Space use, interaction and recursion in a solitary specialized herbivore: a red panda case study

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ABSTRACT: Better understanding of ecology is crucial for the success of endangered species conservation programmes. Little information is available on space use, conspecific interactions and recursions by one such species, the red panda *Ailurus fulgens.* To address this deficiency, we used GPS telemetry to examine their home range, core area, home-range overlap, dynamic interactions and recursive movement, and investigated the effect of sex, age and body mass on these behaviours across seasons. The median annual home range size was 1.41 km^2, with nearly a quarter of this range being used as the core area. Sex and reproductive status were the key determinants of space use patterns on a seasonal scale, while body mass and age remained significant correlates for the core area. The home range of males was nearly double that of females, likely because of the polygynous mating system in red pandas. Females avoided overlapping home ranges, while males overlapped home range with up to 4 females, and neighbouring males overlapped nearly half of their ranges. We found rare interactions between males and females outside the mating season. Red pandas showed site fidelity within their territory, with seasonal variation across sex classes. We also observed high individual variation in patterns of both space use and recursive movement. Taken together, these results suggest that differences in biological requirements across seasons determine red panda space use patterns, conspecific interactions and recursion. However, forage availability and quality, climatic factors, disturbances and habitat fragmentation are also likely to influence these behaviours, and these factors need to be investigated.

KEY WORDS: *Ailurus fulgens* · Core area · Dynamic interaction · Home range · Recursion · Site fidelity · Static interaction · Home-range overlap

1. INTRODUCTION

Space use and conspecific interactions may vary across species due to intrinsic and extrinsic factors (van Beest et al. 2011, Tucker et al. 2014). Solitary species lack cooperative behaviour and maintain distinct territories which may or may not overlap with those of conspecifics (Sandell 1989). These ecological behaviours are influenced by interactions between animals (including but not limited to conspecifics) and their surrounding environment (Korbelová et al. 2016,

Viana et al. 2018). Better understanding of such ecological behaviours is crucial for the success of endangered species conservation programmes. Such information can guide wildlife managers to identify and prioritise ecologically important areas within the environment of the target species and therefore minimize potential threats during critical life cycle phases.

Movement is generally restricted to a specific area known as the home range, in which an animal travels daily to acquire resources for its nutrition, safety and reproduction (Burt 1943, van Beest et al. 2011). Eco-

logical theory suggests that variation in energy requirements drives home range size (Gittleman & Harvey 1982, Larter & Gates 1994). For this reason, home range size scales linearly with body mass for a particular weight range to meet calorie requirements (Jetz et al. 2004, Tucker et al. 2014, Noonan et al. 2019). However, body size may not be the only determinant in species where males have larger range sizes despite equal body mass between males and females.

Several hypotheses have been proposed to explain variation in home range size. For instance, the land-tenure hypothesis suggests that solitary species maintain their density through territoriality, temporal avoidance and communication via chemicals (Seidensticker et al. 1973). Polygynous mating is characteristic of this system, wherein individual males overlap the territories of several females and defend these territories from neighbouring males (Clutton-Brock 2016). The resource-distribution hypothesis proposes that food characteristics determine the range size of females (Larter & Gates 1994, Gehrt & Fritzell 1998), while the social-behaviour hypothesis suggests that spatial organization of males is influenced by food availability outside of the mating season and by the distribution of females during the mating season (Sandell 1989, Larter & Gates 1994, Gehrt & Fritzell 1998). Exclusive ranges are expected in areas with even food distribution, but range sizes may fluctuate with changes in food characteristics across space and time (Sandell 1989). Likewise, the resource-dispersion hypothesis proposes that home-range overlap may increase in areas with high resource availability (Macdonald 1983). However, explanations of space-use patterns cannot be limited within these theoretical frameworks. Several other factors, including local climate (Fisher & Owens 2000, van Beest et al. 2011), habitat productivity (Larter & Gates 1994), predation risk (McLoughlin & Ferguson 2000, van Beest et al. 2011), human disturbances (Šálek et al. 2015, Rus et al. 2021), population density (Clutton-Brock 2016), reproductive status (van Beest et al. 2011) and other resources such as mates, resting and nesting sites, and water availability (McLoughlin & Ferguson 2000, Roshier & Reid 2003, Tucker et al. 2014), may also shape space use patterns at macro and micro scales.

