red fox was 13.28 ± 1.38 SE km/day. The individual F2 showed the highest daily average movement of 20.92 km/day, and the least movement was shown by M4 of 10.54 km/day (Fig. 2). The downscaling of data from 15 minutes GPS fixes to 2-hour interval fixes significantly ($P < 0.05$) reduced the estimated daily average distances walked by red fox (Table . S.2). Since for M3 and M4 individuals, 15 minute GPS locations were obtained for the first 30 days, only these were used to examine the effect of down-sampling.

Directionality in red fox

We found that red fox moved in all directions across different areas of its home range. Except for the M3 individual, the Rayleigh test results showed no significant directionality for the movement of red fox (Table S.1). The M3 individual showed significantly higher movements in the north-east and south-west directions (P<0.05).

Habitat selection

Compared to the random steps, the true steps of F1 were found mainly in agricultural land than other land-use categories, while F2 was mainly found in barren land (Fig. 3). F3 vixen in Hemis National Park selected barren land and but alpine vegetation. The males, M1 and M2 were present in agriculture and barren land majorly. Similarly, M3 and M4 exploited barren and agricultural land. However, they were also found to utilise areas with snow in higher proportions.

Topographic factors influenced the red fox habitat selection and they selected lower elevations and less rugged terrains (P < .001, Fig. 4). With respect to human settlements, only F1 showed significant negative selection (P<0.001), while F3, M2, M3 and M4 selected to be near human settlements (P< 0.01). Individuals F2 and M1 did not exhibit significant selection for or avoidance of human settlements. The red fox tended to select for water bodies, however for M3 and M4 individuals, it was non-significant. Except for F2 and F1, all individuals avoided roads and slope (P< 0.001).

Discussion

Home range

Most studies pertaining to home ranges refer to the traditional use of minimum convex polygon (MCP) or the Kernel method and hence may be appropriate for comparison. Rugged terrains, such as cliffs and rigid boundaries, often force animals to follow a fixed path. In such areas, Localized convex hull (LoCoH) gives a reliable home range of animals as this method can identify rigid boundaries such as rivers, lakes or otherwise inhospitable terrain (Getz et al., 2007). The BBMM is the most recent method which incorporates the time and probability of movement, thereby models the animal movements and helps determine animal home ranges more robustly (Horne et al., 2007). Since each method has its own advantages, we estimated home ranges using all of these methods. In our study, the average LoCoH and BBMM methods had a smaller estimation of home ranges (LoCoH 17.33 ± 6.24 SE km^2 and BBMM 22.40 ± 4.94 SE km^2) compared to MCP and Kernel methods (MCP 43.24 ± 16.54 SE km^2 and Kernels 23.20 ± 6.34 SE km^2).

The home range sizes of red fox are known to have significant variations ranging from as small as 0.40 km^2 in urban areas of Oxford to as large as 40 km^2 (MCP) in the Arctic or even more extensive which are determined majorly by the type of habitat (Sillero-Zubiri, Hoffmann & Macdonald, 2004). Moreover, at higher latitudes and altitudes, animals tend to have larger home ranges (Mattisson et al., 2013; Morellet et al., 2013). Foxes living at higher elevations are reported to have four times more extensive home ranges than at lower elevations (Walton et al., 2017). In Australia, larger home ranges of red fox were reported in the arid Simpson Desert (Newsome, Spencer & Dickman, 2017). However, the use of smaller home ranges by medium-sized canids near human settlements are also 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 anthropogenic food subsidies (Reshamwala et al., 2018). Hence, we speculate a mixed 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 32.93 km^2 (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 km^2 (Gosselink et al., 2003).

The individual F3 collared in Hemis National Park moved to a different place after its release. Studies caution against nomadic foxes while calculating home ranges (Meia, 1995). Similarly, we suspect, F3 was either nomadic or dispersing vixen as it once again relocated from its place. It showed large displacements twice from its initial place of collaring (Fig. S. 3). Hence, we excluded this individual from our home range analysis.

Daily movement

Fox's daily average movement ability could be a key factor in understanding 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 be the same as compared to that of an individual having a 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 km^2, BBMM), but its average daily movement was 11.10 ± 0.81 SE km/day. It is also essential to have the GPS fixes at fine-scale time intervals to calculate the average daily distance travelled by red fox. Our data suggest that increasing the time interval of GPS fixes decreases the daily movement of red fox significantly (P

< 0.01, Table S.2). On the other hand, fixes at a very small time interval may overestimate the average daily distance travelled due to location error (Poulin, Clermont & Berteaux, 2021). The average daily movement of red fox from our study was 13.28 ± 1.38 km/day. Only one study has reported the average daily movement of red fox, which was 4.8 to 16 km/day. However, the study used VHF telemetry, which has its own limitations (Carter, Luck & McDonald, 2012). The average daily movement travelled by arctic fox is comparatively well studied and is reported to be 51.9 ± 11.7 km/day (Poulin, Clermont & Berteaux, 2021).

