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

Hussain S Reshamwala [1] , **Pankaj Raina** [2] , **Zehidul Hussain** [1] , **Shaheer Khan** [1] , **Rodolfo Dirzo** [3] , **Bilal Habib** [Corresp. 1]

[1] Wildlife Institute of India, Dehradun, Uttarakhand, India

[2] Department of Wildlife Protection, Leh, Ladakh Union Territory, India

[3] Stanford University, Stanford, United States

Corresponding Author: Bilal Habib
Email address: bh@wii.gov.in

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), local convex hull (LoCoH) and Brownian-bridge movement model (BBMM). We analysed the daily movement and assessed 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 estimated average daily movement of red fox was 17.76 ± 8.45 SD km/d (range 10.91-34.22 km/d). Red fox significantly selected lower elevations with less rugged terrain 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 ecosystem functioning and landscape management.

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

2 **desert**

4 **Authors:** Hussain Saifee Reshamwala[a], Pankaj Raina[b], Zehidul Hussain[a], Shaheer Khan[a],

5 Rodolfo Dirzo[c], Bilal Habib[a*]

7 Author affiliations

8 [a] Department of Animal Ecology and Conservation Biology, Wildlife Institute of India, Dehradun, India

9 [b] Department of Wildlife Protection, Leh, Ladakh Union Territory, India

10 [c] Department of Biological Sciences, Stanford University, Stanford, California, USA

13 * Corresponding author
14 Dr. Bilal Habib
15 Scientist-E
16 Department of Animal Ecology and Conservation Biology
17 Wildlife Institute of India,
18 Chandrabani, Dehradun-248001, Uttarakhand, India
19 Ph no-0135-2646283
20 Mail-ID- bh@wii.gov.in

22 **Abstract**

23 Red fox (*Vulpes vulpes*) is the most widespread wild carnivore globally, occupying diverse

24 habitats. The species is known for its adaptability to survive in dynamic anthropogenic

25 landscapes. Despite being one of the most extensively studied carnivores, there is a dearth of

26 information on red fox from the Trans-Himalayan region. We studied the home range sizes of

27 red fox using the different estimation methods: minimum convex polygon (MCP), kernel density

28 estimator (KDE), local convex hull (LoCoH) and Brownian-bridge movement model (BBMM).

29 We analysed the daily movement and assessed the habitat selection with respect to topographic

30 factors (ruggedness, elevation and slope), environmental factor (distance to water) and

31 anthropogenic factors (distance to road and human settlements). We captured and GPS-collared

32 six red fox individuals (3 males and 3 females) from Chiktan and one female from Hemis

33 National Park, Ladakh, India. The collars were programmed to record GPS fixes every 15-min.

34 The average BBMM home range estimate (95% contour) was 22.40 ± 12.12 SD km^2 (range 3.81-

35 32.93 km^2) and the average core area (50% contour) was 1.87 ± 0.86 SD km^2 (range 0.55-2.69

36 km^2). The estimated average daily movement of red fox was 17.76 ± 8.45 SD km/d (range 10.91-

37 34.22 km/d). Red fox significantly selected lower elevations with less rugged terrain and were

38 positively associated with water. This is the first study in the Trans-Himalayan landscape which

39 aims to understand the daily movement of red fox at a fine temporal scale. Studying the

40 movement and home range sizes helps understand the daily energetics and nutritional

41 requirements of red fox. Movement information of a species is important for the prioritisation of

42 areas for conservation and can aid in understanding ecosystem functioning and landscape

43 management.

44

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

46

47 **Introduction**

48 One of the basic fundamentals for understanding an animal's ecology is its home range size,

49 which is defined as an individual's area where movement occurs for normal activities like

50 gathering food, mating and raising the young (Burt, 1943). The causes of these movements and

51 their consequences are of great significance for understanding several aspects of an animal's

52 behaviour like dispersal (Small & Rusch, 1989), social interactions (Minta, 1993), space-use

53 (Kenward et al., 2001) and population distributions (Turchin, 1991). Home ranges incorporate all

54 individual's movements and depend upon species behavioural and physiological responses to the

55 environment (Horne et al., 2007; Vanak & Gompper, 2010). A mosaic of different habitat types

56 is required to fulfil various life requisites, and these are reflected in the animal's movement at

57 larger spatial scales (Ims, 1995; Benson & Chamberlain, 2007). Intra and inter-specific

58 interactions in terms of competition, predation or facilitation also determine animal spatial

59 distributions. Estimating the continuous movement of an animal is a powerful tool to quantify an

60 animal's daily movement and home-range size (Turchin, 1998). However, in nature, it is

61 impossible to visually monitor animals continuously, especially in rugged terrain with adverse

62 climatic conditions. The advancement of GPS telemetry is now commonly used to understand

63 fine-scale movement and space use. It aids in continuous monitoring of animals over large

64 distances and is particularly helpful for species that are elusive, nocturnal, or present in areas that

65 are otherwise not accessible to researchers.

66

67   Red fox (*Vulpes vulpes*) is the most widespread wild carnivore in the world (Hoffmann &

68   Sillero-Zubiri, 2016) and is known for its adaptability to survive in all sorts of environments

69   (Geffen et al., 1996). The generalist and opportunistic nature of red fox in terms of their diet,

70   habitat and movement patterns have contributed to its success (Geffen et al., 1996; Walton et al.,

71   2017; Reshamwala et al., 2018). However, such mid-sized carnivores are also facing competition

72   because of their broad diet, which overlaps with the energetic needs of myriad other sympatric

73   competitors (Caro & Stoner, 2003). For example, a previous study reports a high diet-overlap of

74   red fox with wolves and dogs from the Trans-Himalayan region (Reshamwala et al., 2021). As a

75   result, they may have to make trade-offs either temporally or spatially (Schuette et al., 2013).

76   Also, compared to the large carnivores, there have been fewer studies of meso-carnivores.

77

78   In this study, we first explore the home range sizes of red fox as estimated by different methods.

79   We then estimate the average daily movement and assess the habitat use and selection in the arid

80   Trans-Himalayan cold desert.

81

82   **Materials and methods**

83   **Study area**

84   The study was conducted in Ladakh, which belongs to the northwestern Trans-Himalayan region

85   of India (Fig. 1). The area is characterised by dry rugged terrain with precipitation amounting to

86   only 100 mm/year (Bharti et al., 2016). The cold desert has an elevation of 3000 to 7000 m

87   above sea level and harsh winter temperatures, which go down to -30 °C. The vegetation is very

88   sparse and patchy, with alpine meadows in certain areas (Kachroo & Dhar, 1977). The place is

89   also sparsely populated with a human density of 4.9 individuals/km^2 (Chandramouli, 2013).

90 Foxes were GPS collared at two sites: Chiktan and Rumbuck. Chiktan is a small hamlet about 80

91 km from the city of Kargil. The people belong to the Muslim community and due to higher non-

92 vegetarian food consumption, there is more anthropogenic food subsidy and greater fox

93 abundance in this area as compared to other parts of Ladakh (Reshamwala et al., 2018,

94 Reshamwala et al., 2021). Rumbuck is a village with few scattered human settlements within

95 Hemis National Park, and the people belong to the Buddhist community. People are primarily

96 associated with agriculture or agro-pastoralism and are sometimes involved with tourism,

97 especially in Hemis National Park (Reshamwala et al., 2021). Besides red fox, snow leopard

98 (*Panthera uncia*), wolf (*Canis lupus*), Ladakh urial (*Ovis vignei*), blue sheep (*Pseudois nayaur*),

99 ibex (*Capra ibex*), weasel (*Mustela altaica*), and stone marten (*Martes foina*) occur in this area.

