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 its 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. We studied the home range sizes of red fox using the different estimation methods: minimum convex polygon (MCP), kernel density estimator (KDE), localized convex hull (LoCoH) and brownian-bridge movement model (BBMM). We analyzed the daily movement and assess the habitat selection with respect to topographic factors (ruggedness, elevation and slope), environmental factor (distance to water) and anthropogenic factors (distance to road and human settlements). We captured and GPS-collared six red fox individuals (3 males and 3 females) from Chiktan and one female from Hemis National Park, Ladakh, India. The collars were programmed to record GPS fixes every 15-min. The average BBMM home range estimate (95% contour) was 22.40 ± 12.12 SD km^2 (range 3.81 - 32.93 km^2) and the average core area (50% contour) was 1.87 ± 0.86 SD km^2 (range 0.55 - 2.69 km^2). The average daily movement of red fox was 13.28 ± 3.67 SD km/d (range 10.54 – 20.92 km/d). Red fox significantly selected lower elevations with less rugged terrains and were positively associated with water. This is the first study in the Trans-Himalayan landscape which aims to understand the daily movement of red fox at a fine temporal scale. Studying the movement and home range sizes helps understand the daily energetics and nutritional requirements of red fox. Movement information of a species is important for the prioritisation of areas for conservation and can aid in understanding the ecosystem functioning and ladscape management.

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Abstract

Red fox (*Vulpes vulpes*) is the most widespread wild carnivore globally, occupying diverse habitats. The species is known for its 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. We studied the home range sizes of red fox using the different estimation methods: minimum convex polygon (MCP), kernel density estimator (KDE), localized convex hull (LoCoH) and brownian-bridge movement model (BBMM). We analyzed the daily movement and assess the habitat selection with respect to topographic factors (ruggedness, elevation and slope), environmental factor (distance to water) and anthropogenic factors (distance to road and human settlements). We captured and GPS-collared six red fox individuals (3 males and 3 females) from Chiktan and one female from Hemis National Park, Ladakh, India. The collars were programmed to record GPS fixes every 15-min. The average BBMM home range estimate (95% contour) was 22.40 ± 12.12 SD km^2 (range 3.81 - 32.93 km^2) and the average core area (50% contour) was 1.87 ± 0.86 SD km^2 (range 0.55 - 2.69 km^2). The average daily movement of red fox was 13.28 ± 3.67 SD km/d (range 10.54 – 20.92 km/d). Red fox significantly selected lower elevations with less rugged terrains and were positively associated with water. This is the first study in the Trans-Himalayan landscape which aims to understand the daily movement of red fox at a fine temporal scale. Studying the movement and home range sizes helps understand the daily energetics and nutritional requirements of red fox. Movement information of a species is important for the prioritisation of areas for conservation and can aid in understanding the ecosystem functioning and ladscape management.

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

Introduction

One of the basic fundamentals for understanding an animal's ecology is its 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 for understanding 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). 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. Estimating 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. The advancement of GPS telemetry is now commonly used to understand fine-scale movement and space. It aids in continuous monitoring of animals over large distances and is particularly helpful for species that are elusive, nocturnal, or present in areas that are otherwise not accessible to 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 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 of meso-carnivores.

In this study, we first explore the home range sizes of red fox as estimated by different methods. We then estimate the average daily movement and assess the habitat-use in the arid Trans-Himalayan cold desert. This is the first study that aims to understand the red fox's daily movements to the best of our knowledge.

Materials and methods

Study area

The study was conducted in Ladakh, which belongs to the northwestern Trans-Himalayan region of India (Fig. 1). The area is characterized by dry rugged terrain with precipitation amounting to only 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. The vegetation is very sparse and patchy, with alpine meadows in certain areas (Kachroo & Dhar, 1977). The place is also scarcely populated with a human density of 4.9 individuals/km^2 (Chandramouli, 2013). Foxes were GPS collared at two sites: Chiktan and Rumbuck. Chiktan is a small hamlet about 80 km from the city of Kargil. The people comprise of the Muslim community and due to higher non-vegetarian food consumption, there is a high amount of anthropogenic food subsidy and fox abundance in this area as compared to other parts of Ladakh (Reshamwala et al., 2018, Reshamwala et al., 2021). Rumbuck is a village with few scattered human settlements in Hemis National Park and the people belong to the Buddhist community. 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*), blue sheep (*Pseudois nayaur*), ibex (*Capra ibex*), weasel (*Mustela altaica*), and stone marten (*Martes foina*) occur in this landscape.