Directionality

Following our a priori hypothesis of higher movements in the north-east and south-west directions, we found significant results for M3 individual ($P < 0.05$). Since our data was not confined to the hunting activity and comprised of the overall movement of red fox, we could not find any significant directional preference except for one individual (Table S.2). We presume that the higher movements in the northwest and southeast directions for other individuals were because of the orientation of the valley (Fig. S.4).

Habitat selection

Red fox are known for their highly adaptive behaviour 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 which were smaller in size were found in barren and snow-covered land. 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 a more advantageous overpopulation level (Thurfjell, 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, except for F1 and F2, all the other individuals were positively associated with human settlements. The presence of water bodies is also known to influence rodents and lagomorphs positively, and has been reported in previous studies (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 that 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 presume that they avoided human settlements and preferred slopes as compared to others.

Limitations of study

Data on average speeds travelled by red fox is entirely lacking, but the average speed with which wolves travel ranges from 0.8 to 1.1 km/h (Burkholder, 1959; Bibikov, Kudaktin, & Filimonov, 1985; Ciucci *et al.*, 1997; Jedrzejewski *et al.*, 2001). Studies on wolves with 15 min GPS location data of individuals have reported their maximum travel speeds from 9.6 to 13 km/h (Mech, 1994). Hence, our method of restraining the maximum speed limit of 9.35 km/h for red fox may be a fair estimate. The use of speed to identify GPS errors, especially for calculating daily movements, has been reported in other studies (Bjørneraas et al., 2010; Wysong et al., 2020). However, further studies with a greater sample size are warranted to enhance our knowledge of the maximum speed of red fox.

The actual distance travelled by an animal as compared to the straight-line distances obtained from the GPS fixes may be an underestimate. However, there are false positive errors due to the accuracy of GPS fixes in the short 15 minute time interval. For example, the GPS fixes may vary and show a continuous movement despite the red fox being stationary. Although we found the average daily movement for F2 to be as high as 20.92 ± 2.02 SE km/day and as low as 10.54 ± 0.74 SE km/day for M4 individuals, respectively, this could be an effect of sampling bias. The GPS-collar for F2 individuals worked for fewer days (56 days). In addition, for the individuals M3 and M4, the collars were reprogrammed for a longer battery life from 15 minutes for the first month to 2 hours, which further decreased their daily movements (199 and 212 days, respectively). However, based on our field observations, we could confirm that F2 showed more significant movements than other individuals and could be an exception. We also presume the movements for F2 to have reduced after the short collaring period; however, we lack the GPS data to confirm the same.

Further, when we compare the average daily movement of F2 with 30 days data of M3, M3 showed a higher daily average movement (34.22 ± 3.71 SE km/day, Table S.2). This is also because M3 made many forays outside its normal home range during this period. At four instances, the individual M3 has moved about 60 km or more in one day. Such long distances are not uncommon, and in arctic fox, the maximum distance travelled in a day was reported to be 154 km (Fuglei &

Tarroux, 2019). Long-distance dispersal events are even reported in red fox where foxes have travelled over a distance of 132-1036 km in a short period (Walton et al., 2018).

The average daily movement in the case of wolves showed a great variation, ranging from 17 to 38 km/day (Ciucci et al., 1997). It is reported that the average daily movement travelled during the mating season for wolves may go as high as 34 km/day (Jedrzejewski et al., 2001). During the 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 extended 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. We found directional persistence for only one individual. The daily movements are crucial for understanding the individual and species requirements at the population level. The daily movements further aid in understanding the daily energetics and nutritional requirements of species (Miller et al., 2014). Despite the red fox being one of the most extensively studied carnivores, there is no literature available for the daily movement of red fox. Further studies regarding the movements of 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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Conflicts of interest

The authors declare that they have no competing interests.

Author Contributions

HSR did the fieldwork, procured data, analyzed, and wrote the first draft. SK, ZH and PR helped analyse and write the manuscript. BH and PR procured the funding. BH conceptualised the study. BH and RD supervised the project and discussed the results to improve and produce the final manuscript.