100

101 **Fox capture and GPS-collaring**

102 We captured seven adult red foxes from October 2018 to January 2019 using five Victor soft

103 catch #3 leg hold traps. Six individuals were captured in Chiktan and one in Hemis National

104 Park. The animals were immediately collared with Sirtrack collars (Litetrack 150 iridium,

105 weighing ~ 200 g) and released within 20-30 min at the place of capture. Animal handling,

106 capture and release were approved by the Department of Wildlife Protection, Jammu and

107 Kashmir (CCFWL\Permission\2016\575-76). No drugs were administered to the animals, and the

108 methodology was refined to ensure minimum stress, handling time, and injury to the captured

109 individual, approved by Wildlife Institute of India, animal ethics committee. The foxes were

110 weighed and sexed before release (Table 1). Weight was determined by weighing a researcher

111 holding the fox and then subtracting the researcher's weight. The collars were programmed to

112 record GPS fixes at 15-min intervals and transmit the same at 3-h intervals. We chose a 15-min

113   interval as previous studies recommend this time for calculating the daily distance travelled by

114   animals (Musiani, Okarma & Jędrzejewski, 1998). The collars had an auto drop-off scheduled

115   for 364 days and none of the foxes died during the study duration. Due to the 15-min fixes the

116   battery lasted from 56 to 90 days for five individuals. The GPS fixes from F2 were most irregular

117   and hence the battery lasted only 56 days. For individuals M3 and M4, the collars were

118   reprogrammed to take GPS fixes at 130-min intervals after one month to increase the battery life.

119   These collars gave data for 198 and 212 days, respectively. At the time of collaring, none of the

120   individuals had pups. Later while tracking, F1 and F2 were sighted with pups in the month of

121   April. The collaring process was conducted in winter, which coincides with the breeding time of

122   foxes in Trans-Himalayas.

123

124   **Data analysis**

125   The data from seven red foxes included 31,261 GPS fixes and were filtered in ArcGIS 9.2.1 with

126   the ArcMET filter tools (Wall, 2014). The filtered data consisted of 28,163 GPS fixes and

127   excluded fox locations that exceeded 48 km/h as this is the highest speed of the red fox

128   (Haltenorth, & Roth, 1968). Home ranges were estimated using minimum convex polygon

129   (MCP), kernel density estimator (KDE), local convex hull (LoCoH) and Brownian-bridge

130   movement model (BBMM) from the ArcMET utilisation distribution and range tools (Wall,

131   2014). We used MCP and KDE methods as they are used widely to estimate home range size of

132   red fox, allowing comparison with other studies. Rugged terrain often force animals to follow a

133   fixed path. In such areas, LoCoH gives a reliable home range for animals as this method can

134   identify rigid boundaries such as rivers, lakes or otherwise inhospitable terrain (Getz et al.,

135   2007). The BBMM is the most recent method which incorporates the time and probability of

136   movement; it thereby models the animal movements and helps determine animal home ranges

137   more robustly (Horne et al., 2007). Since each method has its own advantages, we estimated

138   home ranges using all of these methods. We used each of these different methods to evaluate the

139   home ranges (95% contour) and core areas (50% contour) of each individual. We also calculated

140   the net square displacement from our collaring location using the path tool details to identify

141   dispersing individuals.

142

143   We calculated daily movements, i.e., the sum of displacement in one day, with the help of

144   trajectory details from the ArcMET path statistics tool in ArcGIS. We considered the daily

145   movement as the sum of linear distances obtained from each consecutive GPS fix from the first

146   location of midnight and the last location of the same day. For M3 and M4 individuals, we use

147   only the 15-min data for estimating the daily movement. While estimating the daily movements,

148   we found an abrupt change in trajectories in certain instances. On inspecting the spatial data

149   further, we could identify irregular spikes in the speed of these trajectories. Hence to remove

150   these high movements, we truncated data above 98% (Fig. S1). It is possible that some of these

151   data were actual movements, but to avoid errors while estimating daily movement, we have

152   removed them from the analysis.

153

154   Since GPS fixes obtained from larger time intervals can affect the estimation of daily movement

155   of animals, we also down-sampled our data to estimate the reduction in the movement. Most

156   GPS telemetry studies have GPS fixes scheduled for time intervals of 1-h or greater for longer

157   battery life. However, the daily average movement may be greatly under-estimated at this time

158   interval (Poulin, Clermont & Berteaux, 2021). Hence, to evaluate this effect of GPS fixes, we

159   resampled our 15-min GPS fixes data at 30, 60 and 120-min time intervals and calculated the

160   daily average movement. We used one-sample t-test to evaluate the differences.

161

162   To understand habitat use, we assessed the percentage of steps in each land cover category for

163   every individual. We used the Biodiversity Information System portal of the Indian Institute of

164   Remote Sensing (http://bis.iirs. gov.in) for land cover data which consisted of nine classes (Roy

165   et al., 2015). We then re-classified land cover data into agriculture, vegetation, barren and snow.

166   Agriculture consisted of cultivated land, whereas vegetation consisted of moist alpine scrub, dry

167   alpine scrub, moist alpine pasture and dry alpine pasture. Barren land consists of no vegetation

168   and snow refers to areas covered with permanent snow.

169

170   For habitat selection in relation to topography (ruggedness, elevation, and slope), an

171   environmental factor (distance to water) and anthropogenic disturbances (distance to road and to

172   human settlements), we used integrated step-selection functions (iSSF) from the amt package in

173   R (Signer, Fieberg & Avgar, 2019). iSSF jointly estimates habitat selection and animal

174   movement parameters (e.g., step length and turn angle) by relaxing the implicit assumption that

175   these are independent (Signer, Fieberg & Avgar, 2019). This method assesses habitat preference

176   in animals by comparing each used step (i.e., movement between two consecutive GPS fixes) to

177   those of randomly placed steps (i.e., that animal could have taken) within the movement path.

178   The random steps are generated using distances sampled from a gamma distribution fitted to the

179   empirical step length distribution and random turning angles by von Misses distribution. We

180   generated both true and random steps for 15-min intervals for all the individuals. We produced

181 10 random steps per used step, based on the recommendations of Thurfjell et al. (2014). At the

182 end of each step, we extracted environmental covariates. All variables were scaled, centred and

183 screened for collinearity using Pearson's correlation coefficient with a threshold of $|r| > 0.7$. We

184 performed an iSSF using conditional logistic regression for the variables: - distance to road,

185 distance to water, distance to human settlements, ruggedness, elevation, and slope. We

186 performed the step selection modelling at an individual level as it is preferred over the

187 population level (Thurfjell, Ciuti & Boyce, 2014). Further, our sample size of seven individuals

188 also advocates for individual modelling.

189

190 **Results**

191 **Home range**

192 The red foxes we observed showed high variation in the size of their home ranges and core areas

193 (Table 2). We also observed overlapping home ranges at Chiktan. F3 showed large displacement

194 from its initial place of collaring (Fig. S2), suggesting that it was either nomadic or dispersing.

195 Similar displacements were not shown by any other individual. Because it is important not to

196 include nomadic foxes while calculating home ranges (Meia & Weber, 1995), we excluded F3

197 from our home range calculations. The average BBMM home range (95% contour) was $22.40 \pm$

198 12.12 SD km^2 and the average core area (50% contour) was 1.87 ± 0.86 SD km^2. The smallest

199 home range was for individual F1 (3.81 km^2) whilst M1, M2, and F3 utilised multiple core areas

200 (Fig. S3). The average female home range was smaller (16.78 km^2, BBMM) than that of males

201 (25.22 km^2, BBMM). However, the difference between sexes was not statistically significant,

202 probably due to the limited sample size and high variability among individuals. In our study, the

203 average LoCoH and BBMM methods had a smaller estimated home ranges (LoCoH 17.33 $\pm$

204 15.29 SD km^2 and BBMM 22.40 ± 12.12 SD km^2) than MCP method (MCP 43.24 ± 40.52 SD

205 km^2).

206

Daily movement

208 The estimated average daily movement of red fox was 17.76 ± 8.45 SD km/d (Table 2). The

209 daily average movements of males were larger (19.39 ± 10.87 km/d, n=4) than those of females

210 (15.58 ± 4.96 km/d, n=3). Individual M3 showed the highest variation and average daily

211 movement (34.22 ± 20.85km/d). The daily movement of our largest individual M2, was least

212 (10.91 ± 7.69 SD km/d, Fig. 2). The downscaling of data from 15-min GPS fixes to 2-h interval

213 fixes significantly reduced the estimated daily average movements ($P < 0.05$, Table S1).