Fox capture and GPS-collaring

We captured seven adult red foxes from October 2018 to January 2019 using five Victor soft catch #3 leg hold traps. Six individuals were captured in Chiktan and one from Hemis National Park. The animals were immediately collared with Sirtrack (Litetrack 150 iridium, weighing ~ 200 g) collars and released within 20 - 30 min at the place of capture. Animal handling, capture and release were approved by the Department of Wildlife Protection, 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 weighed and sexed before release (Table. 1).Weight was determined by weighing a researcher holding the fox and then substracting the researcher's weight. The collars were programmed to record GPS fixes at 15-min intervals and transmit the same at 3-h intervals. We chose a 15-min interval as previous studies recommend this time for calculating the daily distance travelled by animals (Musiani, Okarma & Jędrzejewski, 1998). The collars had an auto drop-off scheduled for 364 days and none of the foxes died during the study duration. Due to the 15-min fixes the battery lasted from 56 to 90 days for five individuals. The GPS fixes from F2 were most irregular and hence the battery lasted only for 56 days. For individuals M3 and M4, the collars were reprogrammed to take GPS fixes every 130-min intervals after one month to increase the battery life. These collars gave data for 198 and 212 days respectively. At the time of collaring, none of the individuals had pups. Later while tracking, F1 and F2 were sighted with pups in the month of April. The collaring process was conducted in winters which coincides with the breeding time of foxes in Trans-Himalayas.

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 consisted of 28,163 GPS fixes and 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 utilisation distribution and range tools (Wall, 2014). We used MCP and KDE methods as they are used widely to estimate home range size of red fox and allows comparison with other studies. 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. We used each of these different methods to evaluate the home ranges (95% contour) and core areas (50% contour) of each individual.

We calculated daily movements, 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 encountered two types of 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 $\leq$ 9.35 km/h (Fig. S.1). Since GPS fixes obtained from larger time intervals can affect the daily movement of animals, we also downsampled our data to estimate the reduction in movement. Most GPS telemetry studies have GPS fixes scheduled for time intervals of 1-hr or greater for longer battery life. However, the daily average movement may be greatly under-estimated at this time interval. Hence, to evaluate this effect of GPS fixes, we resampled our 15-min GPS fixes data to 30, 60 and 120-min time intervals and calculated the daily average movement. We did a one-sample t-test for evaluating the differences. Since for M3 and M4 individuals, 15-min GPS locations were obtained for the first 30 days, only these were used to examine the effect of down-sampling.

To assess habitat selection in relation to topography (ruggedness, elevation, and slope), environmental factor (distance to water) and anthropogenic disturbances (distance to road and human settlements), we used Integrated Step-Selection Functions (iSSF) from the amt package in R (Signer, Fieberg & Avgar, 2019). iSSF 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-mises distribution. We generated both true and random steps for 15-min 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) for 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, centred and screened for collinearity using Pearson's correlation coefficient with a threshold of |r| > 0.7. We performed an iSSF 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

Red fox showed high variation in the size of their home ranges and core area utilisation (Table. 2). The average BBMM home range (95% contour) was 22.40 ± 12.12 SD km^2 and the average core area (50% contour) was 1.87 ± 0.86 SD km^2. The smallest home range was for the individual F1 (3.81 km^2) whilst M1, M2, and F3 individuals utilised multiple core areas (Fig. S.2). The average female home range was lower (16.78 km^2, for F1 and F2 BBMM) as compared to males (25.22 km^2 , for M1, M2, M3,and M4 BBMM). However, due to the lower sample size and high variability amongst individuals, we could not significantly conclude the variation in home ranges across sexes. In our study, the average LoCoH and BBMM methods had a smaller estimation of home ranges (LoCoH 17.33 ± 15.29 SD km^2 and BBMM 22.40 ± 12.12 SD km^2) compared to MCP and kernel methods (MCP 43.24 ± 40.52 SD km^2 and kernal 23.20 ± 15.53 SD km^2).

Daily movement

The average daily movement of red fox was 13.28 ± 3.67 SD km/d (Table. 2). Individual F2 showed the highest daily average movement (20.92 km/d), and M4 had the least (10.54 km/d) (Fig. 2). The daily movement of the largest individual was 10.91 ± 7.69 SD km/d. The highest variation was observed for M3 individual (13.20 ± 14.67 SD km/d). The daily average movements of females was larger (15.58 km/d, n=3) as compared to males (11.56 km/d, n=4). The downscaling of data from 15-min GPS fixes to 2-h interval fixes significantly reduced the estimated daily average distances walked by red fox ($P < 0.05$, Table. S.1).