Animal Ethics

All red foxes were captured following standard and approved protocols after due permission from the Ministry of Environment, Forests and Climate Change, Government of India, and Department of Wildlife Protection, Ladakh, Jammu and Kashmir. The permit details are as follows: CCFWL\Permission\2016\575-76

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List of Figures and Tables

Figure 1

Study area of collared red foxes in the trans-Himalayan cold desert, Ladakh, India.

(a) 95% MCP home ranges of six red foxes at Chiktan, Kargil. (b) 95% MCP home range of a female at Hemis National Park, Leh.

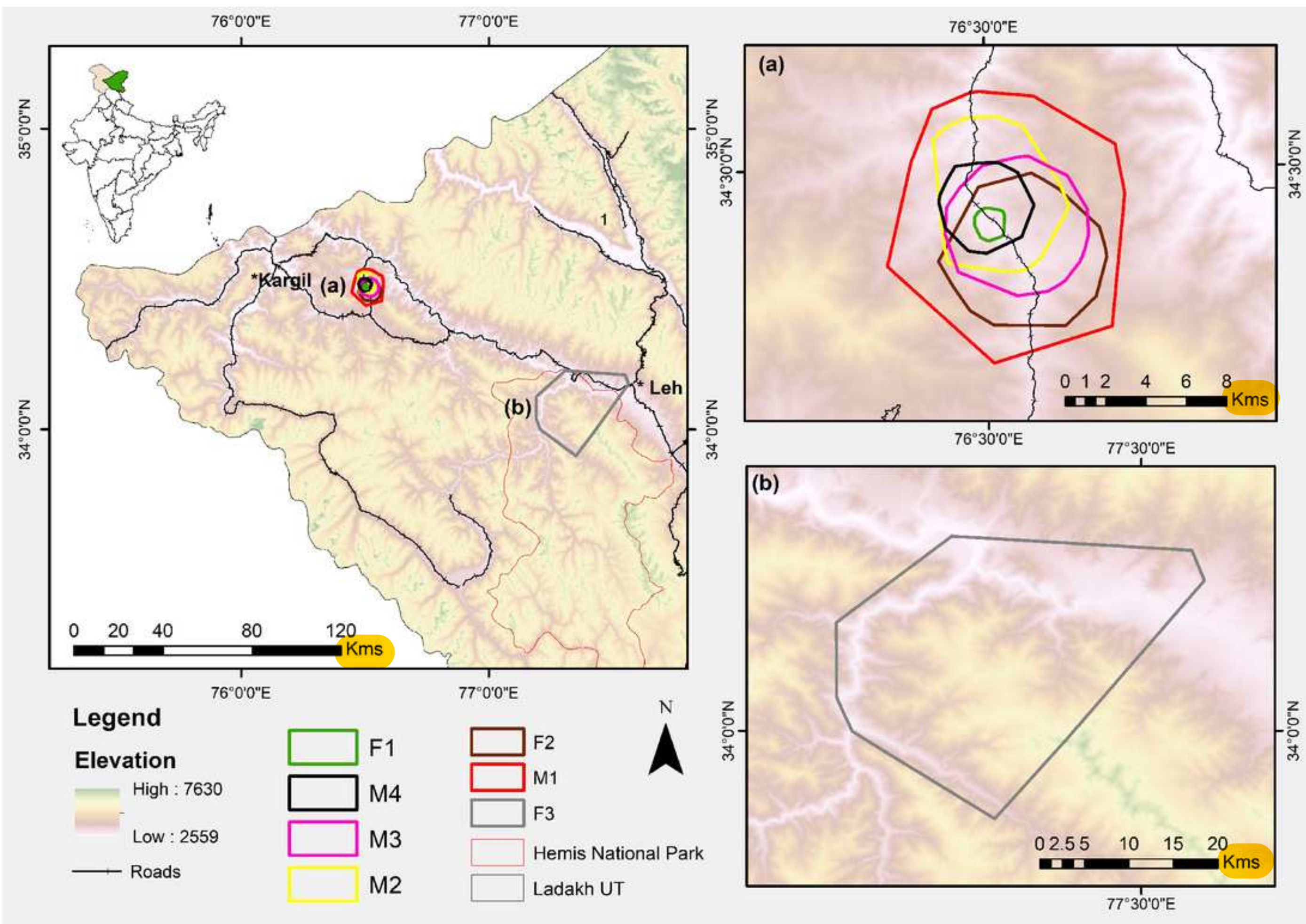

Figure 2

Estimated daily movement per day of red fox in the trans-Himalayan cold desert, Ladakh, India