214

Habitat use and selection

216 The barren land is most prevalent in the Trans-Himalayan cold desert and all foxes exploited this

217 land cover category. The individual F1 was found more in agricultural land (83.65%) than other

218 land-use categories, while F2 was mainly found in barren land (70.14%). M1 and M2 were

219 present in agriculture and barren land. Similarly, M3 and M4 exploited agriculture and barren

220 land, but also used areas with snow in higher proportions (50.47% and 63.71%, respectively). F3

221 vixen in Hemis National Park used only barren land (62.32%) and alpine vegetation (37.67%),

222 respectively (Fig. 3).

223

224 For habitat selection, we found the red fox selected lower elevations and less rugged terrain ($P <$

225 0.001, Fig. 4). With respect to human settlements, only F1 showed significant negative selection

226 (P < 0.001), while F3, M2, M3 and M4 selected to be near human settlements (P < 0.01).

227 Individuals F2 and M1 did not exhibit significant selection for or avoidance of human

228 settlements. The red fox tended to select for water bodies. However, for M3 and M4 individuals,

229 this trend was non-significant. Except for F2 and F1, all individuals avoided roads and slope (P <

230 0.001).

231

232 **Discussion**

233 **Home range**

234 We found high variability not only across different methods for home range estimation, but also

235 amongst individuals. Across different methods for home range estimation, the highest variation

236 was found for the individual M1 whose home range varied from 118.77 km^2 (95% MCP) to 8.97

237 km^2 (95% LoCoH). We also found the largest home range for M1 (118.77 km^2 95% MCP) while

238 the largest core area was found for M2 (24.47 km^2 50% MCP). The MCP method is adversely

239 affected by extreme locations resulting in larger home range estimates. However, the core area of

240 M2, the largest individual, overlapped with the core areas of all other individuals. The traditional

241 methods MCP and kernels utilisation distribution allow comparisons between studies but may

242 overpredict the actual home ranges because of exploratory behaviour. Since our study site

243 consists of rugged terrain and we used short interval between GPS fixes, LoCoH and BBMM are

244 likely to be better methods for home range estimation. The LoCoH method identifies steep

245 slopes and inaccessible areas while BBMM incorporates space, time and animal-specific

246 parameters or habitat (Walter, 2015), which accounts for highly autocorrelated movement

247 locations.

248

249 Our collared individuals had extensively overlapping home ranges at 95% MCP (Fig. 1). The

250 high amount of overlap could be related to the small area in which trapping was conducted at

251 Chiktan. However, the core areas had very little to no spatial overlap (50% MCP). The individual

252 F1 consistently had the smallest estimated home range across different methods as compared to

253 the other individuals. F1 and M2 were sighted together in several instances. Unfortunately, the

254 den of this pair was inaccessible due to the dense seabuckthorn (*Hippophae spp.*) shrub.

255 Additionally, due to the high anthropogenic food subsidy prevalent at the study site of Chiktan

256 (Reshamwala et al., 2018; 2021), the foxes may have a high tolerance and overlapping home

257 ranges (Newdick, 1983).

258

259 The home range estimates using the BBMM method varied from 3.81 to 32.93 km². The home

260 range sizes of red fox are known to have significant variations ranging from as small as 0.40 km²

261 in urban areas of Oxford to as large as 40 km² (MCP) in the Arctic or even more extensive which

262 are determined majorly by the type of habitat (Sillero-Zubiri, Hoffmann & Macdonald, 2004).

263 Such results are not uncommon and the home ranges of fox within the same area may often show

264 wide variation. Similarly, in Illinois, U.S.A, the home range of red fox varied from less than 1 to

265 > 35 km² (Gosselink et al., 2003).

266

267 Our study site is a high altitude cold desert with the presence of anthropogenic food subsidies.

268 There have been no studies pertaining to the home range sizes of red fox from the Trans-

269 Himalayan region. However, at higher latitudes and altitudes, animals tend to have larger home

270 ranges (Mattisson et al., 2013; Morellet et al., 2013). A recent study on red foxes living in the

271 Arctic reported home ranges as large as 60-72 km² (Lai et al., 2022). Foxes living at higher

272 elevations are reported to have four times more extensive home ranges than at lower elevations

273 (Walton et al., 2017). In case of deserts, larger home ranges of red fox were reported in the arid

274 Simpson Desert (Newsome, Spencer & Dickman, 2017). In contrast, the use of smaller home

275 ranges by medium-sized canids near human settlements has also been reported (Coman,

276 Robinson & Beaumont, 1991; Saeki, Johnson & Macdonald, 2007; Rotem et al., 2011). In areas

277 with high human impact and food availability in abundance, the home ranges of red fox tends to

278 be smaller (Main et al., 2020; Newdick, 1983). On one hand, the arid Trans-Himalayan cold

279 desert with high elevation suggests larger home ranges. On the other hand, the presence of

280 anthropogenic food subsidies may result in a smaller home range. In the case the foxes we

281 studied, the two factors could together explain the observed high variation in home range sizes.

282

283 **Daily movement**

284 The estimated average daily movement of red fox in our study was 17.76 ± 8.45 SD km/d and

285 ranged between 10.91 km/d and 34.22 km/d (Table 2). A study has reported the average daily

286 movement of red fox, which was 4.8 to 16 km/d with a mean of 9.4 ±3.7 km/d (Carter, Luck &

287 McDonald, 2012). Another study has also reported similar daily movements of 3.9-12 km/day

288 (Meia & Weber 1995). However, the VHF telemetry used in these studies has limitations such as

289 continuous monitoring, inaccessible areas, monitoring multiple individuals, following nocturnal

290 animals, etc. The average daily movement travelled by arctic fox (*Vulpes lagopus*) has been

291 comparatively well studied and is reported to be 51.9 ± 11.7 km/d (Poulin, Clermont & Berteaux,

292 2021). The average daily movement of wolves showed a great variation, ranging from 17 to 38

293   km/d (Ciucci et al., 1997). The daily average movement of wolves travelled during the mating

294   season may go as high as 34 km/d (Jedrzejewski et al., 2001). During the breeding season, male

295   lynx frequently move longer distances and at greater speeds to increase their chances of mating

296   (Schmidt, 1999). Since our data collection period coincides with the breeding time of red fox, we

297   suspect M3 and M4 to have made similar extended forays (Fig. 2).

298

299   We found that our estimated daily average movement data were positively skewed. On most

300   occasions, we observed small daily average distances, but there were a few instances of very

301   high movements. The individual M3 showed the highest daily movement of 81.98 km and 79.64

302   km on two occasions. F2 also showed two events with high movements of 67.61 and 53.54 km.

303   Foxes with smaller home ranges may not necessarily travel less. F1 had a very small home range

304   (3.81 km^2, BBMM) as compared to other individuals, but its average daily movement was 11.10

305   ± 7.72 SD km/d. Daily distance travelled by individuals having a smaller home range may be

306   similar to individuals having a larger home range, and the difference may only reflect the

307   different foraging sites used by the individuals (Carter, Luck & McDonald, 2012).

308

309   It is essential to have the GPS fixes at fine-scale time intervals to calculate the average daily

310   distance travelled by red fox. Our data suggest that increasing the time interval of GPS fixes

311   decreases the estimate of daily movement of red fox significantly ($P < 0.01$, Table S1). The

312   estimated daily average movement of foxes decreased from 17.76 ± 8.45 SD km/d to 14.96 ±

313   7.71 SD km/d on down sampling the data from 15-min to 30-min time intervals. Further down

314   sampling resulted in greater under-estimates of daily average movement (Table S1). On the other

315   hand, fixes at short time intervals may overestimate the average daily distance travelled due to

316   location errors (Poulin, Clermont & Berteaux, 2021).

317

318   The individual M3 showed a higher daily average movement (34.22 ± 20.34 SD km/d, Table

319   S1). This may be because M3 made many forays outside its normal home range during this

320   period. On four occasions, M3 moved about 60 km or more in one day. Such long distances are

321   not uncommon, and in arctic fox, the maximum distance travelled in a day was reported to be

322   154 km (Fuglei & Tarroux, 2019). Long-distance dispersal events are similarly reported in red

323   fox, where foxes have travelled over a distance of 132-1036 km in a short period (Walton et al.,

324   2018).