Habitat selection

Our land-use categories for habitat utilisation of red foxes were agriculture, barren, snow, alpine vegetation and others (Roy et al., 2015). The barren land is most prevalent in the Trans-Himalayan cold desert and all foxes exploited this land-use category. Compared to the random steps, the true steps of F1 were found more in agricultural land than other land-use categories, while F2 was mainly found in barren land (Fig. 3). M1 and M2 were present in agriculture and barren land . Similarly, M3 and M4 exploited agriculture and barren land, but also used areas with snow in higher proportions. F3 vixen in Hemis National Park selected barren land and alpine vegetation.

We found that topographic factors influenced the red fox habitat selection, and they selected lower elevations and less rugged terrain ($P < 0.001$, 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, this trend was non-significant. Except for F2 and F1, all individuals avoided roads and slopes ($P < 0.001$).

Discussion

Home range

We found high variability not only across different methods for home range estimation, but also amongst individuals. Across different methods for home range estimation, the highest variation was found for the individual M1 whose home range varied from 118.77 km^2 (95% MCP) to 8.97

km^2 (95% LoCoH). We found high core area for M2 (24.47 km^2 50% MCP) and home range for M1 (118.77 km^2 95% MCP). The MCP method is adversely affected when extreme locations are present and results in estimating larger home ranges. We speculate that this likely adds to the high values of home range estimation. However, for M2, the largest individual, its core area was found to overlap with the core areas of all other individuals. Thereby, traditional methods MCP and kernels utilisation distribution may be good for comparison with other studies but may overpredict the actual home ranges because of its exploratory behaviour. Since our study site consists of rugged terrains and the short time interval of GPS fixes for estimating daily average movement; we suspect that LoCoH and BBMM could predict the home range sizes better with lower standard deviations. Among these two methods, though the LoCoH method identifies steep slopes and inaccessible areas, BBMM can be concluded to be the most advanced method, considering the time for predicting movement possibilities.

Our collared individuals had high overlapping home ranges at 95% MCP (Fig. 1). The high amount of overlap could be inferred to the small area in which trapping was conducted at Chiktan. Nevertheless, the core areas had very little to no spatial overlap (50% MCP). The individual F1 consistently had the smallest estimated home range across different estimation methods, as compared to the other individuals. F1 and M2 were sighted together in several instances. Unfortunately, the den of this pair was inaccessible due to the dense seabuckthorn shrub. Additionally, due to the high anthropogenic food subsidy prevelant at the study site of Chiktan (Reshamwala et al., 2018; 2021), the foxes may have high tolerance and overlapping home ranges (Newdick, 1983).

The home ranges of individuals in our study varied from 3.81 to 32.93 km^2 (BBMM). 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 km² (MCP) in the Arctic or even more extensive which are determined majorly by the type of habitat (Sillero-Zubiri, Hoffmann & Macdonald, 2004). Such results are not uncommon and the home ranges of fox within the same area may often show wide variation. Similarly, in Illinois, U.S.A, the home range of red fox varied from less than 1 to > 35 km^2 (Gosselink et al., 2003).

Our study site is a high altitude cold desert with the presence of anthropogenic food subsidies (Reshamwala et al., 2018). There have been no studies pertaining to the home range sizes of red fox from the Trans-Himalayan region. But it is reported that at higher latitudes and altitudes, animals tend to have larger home ranges (Mattisson et al., 2013; Morellet et al., 2013). Recent study on red foxes living in the Arctic have reported their home ranges to be as large as 60-72 km^2 (Lai et al., 2022). Foxes living at higher elevations are reported to have four times more extensive home ranges than at lower elevations (Walton et al., 2017). In case of deserts, larger home ranges of red fox were reported in the arid Simpson Desert (Newsome, Spencer & Dickman, 2017). Contrarily, 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). On one hand the arid Trans-Himalayan cold desert with high elevation suggests larger home ranges, on the other hand the presence of anthropogenic food subsidies supports smaller home range. Hence, we speculate a mixed effect of both; the high elevation cold desert and the presence of anthropogenic food subsidies resulting in the variation of home range size.