Most animals also show site fidelity (Lone et al. 2013) and frequently revisit favoured foraging patches, resting sites, nests, water sources and corridors within their home range, which is known as recursion (English et al. 2014, Bracis et al. 2018). Such behaviour has been reported in a wide group of animals including both generalists (English et al. 2014, Nandintsetseg et al. 2019) and habitat specialists such as giant pandas *Ailuropoda melanoleuca* (Hull et al. 2015) and koalas *Phascolarctos cinereus* (Matthews et al. 2007, Rus et al. 2021). Recursive movement may be high in heterogeneous habitat (Berger-Tal & Bar-David 2015). In solitary species, defence movement for territory marking could be one of the major drivers of recursive movement (Berger-Tal & Bar-David 2015). Very little information is available on some of these key ecological aspects of the red panda *Ailurus fulgens*, an Endangered species of the Eastern Himalaya. A recent study has classified red pandas into 2 distinct species: *A. fulgens* and *A. styani* (Hu et al. 2020). *A. fulgens* live only in temperate Himalayan forests with bamboo abundance in the understorey at elevations between 2300 and 4000 m, with only a few records beyond this range (Glatston et al. 2015). Their camouflaged body, montane habitat, low density and elusive nature have made them difficult to study (Yonzon 1989, Bista et al. 2021a). We aimed to test some of the above-mentioned hypotheses on *A. fulgens*, a solitary arboreal mammal which also represents a group of unique members of the Carnivora with a herbivorous diet.

Red pandas are medium-sized mammals mostly restricted to a diet of bamboo (Pradhan et al. 2001, Bista et al. 2022). Available studies on movement ecology of red pandas have been based on VHF telemetry. There are many instances of GPS telemetry revealing more accurate information than revealed by VHF telemetry (Walter et al. 2015). For example, GPS telemetry revealed a nearly 7-fold larger home range size of the snow leopard *Panthera uncia* than estimates based on VHF telemetry (Johansson et al. 2016). Therefore, in this study we set out to fill some knowledge gaps about space use, interaction and recursion patterns in *A. fulgens* using GPS telemetry.

We aimed to examine the effect of morphometric features and life history traits on home range and core areas, analyse conspecific interactions and investigate recursion in red pandas. We attempted to test 4 *a priori* hypotheses: (1) males and adults occupy larger ranges than females and subadults, respectively; (2) the home range of males is larger in the mating season, and female range size increases in the mating season and during cub-rearing; (3) males overlap home ranges of several females but rarely interact with them outside the mating season; and (4) red pandas have several activity centres in which they spend long hours and visit repeatedly.

2. MATERIALS AND METHODS

2.1. Data collection and processing

Using a standard protocol (Bista et al. 2021a), we captured and GPS-collared 10 red pandas in Ilam district, eastern Nepal (27.102° N, 87.982° E) from September 2019 to December 2019. These animals were monitored until March 2021. We followed the guidelines of the American Society of Mammalogists (Sikes & The Animal Care and Use Committee of the American Society of Mammalogists 2016) for animal capturing and handling, which was also approved by the University of Queensland's Animal Ethics Committee (SAFS/133/19/NEPAL). Additionally, the Department of Forests and Soil Conservation, Government of Nepal, also reviewed and approved the protocol (DFSC-521/075/076 and DFSC-244/076/077). The collared animals comprised 4 adult females, 3 adult males, 1 sub-adult male and 2 sub-adult females (Table 1). We set each collar to record 12 GPS fixes per day (1 fix in every 2 h) to be transferred remotely. Telemetry error can be relatively high in areas with dense canopy and steep slopes (D'Eon et al. 2002, Hebblewhite et al. 2007, Hansen & Riggs 2008), features also found in our study area. We therefore omitted imprecise data with positional dilution of precision >5 (Lewis et al. 2007). Our study area was located between 1500 and 3636 m elevation, and we discarded unusual elevation values beyond this elevation range. In addition, we empirically determined in the field that the telemetry error of our collars was up to 25 m.