325

326   Data on average speeds travelled by red fox have not been reported, but the average speed with

327   which wolves travel ranges from 0.8 to 1.1 km/h (Burkholder, 1959; Ciucci *et al.*, 1997;

328   Jedrzejewski *et al.*, 2001). Studies on wolves with 15-min GPS location data have reported

329   maximum travel speeds ranging from 9.6 to 13 km/h (Mech, 1994). Hence, our method of

330   restricting the maximum speed limit of 9.35 km/h for red fox may be reasonable. The use of

331   speed to identify GPS errors, especially for calculating daily movements, has been reported in

332   other studies (Bjørneraas et al., 2010; Wysong et al., 2020). Studies with a greater sample size

333   are warranted to enhance our knowledge of maximum speed of red fox.

334

335   **Habitat use and selection**

336   Multiple land cover categories were exploited by different individuals in our study. Most of the

337   area at our study site is barren due to the arid Trans-Himalayan conditions. The high elevation

338   areas (> 6000 m above sea level) are covered with snow all throughout the year. Agricultural

339   land is scarce and present near the river valleys. We found that the larger foxes, i.e., F1, M1 and

340   M2, exploited agricultural land the most as compared to any other land cover category (Fig. 3).

341   On the other hand, F2, M3 and M4, which were smaller in size were found in barren and snow-

342   covered land (Table 1, Fig. 3). We suspect that the larger individuals are more dominant, giving

343   them greater access to preferred, resource-rich areas such as agricultural land. However, the

344   overlapping home ranges indicate that the larger individuals do not completely exclude others

345   from their home ranges. The individual F3 in Hemis National Park was found in both barren and

346   alpine vegetation areas.

347

348   Red foxes are known for their highly adaptable behaviour and often show large variations in

349   their habitat selection (Walton et al., 2017; Walton, 2020). In our study, except for F1 and F2, all

350   other individuals were positively associated with human settlements. Red fox in the Trans-

351   Himalayan landscape has been reported to be at higher densities and often den near human

352   settlements due to the presence of anthropogenic food subsidies (Reshamwala et al., 2018, 2021).

353   We found that all individuals were positively associated with water. The presence of water

354   bodies is also known to positively influence the abundance of rodents and lagomorphs

355   (Reshamwala et al., 2021). We also found that red fox significantly preferred lower elevations

356   and less rugged terrain. Except for F1 and F2, all other individuals significantly avoided slopes.

357   Other species have been shown to avoid higher elevations, steep slopes and rugged terrain, which

358   are known to be energetically costly to use (Filla et al., 2017; Fullman, Joly & Ackerman, 2017).

359   At the time they were radio-collared, these individuals were without pups, but later field

360 observations showed that both had young ones. They may have avoided human settlements and

361 showed more preference for slopes to avoid anthropogenic disturbances.

362

363 Studies on the red fox population in the Trans-Himalayan region are limited and their current

364 status remains unknown. However, a previous study has reported few retaliatory killings due to

365 predation on poultry (Reshamwala et al., 2018). This study provides an overview of the spatial

366 ecology of red fox in the Trans-Himalayan cold desert. The role of spatial ecology in

367 conservation is well known and information on species movement is important for the

368 prioritisation of areas for conservation (Allen & Singh 2016; Carwardine et al., 2012). While the

369 movement within the home ranges is crucial for understanding the habitat suitability and

370 preferences (Lu et al., 2012), the home range sizes and shapes are essential for managers to

371 understand the scale of management (Schwartz, 1999). From our movement data of GPS-

372 collared individuals, we conclude that they preferred lesser rugged terrain and lower elevations

373 in this region. In addition to home ranges, we provide insights on the daily movements and the

374 need for having short time intervals between locations for calculating daily movements. The

375 movement of species also influences other ecosystem services such as pollination and seed

376 dispersal (Kremen et al., 2007; Nathan and Muller-landau, 2000). Hence, movement ecology can

377 aid in understanding ecosystem functioning and landscape management (Habib et al., 2021;

378 Mitchell, Bennett & Gonzalez et al., 2013).

379

380 **Acknowledgements**

381 We are thankful to the Director and Dean, Wildlife Institute of India, for support and

382 encouragement. We are grateful to the Department of Wildlife Protection, Govt. Jammu and

383   Kashmir for providing the necessary permissions. Gianalberto Losapio is acknowledged for his

384   valuable inputs on the manuscript. Mr. Lavpreet Singh Lahoria, Mr. Hasnain Zargar and Mr. Ali

385   Akbar Zargar are acknowledged for their help in capturing the foxes. Dr. Ajaz Hussain and his

386   family are acknowledged for their constant support during this long-term study. Ms. Keerthi

387   Sudarsan and Dr. Ranjana Pal are acknowledged for helping in editing the manuscript. The

388   authors acknowledge a grant from Idea Wild for providing the necessary field equipment.

389

390   **Funding**

391   This research was supported by the project "Understanding Ladakh's socio-ecological processes

392   to design landscape level development strategies" funded by the Government of India's National

393   Mission on Himalayan Studies and implemented by the Department of Wildlife Protection, Leh.

394

395   **Conflicts of interest**

396   The authors declare that they have no competing interests.

397

398   **Author Contributions**

399   HSR did the fieldwork, procured data, analysed, and wrote the first draft. ZH, SK and PR helped

400   analyse and write the manuscript. BH and PR procured the funding. BH conceptualised the

401   study. BH and RD supervised the project and discussed the results to improve and produce the

402   final manuscript.

403

404   **Animal Ethics**

405 All red foxes were captured following standard and approved protocols after due permission

406 from the Ministry of Environment, Forests and Climate Change, Government of India, and

407 Department of Wildlife Protection, Ladakh, Jammu and Kashmir. The permit details are as

408 follows: CCFWL\Permission\2016\575-76

409

410 **References**

411 Allen AM, Singh NJ. 2016. Linking movement ecology with wildlife management and

412   conservation. *Frontiers in Ecology and Evolution* 3, 155.

413 Benson JF, Chamberlain MJ. 2007. Space-use and habitat selection by female Louisiana Black

414   Bears in the Tensas river basin of Louisiana. *Journal of Wildlife Management* 71:117–126.

415   doi: 10.2193/2005-580.

416 Bharti V, Singh C, Ettema J, Turkington TAR. 2016. Spatiotemporal characteristics of extreme

417   rainfall events over the Northwest Himalaya using satellite data. *International Journal of*

418   *Climatology* 36:3949–3962. doi: 10.1002/joc.4605.

419 Bjørneraas K, Van Moorter B, Rolandsen CM, Herfindal I. 2010. Screening global positioning

420   system location data for errors using animal movement characteristics. *Journal of Wildlife*

421   *Management* 74:1361–1366. doi: 10.2193/2009-405.

422 Burkholder. 1959. Movements and behavior of a wolf pack in Alaska. *The Journal Of Wildlife*

423   *Management* 23:1–11.

424 Burt HW. 1943. Territoriality and home range concepts as applied to mammals. *Journal of*

425   *Mammalogy* 24:346–352.

426 Caro TM, Stoner CJ. 2003. The potential for interspecific competition among African carnivores.

427   *Biological Conservation* 110:67–75. doi: 10.1016/S0006-3207(02)00177-5.

428   Carter A, Luck GW, McDonald SP. 2012. Ecology of the red fox (*Vulpes vulpes*) in an

429   agricultural landscape. 2. Home range and movements. *Australian Mammalogy* 34:175–

430   187. doi: 10.1071/AM11041.

431   Carwardine J, O'Connor T, Legge S, Mackey B, Possingham HP, Martin TG. 2012. Prioritizing

432   threat management for biodiversity conservation. *Conservation Letters* 5, 196–204. doi:

433   10.1111/j.1755-263X.2012.00228.x.