*Numbers indicate the number of days an individual was collared. (Female=orange, Male=Purple)

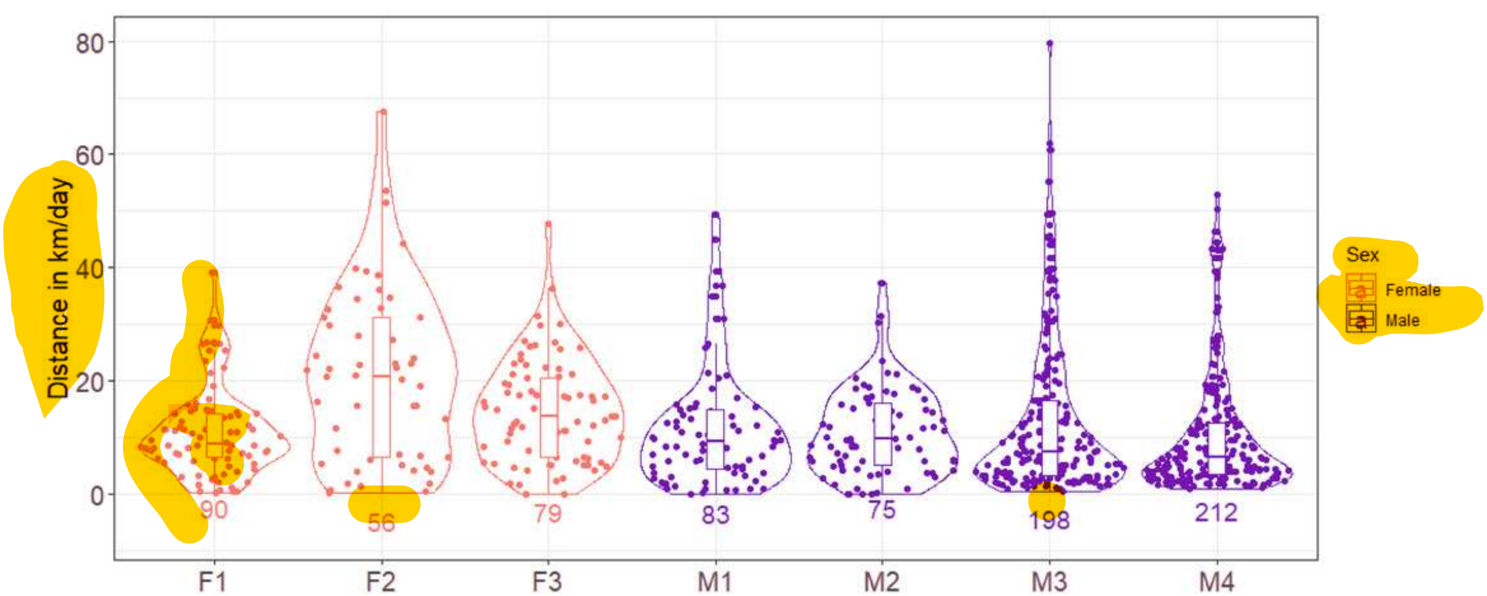

Figure 3

Land-use land cover categories utilised by different red fox individuals in the trans-Himalayan cold desert, Ladakh, India