F3 from our study, 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 found that 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

The average daily movement of red fox from our study was 13.28 ± 3.67 SD km/d and ranged between 10.54 km/d and 20.92 km/d (Table. 2). Only one study has reported the average daily movement of red fox, which was 4.8 to 16 km/d with a mean of 9.4 ±3.7 km/d (Carter, Luck & McDonald, 2012). However, the VHF telemetry used in the study has its own limitations such as continuous monitoring, inaccessible areas, monitoring multiple individuals, following nocturnal animals etc. The average daily movement travelled by arctic fox (*Vulpes lagopus*) is comparatively well studied and is reported to be 51.9 ± 11.7 km/d (Poulin, Clermont & Berteaux, 2021). The average daily movement in the case of wolves showed a great variation, ranging from 17 to 38 km/d (Ciucci et al., 1997). It is reported that the daily average movement travelled during the mating season for wolves may go as high as 34 km/d (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 (Fig. 2).

We found that our daily average movement data was positively skewed. On most occasions we observed smaller daily average distances, and a few instances with very high movements. The individual M3 showed the highest daily movement of 81.98 km and 79.64 km on two occasions. F2 also showed high movements of 67.61 and 53.54 km at two instances. Foxes with smaller home ranges may not necessarily travel less. F1 had a very small home range (3.81 km^2, BBMM) as compared to other individuals, but its average daily movement was 11.10 ± 7.72 SD km/d. Daily distance travelled by individuals having a smaller home range maybe the same in comparison 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).

It is 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 estimate of daily movement of red fox significantly ($P < 0.01$, Table S.1). The daily average movement of foxes reduced from 17.76 ± 8.45 SD km/d to 14.96 ± 7.71 SD km/d on downsampling the data from 15-min to 30-min time interval. Further down-sampling resulted in higher under-estimates of daily average movement (Table S.1). While bigger time intervals may lead to an under-estimate of daily movements, fixes at a very small time interval may overestimate the average daily distance travelled due to location error (Poulin, Clermont & Berteaux, 2021).

Although we found the daily average movement for F2 to be as high as 20.92 ± 15.12 SD km/d, and as low as 10.54 ± 10.79 SD km/d for M4 individual, 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). 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 ± 20.34 SD km/d, Table S.1). 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 parallely reported in red fox where foxes have travelled over a distance of 132-1036 km in a short period (Walton et al., 2018).

Data on average speeds travelled by red fox are entirely lacking, but the average speed with which wolves travel ranges from 0.8 to 1.1 km/h (Burkholder, 1959; 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 ranging 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). Moreover, studies with a greater sample size are warranted to enhance our knowledge of maximum speed of red fox.

Habitat selection

Multiple land-use categories were exploited by different individuals in our study. Most of the area at our study site is barren due to the arid Trans-Himalayan conditions. The high elevation areas (> 6000 m above sea level) are covered with snow all throughout the year. Agricultural land is scarce and present near the river valleys. We found that the dominant larger foxes, i.e. F1, M1 and M2, exploited agricultural land the most as compared to any other land-use category (Fig. 3). Whereas, F2, M3 and M4 which were smaller in size were found in barren and snow-covered land (Table. 1). Since the foxes had overlapping home ranges, we suspect that the dominant individuals may not completely exclude other individuals from their home ranges but prefer to stay in the resource-rich areas such as agriculture. F3 in Hemis National Park was found in both barren and alpine vegetation.

Red fox are known for their highly adaptive behaviour and often show large variations in their habitat selection depending upon various factors (Walton et al., 2017; Walton, 2020). To understand these variations, step selection modelling at an individual level is preferred over the population level (Thurfjell, Ciuti & Boyce, 2014). Further, our sample size of seven individuals also advocates for individual modelling. In our study, except for F1 and F2, all other individuals were positively associated with human settlements. Red fox in the Trans-Himalayan landscape has 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). We found that all individuals were positively associated with water. 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 also found that red fox significantly preferred lower elevations and lesser rugged terrain. Except for F1 and F2, all other individuals significantly avoided slopes. Animals are known to avoid higher elevations, steep slopes and rugged terrain, which are known to be energetically high in cost (Filla et al., 2017; Fullman, Joly & Ackerman, 2017). During our radio-collaring duration, these individuals were adults without pups. Later, from our field observations, we found both F1 and F2 to be breeding vixens and presume that they avoided human settlements and preferred slopes compared to others to avoid anthropogenic disturbances.

The role of spatial ecology in conservation of a species is well known (Allen & Singh 2016). Movement information of a species is important for the prioritisation of areas for conservation (Carwardine et al., 2012). While the movement within the home ranges is crucial for understanding the habitat suitability and preferences (Lu et al., 2012), the home range sizes and shapes are essential for managers to understand the scale of management (Schwartz, 1999). Our study provides a brief overview of the spatial ecology of red fox in the Trans-Himalayan cold desert. From our movement data of GPS collared individuals we could conclude that they preferred lesser rugged terrains and lower elevations in this region. In addition to home ranges, we provide insights on the daily movements and the need for having short time interval for calculating daily movements. The movement of species also explores additional mobile agent-based ecosystem services such as pollination and seed dispersal (Kremen et al., 2007; Nathan and Muller-landau, 2000). Hence, the movement ecology can aid in understanding the ecosystem functioning and ladscape management (Mitchell, Bennett & Gonzalez et al., 2013).