434   Chandramouli C. 2013. Census of India 2011: Primary Census Abstract. New Delhi, India.

435   *Office of the Registrar General & Census Commissioner, India.*

436   Ciucci P, Boitani L, Francisci F, Andreoli G. 1997. Home range, activity and movements of a

437   wolf pack in central Italy. *Journal of Zoology* 243:803–819. doi: 10.1111/j.1469-

438   7998.1997.tb01977.x.

439   Coman BJ, Robinson J, Beaumont C. 1991. Home range, dispersal and density of red foxes

440   (*Vulpes vulpes l.*) in central Victoria. *Wildlife Research* 18:215–223. doi:

441   10.1071/WR9910215.

442   Filla M, Premier J, Magg N, Dupke C, Khorozyan I, Waltert M, Bufka L, Heurich M. 2017.

443   Habitat selection by Eurasian lynx (*Lynx lynx*) is primarily driven by avoidance of human

444   activity during day and prey availability during night. *Ecology and Evolution* 7:6367–6381.

445   doi: 10.1002/ece3.3204.

446   Fuglei E, Tarroux A. 2019. Arctic fox dispersal from Svalbard to Canada: One female's long run

447   across sea ice. *Polar Research* 38:1–7. doi: 10.33265/polar.v38.3512.

448   Fullman TJ, Joly K, Ackerman A. 2017. Effects of environmental features and sport hunting on

449   caribou migration in northwestern Alaska. *Movement Ecology* 5:1–11. doi: 10.1186/s40462-

450   017-0095-z.

451   Geffen E, Gompper ME, Gittleman JL, Luh H, David W, Wayne RK, Geffen ELI, Macdonald

452   DW. 1996. Size, life-history traits, and social organization in the Canidae : A re-evaluation.

453   *The American Naturalist* 147(1), 140-160.

454   Getz WM, Fortmann-Roe S, Cross PC, Lyons AJ, Ryan SJ, Wilmers CC. 2007. LoCoH:

455   Nonparameteric Kernel methods for constructing home ranges and utilization distributions.

456   *PLoS ONE* 2(2). doi: 10.1371/journal.pone.0000207.

457   Gosselink TE, Deelen TR Van, Warner RE, Joselyn MG. 2003. Temporal habitat partitioning

458   and spatial use of coyotes and red foxes in East-Central Illinois. *The Journal of Wildlife*

459   *Management* 67:90. doi: 10.2307/3803065.

460   Habib B, Ghaskadbi P, Khan S, Hussain Z, Nigam P. 2021. Not a cakewalk: Insights into

461   movement of large carnivores in human-dominated landscapes in India. *Ecology and*

462   *evolution* 11(4), 1653-1666.

463   Haltenorth T, Roth HH. 1968. Short review of the biology and ecology of the red fox.

464   *Saugetierkunde Mitteilungen* 16:339–352.

465   Hoffmann M, Sillero-Zubiri C. 2016. *Vulpes vulpes*. The IUCN Red List of Threatened Species

466   2016. doi.org/10.2305/IUCN.UK.

467   Horne JS, Garton EO, Krone SM, Lewis JS. 2007. Analyzing animal movements using Brownian

468   bridges. *Ecology* 88:2354–63.

469   Ims RA. 1995. Movement patterns related to spatial structures. *Mosaic landscapes and*

470   *ecological processes*. Springer, Dordrecht 85-109.

471   Jedrzejewski W, Schmidt K, Theuerkauf J, Jedrzejewska B, Okarma H. 2001. Daily movements

472   and territory use by radio-collared wolves (*Canis lupus*) in Bialowieza Primeval Forest in

473   Poland. *Canadian Journal of Zoology* 79:1993–2004. doi: 10.1139/cjz-79-11-1993.

474   Kachroo P, Dhar U SB. 1977. Flora of Ladakh. *Bishen Singh Mahendra Pal Singh, Dehradun*

475   15:4253-4270.

476   Kenward RE, Clarke RT, Hodder KH, Walls SS. 2001. Density and linkage estimators of home

477   range: Nearest-neighbor clustering defines multinuclear cores. *Ecology* 82:1905–1920. doi:

478   10.1890/0012-9658(2001)082[1905:DALEOH]2.0.CO;2.

479   Kremen C, Williams NM, Aizen MA, Gemmill-Herren B, LeBuhn G, Minckley R, Ricketts TH.

480   2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual

481   framework for the effects of land-use change. *Ecology letters* 10(4), 299-314. doi:

482   10.1111/j.1461-0248.2007.01018.x.

483   Lai S, Warret Rodrigues C, Gallant D, Roth JD, Berteaux D. 2022. Red foxes at their northern

484   edge: competition with the Arctic fox and winter movements. *Journal of Mammalogy*

485   doi.org/10.1093/jmammal/gyab164.

486   Lu N, Jia CX, Lloyd H, Sun YH. 2012. Species-specific habitat fragmentation assessment,

487   considering the ecological niche requirements and dispersal capability. *Biological*

488   *Conservation* 152, 102–109. doi: 10.1016/j.biocon.2012.04.004.

489   Main MT, Davis RA, Blake D, Mills H, Doherty TS. 2020. Human impact overrides bioclimatic

490   drivers of red fox home range size globally. *Diversity and Distributions* 26(9), 1083-1092.

491   doi: 10.1111/ddi.13115.

492   Mattisson J, Sand H, Wabakken P, Gervasi V, Liberg O, Linnell JDC, Rauset GR, Pedersen HC.

493   2013. Home range size variation in a recovering wolf population: Evaluating the effect of

494   environmental, demographic, and social factors. *Oecologia* 173:813–825. doi:

495   10.1007/s00442-013-2668-x.

496   Mech D. 1994. Regular and homeward travel speeds of Arctic wolves. *Journal of Mammalogy*

497   75:741–742.

498 Meia JS, Weber JM. 1995. Home ranges and movements of red foxes in central Europe: stability

499   despite environment changes. *Canadian Journal of Zoology* 73:1960–1966.

500 Minta SC. 1993. Sexual differences in spatio-temporal interaction among badgers. *Oecologia*

501   96:402–409. doi: 10.1007/BF00317511.

502 Mitchell MGE, Bennett EM, Gonzalez A. 2013. Linking landscape connectivity and ecosystem

503   service provision: current knowledge and research gaps. *Ecosystems* 16, 894–908. doi:

504   10.1007/s10021-013-9647-2.

505 Morellet N, Bonenfant C, Börger L, Ossi F, Cagnacci F, Heurich M, Kjellander P, Linnell JDC,

506   Nicoloso S, Sustr P, Urbano F, Mysterud A. 2013. Seasonality, weather and climate affect

507   home range size in roe deer across a wide latitudinal gradient within Europe. *Journal of*

508   *Animal Ecology* 82:1326–1339. doi: 10.1111/1365-2656.12105.

509 Musiani M, Okarma H, Jędrzejewski W. 1998. Speed and actual distances travelled by

510   radiocollared wolves in Bialowieza Primeval Forest (Poland). *Acta Theriologica* 43:409–

511   416. doi: 10.4098/AT.arch.98-51.

512 Nathan R, Muller-landau HC. 2000. Spatial patterns of seed dispersal, their determinants and

513   consequences for recruitment. *Trends in Ecology and Evolution* 15, 278–285. doi:

514   10.1016/S0169-5347(00)01874-7.

515 Newdick MT. 1983. The behavioural ecology of urban foxes, *Vulpes vulpes*, in Oxford. Ph.D.

516   dissertation, University of Oxford.

517 Newsome TM, Spencer EE, Dickman CR. 2017. Short-term tracking of three red foxes in the

518   Simpson Desert reveals large home-range sizes. *Australian Mammalogy* 39:238–242. doi:

519   10.1071/AM16037.

520 Poulin M-PP, Clermont J, Berteaux D. 2021. Extensive daily movement rates measured in

521   territorial arctic foxes. *Ecology and Evolution* 11(6), 2503–2514. doi: 10.1002/ece3.7165.

522 Reshamwala HS, Mahar N, Dirzo R, Habib B. 2021. Successful neighbour : Interactions of the

523   generalist carnivore red fox with dogs, wolves and humans for continued survival in

524   dynamic anthropogenic landscapes. *Global Ecology and Conservation* 25:e01446. doi:

525   10.1016/j.gecco.2020.e01446.