*Case; actual steps = orange, random steps = purple

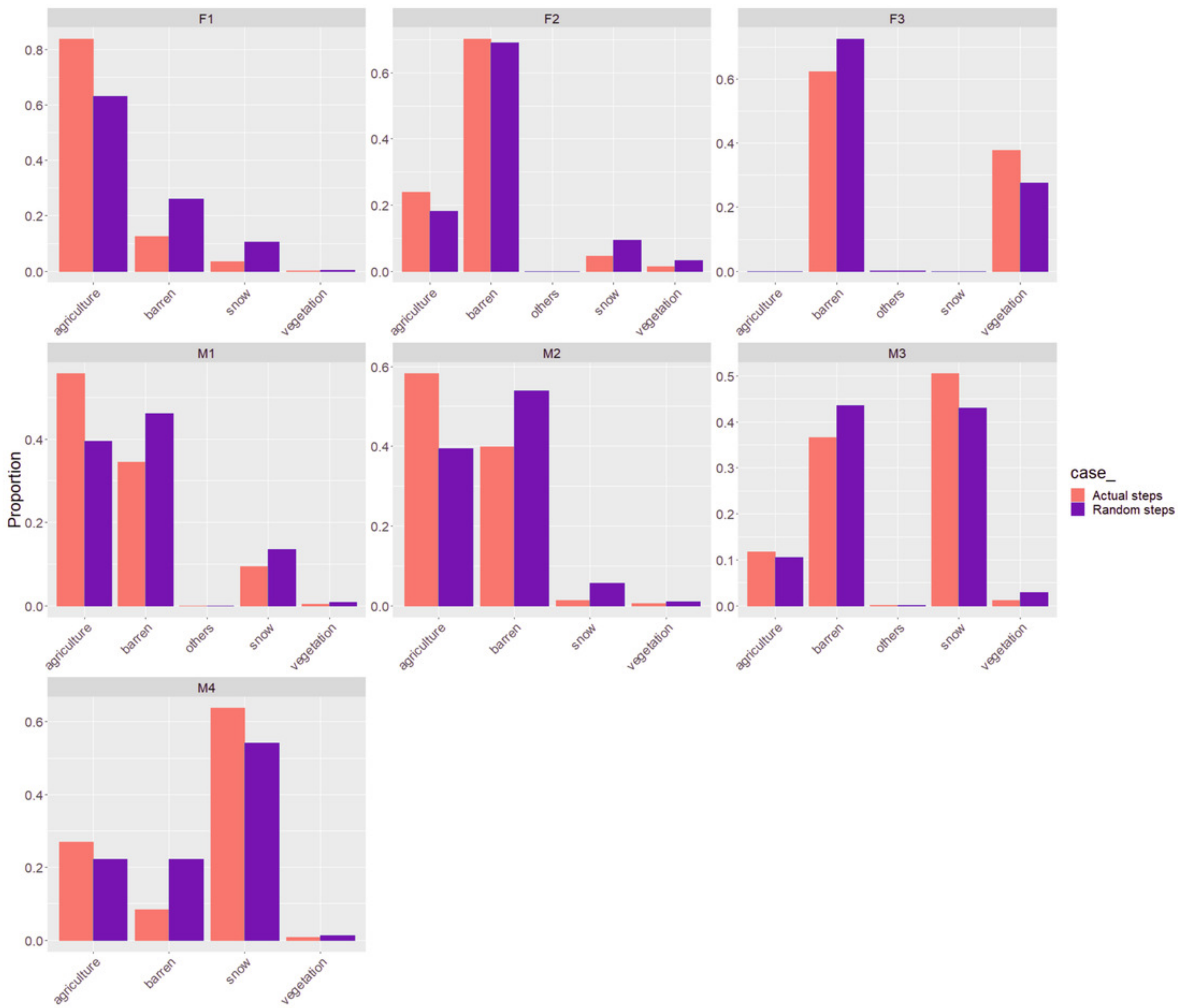

Figure 4

Step-Selection function beta coefficients of different red fox individuals

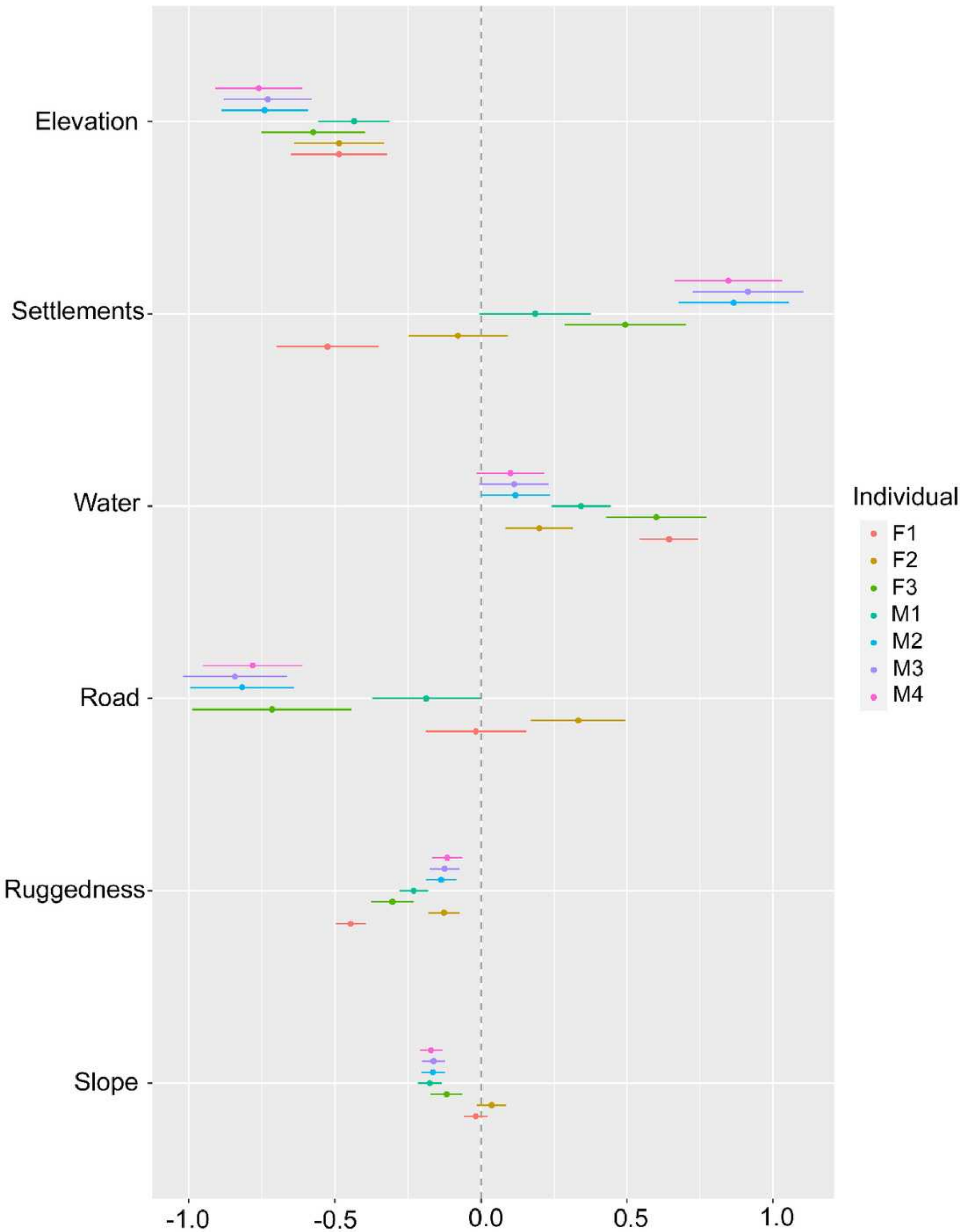
Elevation
Settlements
Water
Road
Ruggedness
Slope
-1.0
-0.5
0.0
0.5
1.0
Individual
F1
F2
F3
M1
M2
M3
M4

Table 1 (on next page)

Details of GPS-collared individuals, date of collaring, active days, and total GPS fixes received to study the spatial ecology of red fox in Ladakh, India

ID	Sex	Weight (kg)	Date of collaring	No. of days collared	Total GPS fixes
F1	F	6	27.10.2018	90	6820
F2	F	5.6	17.12.2018	56	3613
F3	F	5.2	24.12.2018	79	3208
M1	M	7.1	29.10.2018	83	5120
M2	M	8.2	17.11.2018	75	4425
M3	M	6.2	19.01.2019	198	4235
M4	M	6.4	22.01.2019	212	3840

Table 2(on next page)