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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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Supplementary

Figure S.1 Distribution of speed data from trajectory details of all red fox individuals and the cut-off line (in red) at 9.35km/hr to eliminate errors.

Figure S.2 BBMM home ranges of red fox individuals and their core areas (red).
**Scales for individuals are different.*

Figure S.3 Displacement of individuals from their collared location to each GPS fix.

**Trendline of F3 in green showing continuous displacement of this individual.*

Table S.1 Effect of down-sampling GPS fixes from 15-min to 2-hr time interval on the estimated daily movement of red fox and t-test results.

Figure 1

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

(A) Location of the study sites in India. (B) 95% MCP home ranges of six red foxes at Chiktan, Kargil. (C) 95% MCP home range of a female at Hemis National Park.

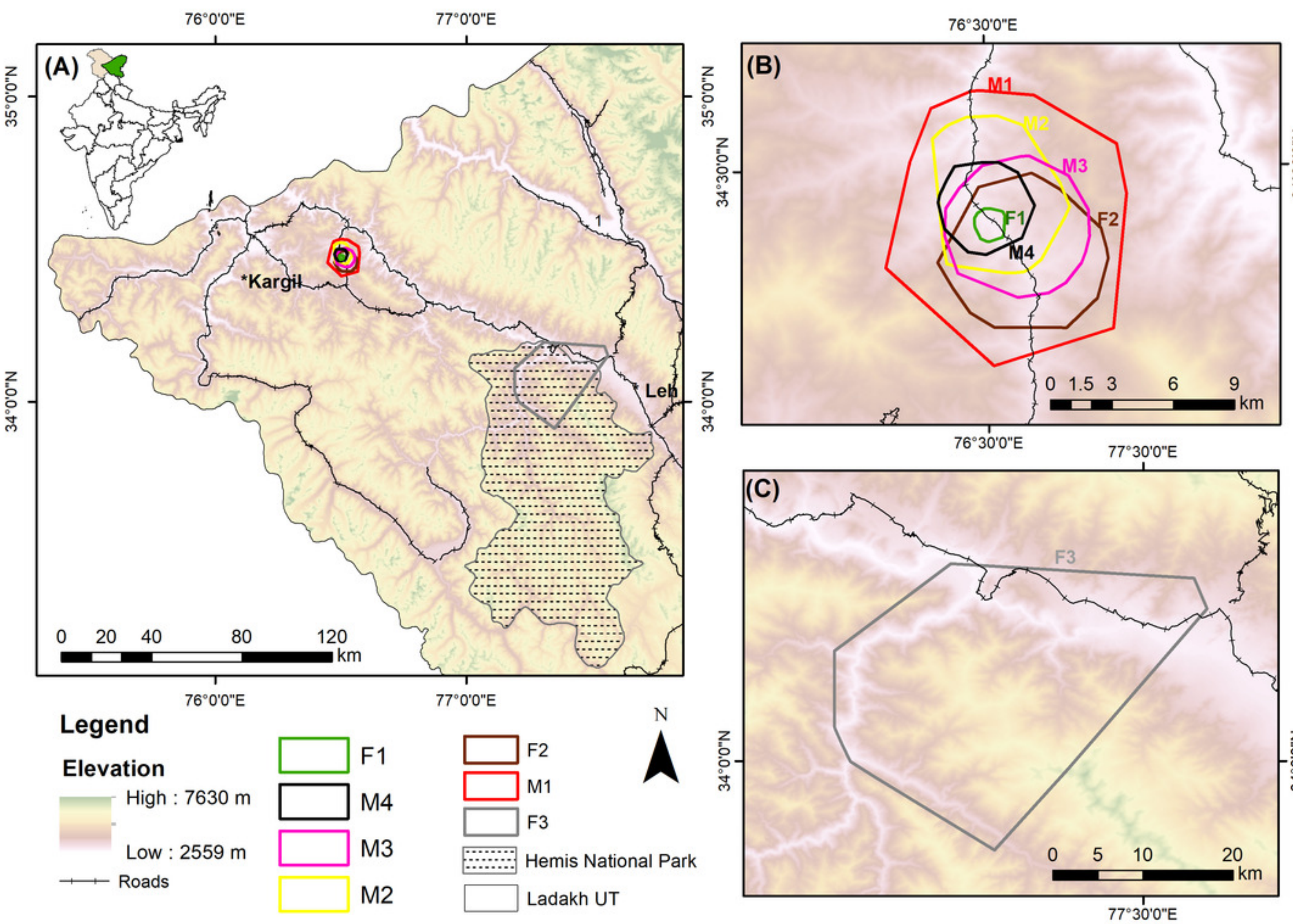

Figure 2

Violin plots showing the estimated daily movement per day of red fox in the Trans-Himalayan cold desert, Ladakh, India.