526 Reshamwala HS, Shrotriya S, Bora B, Lyngdoh S, Dirzo R, Habib B. 2018. Anthropogenic food

527   subsidies change the pattern of red fox diet and occurrence across Trans-Himalayas, India.

528   *Journal of Arid Environments* 150:15–20. doi: 10.1016/j.jaridenv.2017.12.011.

529 Rotem G, Berger H, King R, Bar P, Saltz D. 2011. The effect of anthropogenic resources on the

530   space-use patterns of golden jackals. *Journal of Wildlife Management* 75:132–136. doi:

531   10.1002/jwmg.9.

532 Roy PS, Behera MD, Murthy MSR, Roy A, Singh S, Kushwaha SPS, Jha CS, Sudhakar S, Joshi

533   PK, Reddy CS, Gupta S, Pujar G, Dutt CBS, Srivastava VK, Porwal MC, Tripathi P, Singh

534   JS, Chitale V, Skidmore AK, Rajshekhar G, Kushwaha D, Karnatak H, Saran S, Giriraj A,

535   Padalia H, Kale M, Nandy S, Jeganathan C, Singh CP, Biradar CM, Pattanaik C, Singh DK,

536   Devagiri GM, Talukdar G, Panigrahy RK, Singh H, Sharma JR, Haridasan K, Trivedi S,

537   Singh KP, Kannan L, Daniel M, Misra MK, Niphadkar M, Nagabhatla N, Prasad N,

538   Tripathi OP, Rama Chandra Prasad P, Dash P, Qureshi Q, Tripathi SK, Ramesh BR, Gowda

539   B, Tomar S, Romshoo S, Giriraj S, Ravan SA, Behera SK, Paul S, Das AK, Ranganath BK,

540   Singh TP, Sahu TR, Shankar U, Menon ARR, Srivastava G, Neeti, Sharma S, Mohapatra

541   UB, Peddi A, Rashid H, Salroo I, Hari Krishna P, Hajra PK, Vergheese AO, Matin S,

542   Chaudhary SA, Ghosh S, Lakshmi U, Rawat D, Ambastha K, Malik AH, Devi BSS, Sharma

543   KC, Mukharjee P, Sharma A, Davidar P, Raju RRV, Katewa SS, Kant S, Raju VS, Uniyal

544   BP, Debnath B, Rout DK, Thapa R, Joseph S, Chhetri P, Ramachandran RM. 2015. New

545   vegetation type map of India prepared using satellite remote sensing: Comparison with

546   global vegetation maps and utilities. *International Journal of Applied Earth Observation*

547   *and Geoinformation* 39:142–159. doi: 10.1016/j.jag.2015.03.003.

548 Saeki M, Johnson PJ, Macdonald DW. 2007. Movements and habitat selection of raccoon dogs

549   (*Nyctereutes procyonoides*) in a mosaic landscape. *Journal of Mammalogy* 88:1098–1111.

550   doi: 10.1644/06-MAMM-A-208R1.1.

551 Schmidt K. 1999. Variation in daily activity of the free-living Eurasian lynx (*Lynx lynx*) in

552   Bialowieza Primeval Forest, Poland. *Journal of Zoology* 249:417–425. doi:

553   10.1017/S0952836999009851.

554 Schuette P, Wagner AP, Wagner ME, Creel S. 2013. Occupancy patterns and niche partitioning

555   within a diverse carnivore community exposed to anthropogenic pressures. *Biological*

556   *Conservation* 158:301–312. doi: 10.1016/j.biocon.2012.08.008.

557 Schwartz MW. 1999. Choosing the appropriate scale of reserves for conservation. *Annual*

558   *Review of Ecology and Systematics* 30, 83–108. doi: 10.1146/annurev.ecolsys.30.1.83.

559 Signer J, Fieberg J, Avgar T. 2019. Animal movement tools (amt): R package for managing

560   tracking data and conducting habitat selection analyses. *Ecology and Evolution* 9:880–890.

561   doi: 10.1002/ece3.4823.

562 Sillero-Zubiri C, Hoffmann M, Macdonald DW. 2004. Canids: foxes, wolves, jackals, and dogs:

563   status survey and conservation action plan. *Gland, Switzerland: IUCN*.

564 Small RJ, Rusch DH. (1989). The natal dispersal of ruffed grouse. *The Auk*, *106*(1), 72-79.

565 Thurfjell H, Ciuti S, Boyce MS. 2014. Applications of step-selection functions in ecology and

566   conservation. *Movement ecology* 2(1), 1-12.

567 Turchin, P. 1991. Reconstructing endogenous dynamics of a laboratory Drosophila population.

568   *Journal of Animal Ecology* 60(3), 1091-1098.

569 Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population

570   redistribution in animals and plants. *Sinauer Associates*.

571 Vanak AT, Gompper ME. 2010. Multi-scale resource selection and spatial ecology of the Indian

572   fox in a human-dominated dry grassland ecosystem. *Journal of Zoology* 281:140–148. doi:

573   10.1111/j.1469-7998.2010.00690.x.

574 Wall J. 2014. *Movement ecology tools for ArcGIS (arcmet) version,* 10(2), V3.

575 Walter WD, Onorato, DP, Fischer JW. 2015. Is there a single best estimator? Selection of home

576   range estimators using area-under-the-curve. *Movement Ecology* 3(1) 1-11. doi

577   10.1186/s40462-015-0039-4.

578 Walton Z. 2020. *Movement across scales: red fox spatial ecology*. Ph.D. Dissertation. Innland

579   Norway University of Applied Sciences. *Høgskolen i Innlandet.*

580 Walton Z, Samelius G, Odden M, Willebrand T. 2017. Variation in home range size of red foxes

581   *Vulpes vulpes* along a gradient of productivity and human landscape alteration. *PLoS ONE*

582   12:1–14. doi: 10.1371/journal.pone.0175291.

583 Walton Z, Samelius G, Odden M, Willebrand T. 2018. Long-distance dispersal in red foxes

584   *Vulpes vulpes* revealed by GPS tracking. *European Journal of Wildlife Research* 64. doi:

585   10.1007/s10344-018-1223-9.

586 Wysong ML, Hradsky BA, Iacona GD, Valentine LE, Morris K, Ritchie EG. 2020. Space use

587   and habitat selection of an invasive mesopredator and sympatric, native apex predator.

588   *Movement Ecology* 8:1–14. doi: 10.1186/s40462-020-00203-z.

589 **List of Figures and Tables**

590 *Figure 1 Study area of collared red foxes in the Trans-Himalayan cold desert, Ladakh, India. (A)*

591 *Location of the study sites in India. (B) 95% MCP home ranges of six red foxes at Chiktan,*

592 *Kargil. (C) 95% MCP home range of a female at Hemis National Park*

593

594 *Figure 2 Violin plots showing the estimated daily movement of red fox in the Trans-Himalayan*

595 *cold desert, Ladakh, India*

596 **Values below the violin indicate the number of days used for estimating the average daily*

597 *movement. Each dot in the violin plot represents the distance walked in a day. (Females=F1, F2,*

598 *F3; Males=M1, M2, M3, M4)*

599

600 *Figure 3 Percentage of land cover categories utilised by different red fox individuals in the*

601 *Trans-Himalayan cold desert, Ladakh, India*

602

603 *Figure 4 Step-selection function beta coefficients* of different red fox individuals for*

604 *topographic factors (ruggedness, elevation and slope), an environmental factor (distance to*

605 *water) and anthropogenic factors (distance to road and human settlements)*

606 **Beta coefficients derived from step selection function analysis. Positive values show preference*

607 *and negative values show avoidance*

608

609 *Table 1 Details of GPS-collared individuals, date of collaring, active days, and the number of*

610 *locations received to study the spatial ecology of red fox in Ladakh, India*

611

612 *Table 2 Estimated home range sizes by minimum convex polygon (MCP), kernel density estimate*

613 *(KDE), local convex hull (LoCoH), Brownian-bridge movement model (BBMM), and estimated*