Estimation of home range sizes by different methods and daily average movement of red fox in Ladakh, India

Individual	MCP (km^2)		Kernel (km^2)		LoCoH (km^2)		BBMM (km^2)		Daily average movement (km)
	Core area	*HR*	*Core area*	*HR*	*Core area*	*HR*	*Core area*	*HR*	(±SE)
F1	0.14	1.95	0.22	1.62	0.05	1.17	0.55	3.81	11.10 (0.81)
F2	0.36	45.99	1.27	41.59	0.32	37.57	2.33	29.75	20.92 (2.02)
M1	1.74	118.77	1.5	18.49	0.18	8.97	1.93	31.02	11.61 (1.13)
M2	2[illegible]	39.36	4.02	26.65	0.26	10.63	2.62	26.19	10.91 (0.88)
M3	1.01	37.50	1.57	38.83	0.43	35.57	2.69	32.93	13.20 (1.04)
M4	0.51	15.90	0.77	12.07	0.36	10.11	1.15	10.75	10.54 (0.74)
F3									14.72 (1.02)
Average (± SE)	**4.70 (3.95)**	**43.24 (16.54)**	**1.55 (0.53)**	**23.20 (6.34)**	**0.26 (0.05)**	**17.33 (6.24)**	**1.87 (0.35)**	**22.40 (4.94)**	**13.28 (1.38)**