**Numbers below the violin indicate the number of days an individual was collared. Each dot in the violin plot represents the distance walked in a day (Female=F1,F2,F3 Male=M1,M2,M3,M4)*

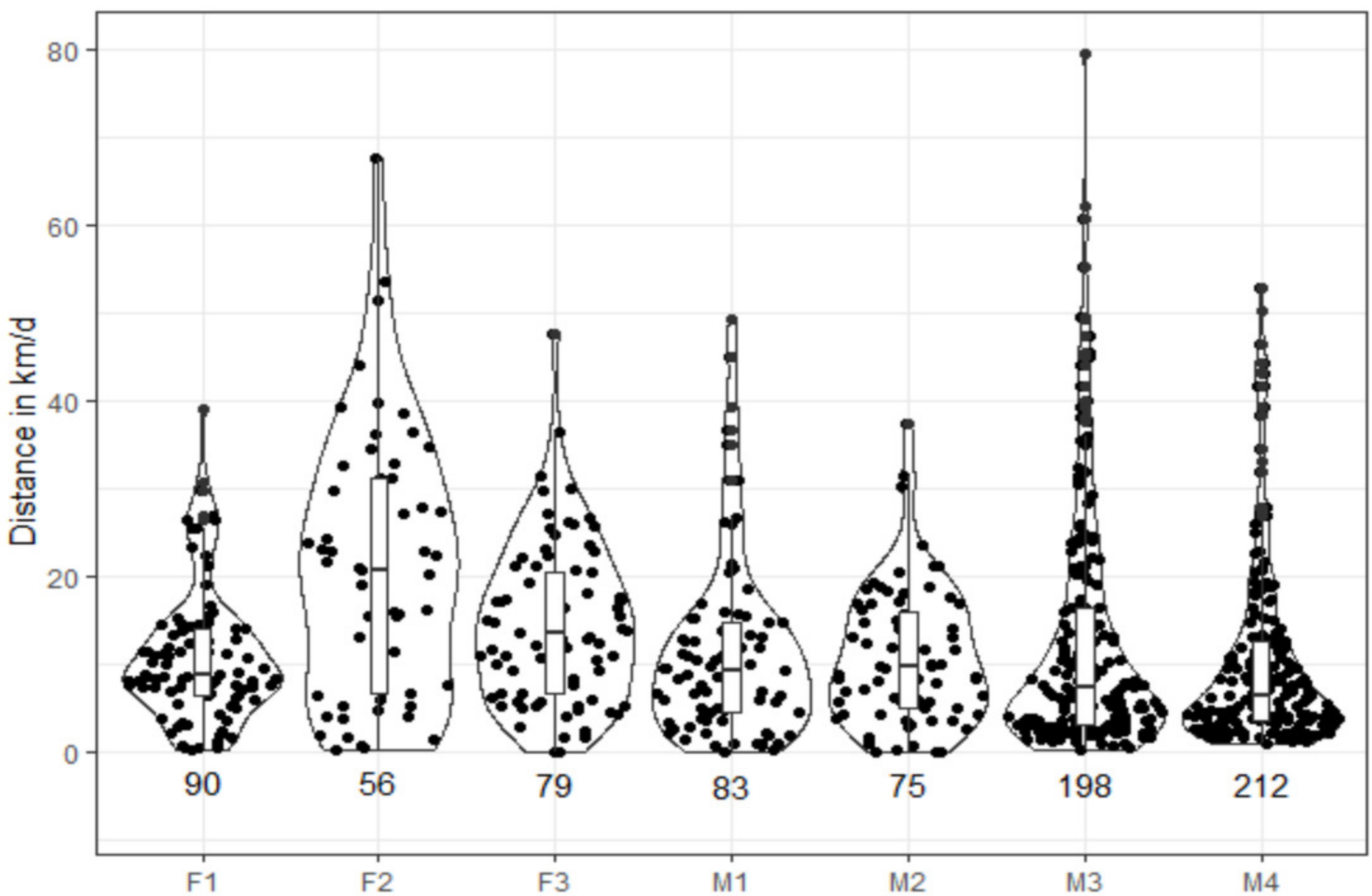

Figure 3

Percentage of different land-use land cover categories utilised by different red fox individuals in the Trans-Himalayan cold desert, Ladakh, India.