614 *average daily movement of red fox in Ladakh, India*

615 **Supplementary**

616 *Figure S1 Density distribution of speed data (values are log-transformed) from trajectory details*

617 *of all red fox individuals and the cut-off line in red at 98% (9.35km/h) of the data to eliminate*

618 *movement errors*

619

620 *Figure S2*

621 *Net square displacement (km²) of collared individuals, 3 females (F1, F2, F3) and 4 males (M1,*

622 *M2, M3, M4) in Ladakh, India. Dashed lines show the trendline for each individual*

623

624 *Figure S3*

625 *Brownian-bridge movement model (BBMM) utilisation distribution of home ranges (95% contour;*

626 *black outline) and core areas (50% contour; red) of red foxes obtained from home range analysis*

627 *done in ArcGIS*

628 **Map scales for each individual are different*

629

630 *Table S1 Effect of down-sampling GPS fixes from 15-min to 2-h time interval on the estimated*

631 *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

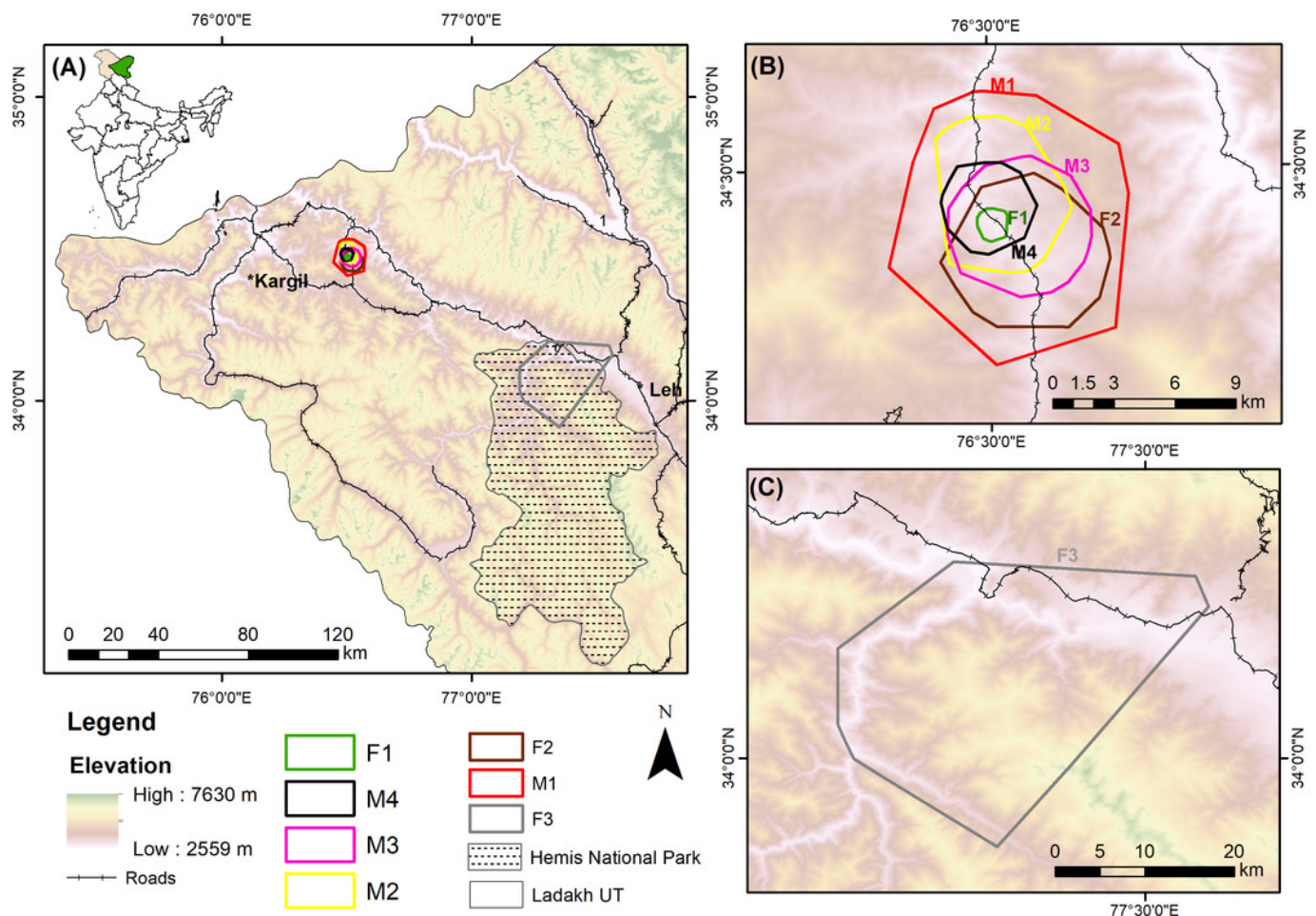



Figure 2

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

*Values below the violin indicate the number of days used for estimating the average daily movement. Each dot in the violin plot represents the distance walked in a day. (Females=F1, F2, F3; Males=M1, M2, M3, M4)

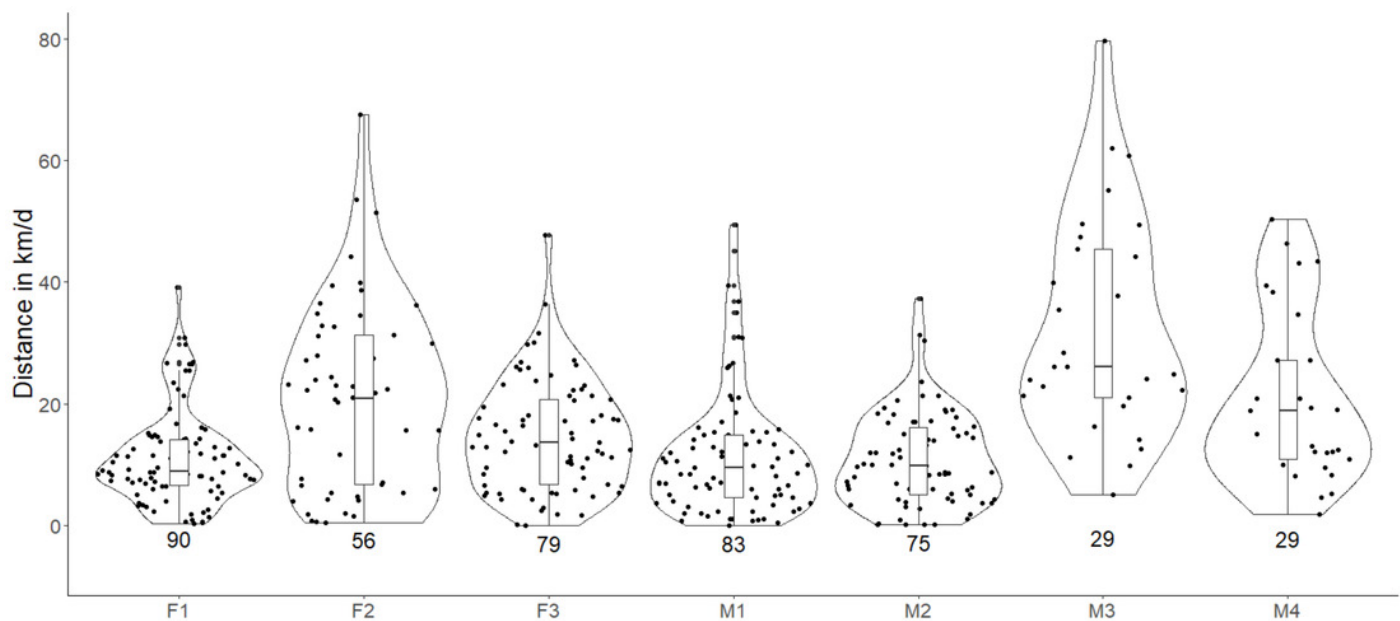



Figure 3

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

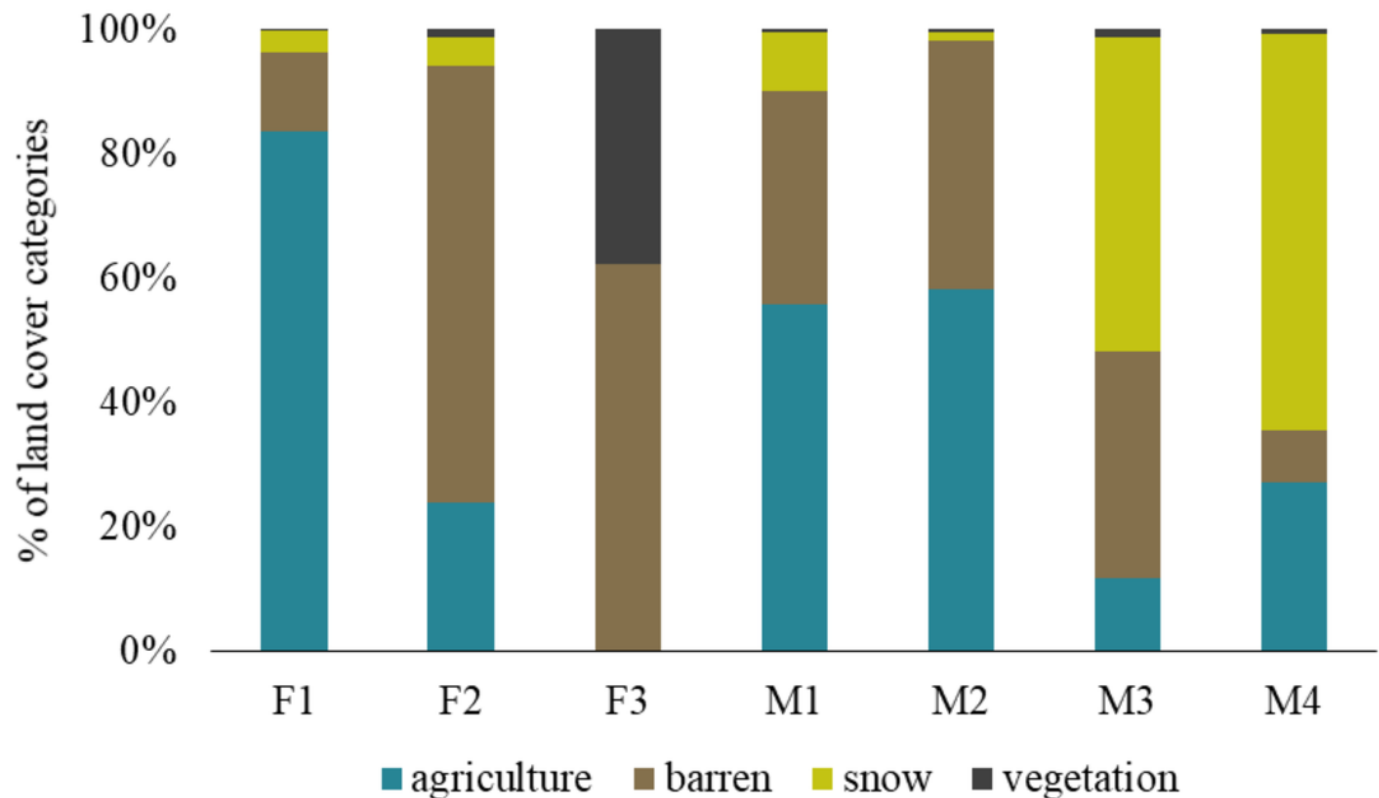
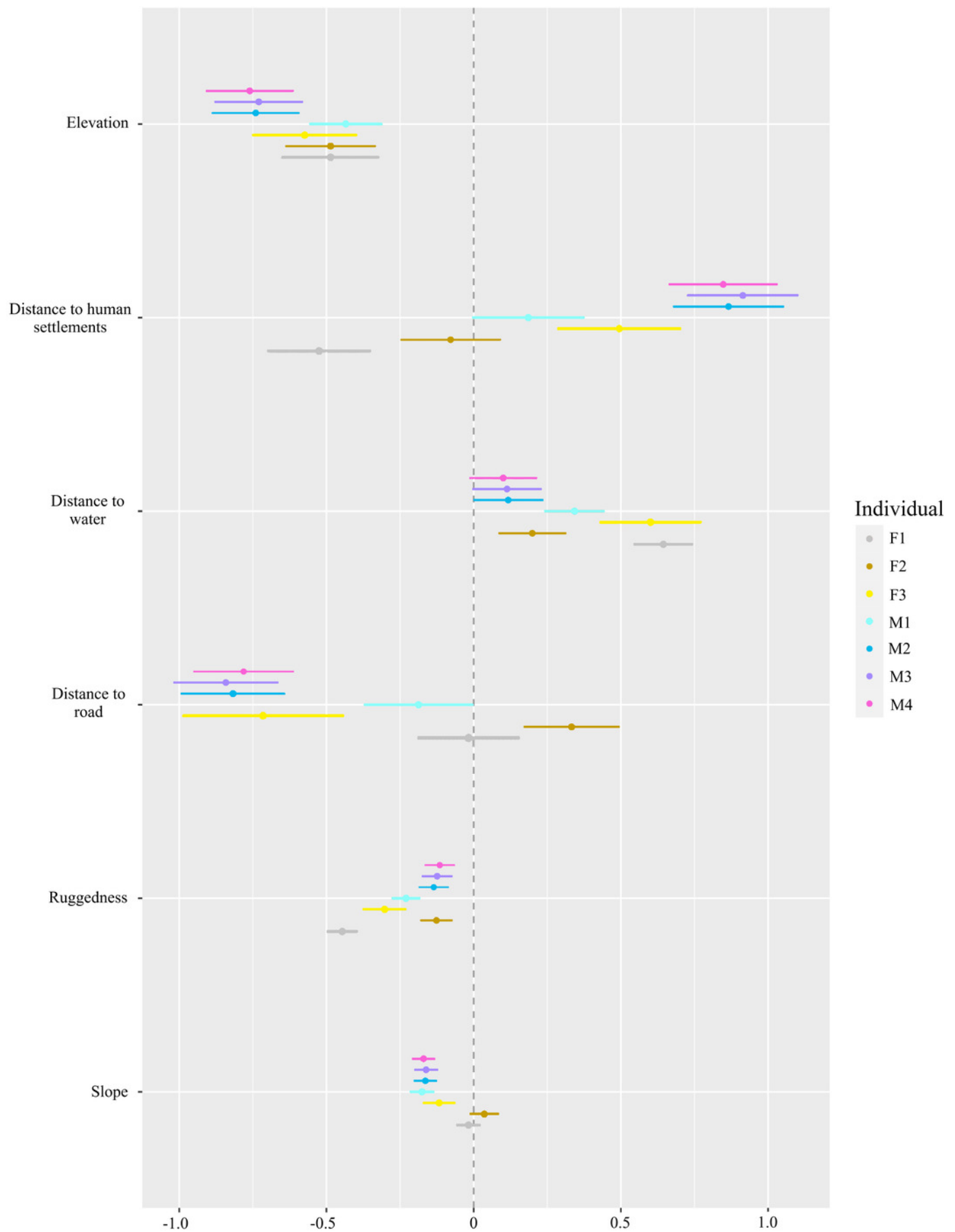



Figure 4

Step-selection function beta coefficients* of different red fox individuals for topographic factors (ruggedness, elevation and slope), an 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

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

1   *Table 1 Details of GPS-collared individuals, date of collaring, active days, and the number of*

2   *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

Estimated home range sizes by minimum convex polygon (MCP), kernel density estimate (KDE), local convex hull (LoCoH), Brownian-bridge movement model (BBMM), and estimated average daily movement of red fox in Ladakh, India

1   *Table 2 Estimated home range sizes by minimum convex polygon (MCP), kernel density estimate*

2   *(KDE), local convex hull (LoCoH), Brownian-bridge movement model (BBMM), and estimated*

3   *average daily 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	34.22 (20.85)
M4	0.51	15.90	0.77	12.07	0.36	10.11	1.15	10.75	20.85 (13.88)
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)**	**17.76 (8.45)**