**TS = True actual steps of red fox, RS = random steps generated by the step selection function*

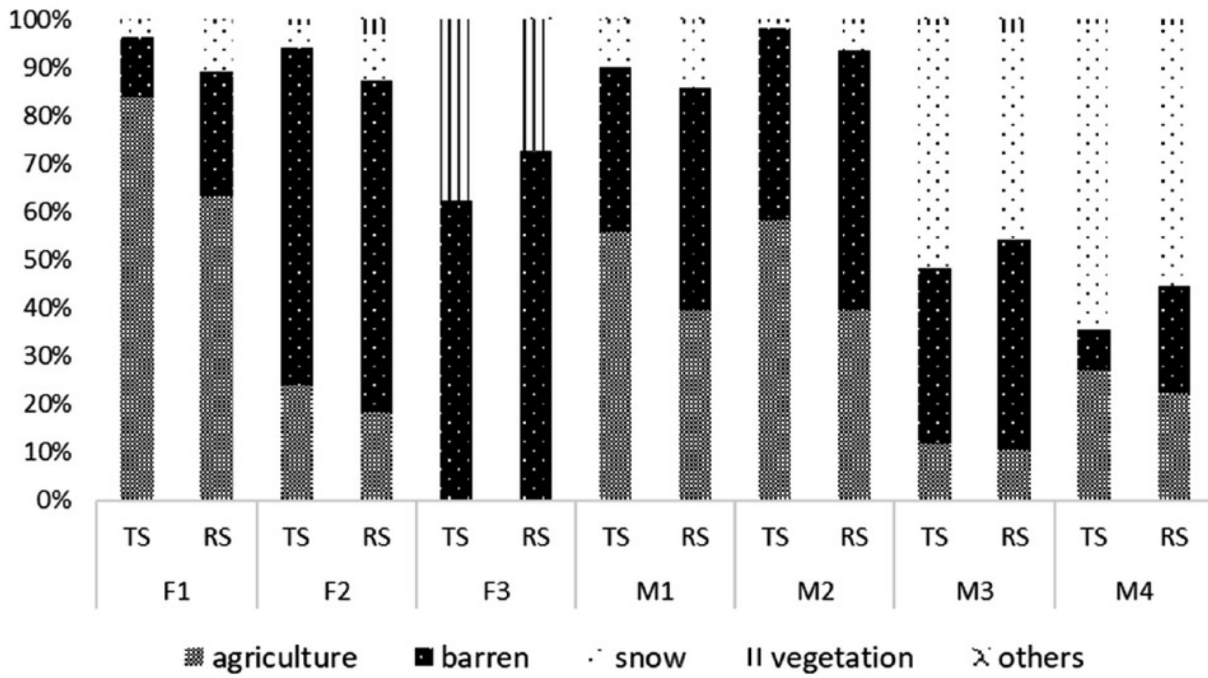

Figure 4

Step-Selection function beta coefficients of different red fox individuals for topographic factors (ruggedness, elevation and slope), environmental factor (distance to water) and anthropogenic factors (distance to road and human settlements)*

**Beta coefficients derived from step selection function analysis. Positive values show preference and negative values show avoidance*

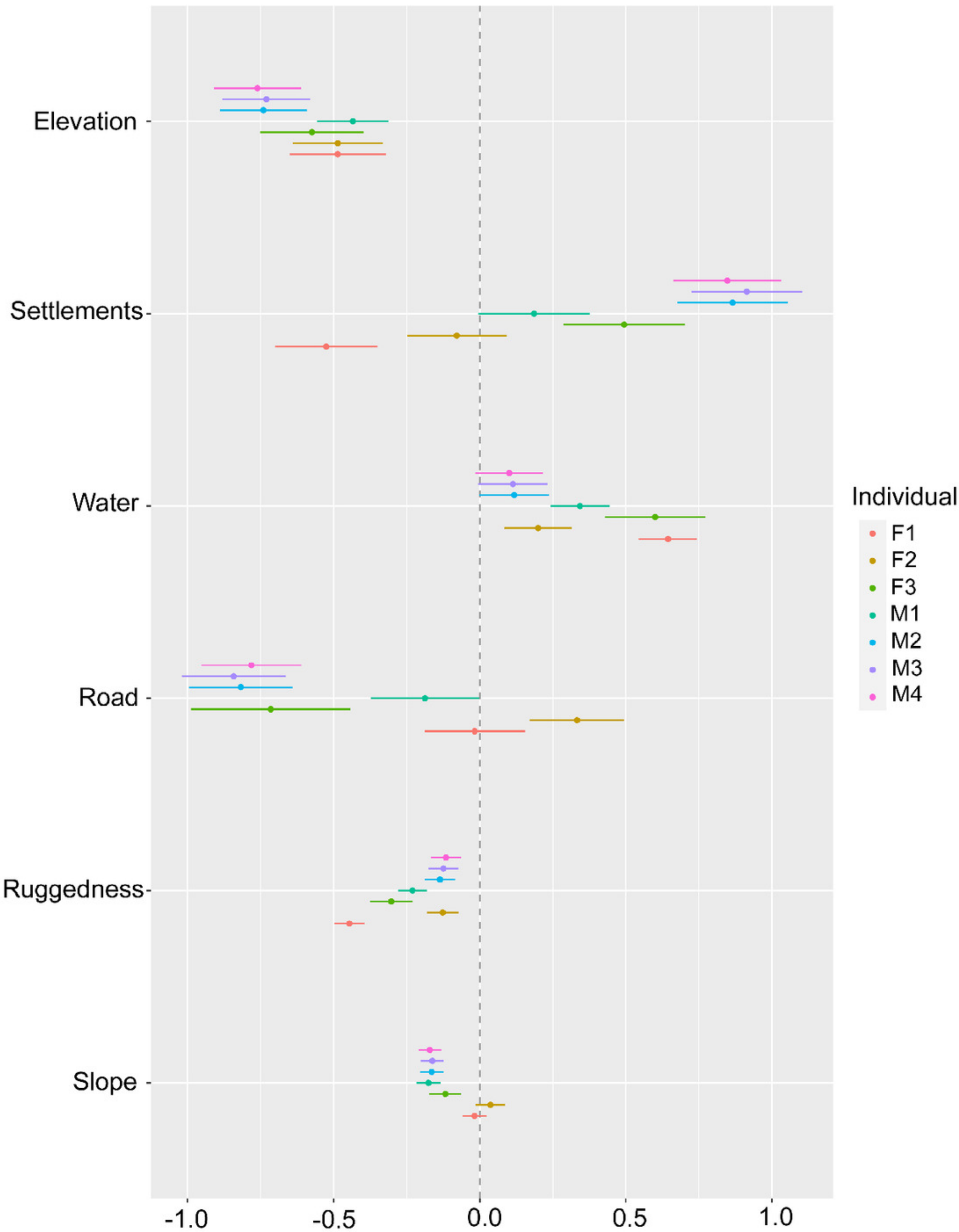
Elevation
Settlements
Water
Road
Ruggedness
Slope
-1.0
-0.5
0.0
0.5
1.0
Individual
F1
F2
F3
M1
M2
M3
M4

Table 1(on next page)

Details of GPS-collared individuals, date of collaring, active days, and the number of locations 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	6.0	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)

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

Individual	MCP (km²)		Kernel (km²)		LoCoH (km²)		BBMM (km²)		Daily average movement (km/d ±SD)
	Core area (50%)	*Home Range (95%)*	*Core area (50%)*	*Home Range (95%)*	*Core area (50%)*	*Home Range (95%)*	*Core area (50%)*	*Home Range (95%)*	
F1	0.14	1.95	0.22	1.62	0.05	1.17	0.55	3.81	11.10 (7.72)
F2	0.36	45.99	1.27	41.59	0.32	37.57	2.33	29.75	20.92 (15.12)
M1	1.74	118.77	1.50	18.49	0.18	8.97	1.93	31.02	11.61 (10.38)
M2	24.47	39.36	4.02	26.65	0.26	10.63	2.62	26.19	10.91 (7.69)
M3	1.01	37.50	1.57	38.83	0.43	35.57	2.69	32.93	13.20 (14.67)
M4	0.51	15.90	0.77	12.07	0.36	10.11	1.15	10.75	10.54 (10.79)
F3	-	-	-	-	-	-	-	-	14.72 (9.10)
Average (± SD)	**4.70 (9.69)**	**43.24 (40.52)**	**1.55 (1.30)**	**23.20 (15.53)**	**0.26 (0.13)**	**17.33 (15.29)**	**1.87 (0.86)**	**22.40 (12.12)**	**13.28 (3.67)**