2.2. Home range estimation

GPS telemetry data suffer from autocorrelation (Noonan et al. 2019). Therefore, we plotted a variogram for all individuals (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/n047p131_supp.pdf) to examine the autocorrelation structure of the data and movement behaviour by fitting continuous-time stochastic process movement models (Fleming et al. 2014, Calabrese et al. 2016). We then fitted the models with maximum likelihood estimation and selected the appropriate movement model (Calabrese et al. 2016). Weight optimization is important for optimal estimation of distribution in autocorrelated data (Fleming et al. 2018). Therefore, we optimized weight and estimated bias-corrected autocorrelated kernel density estimation (AKDEc) as a home range estimator (Fleming et al. 2018) in the R package 'ctmm' (Fleming & Calabrese 2021). We considered the area encompassed by the 95% contour line of the utilization distribution as the home range with lower and upper bounds of the 95% confidence interval. We estimated core home range within the 50% contour. We analysed data across 4 seasons based on red panda biology: pre-mating (November–December), mating (January–March), gestation and birthing (hereafter birthing, April–July) and cub-rearing (August–October).

Two sub-adults showed non-stationary behaviour during their dispersal (Fig. S1). Therefore we fragmented their data using the R package 'segclust2d' (Patin et al. 2019), identified stationary phases (Fig. S2) and averaged the resulting estimations (Calabrese et al. 2016).

Previous studies have used minimum convex polygon (MCP) calculations in home range estimations of red pandas (Yonzon 1989, Reid et al. 1991). Therefore, to allow comparison with previous studies, we estimated the home range of red pandas using the MCP method with 95 and 100% isopleths in the R package 'adehabitatHR' (Calenge 2006).

We evaluated the variation in home range size and core area across sex, age and body mass of red pandas and season using a linear mixed model (LMM) in the R package 'lme4' (Bates et al. 2005). Initially, we checked for correlations among variables using the variance inflation factor (VIF) but all variables had VIF <10. We therefore retained all variables in the final analyses (Quinn & Keough 2002). We included the effect of predictors (sex, age, body mass and season) as fixed factors and individual animal as the random intercept. The behaviour of

Table 1. Study animals and data used in analyses. We collared 10 red pandas in Ilam, eastern Nepal, in 2019. Dates are given as d/mo/yr

Animal ID	Sex	Age	Total GPS fixes used	Monitoring date Start	End
F1	Female	Adult	2589	30/10/2019	13/07/2020
F2	Female	Adult	723	17/12/2019	21/11/2020
F3	Female	Adult	1530	21/09/2019	25/06/2020
F4	Female	Adult	209	19/12/2019	7/02/2021
M1	Male	Adult	184	16/12/2019	19/10/2020
M2	Male	Adult	1375	1/12/2019	9/09/2020
M3	Male	Adult	1659	11/12/2019	14/02/2021
S_M1	Male	Sub-adult	57	10/12/2019	3/10/2020
S_F1	Female	Sub-adult	1389	10/12/2019	1/11/2020
S_F2	Female	Sub-adult	721	4/12/2019	17/10/2020

males and females is likely to vary with changes in biological requirements across seasons (Michel et al. 2018). Therefore, we included an interaction effect of sex with season in the global models for home range and core area. We selected the candidate model based on the smallest corrected Akaike's information criterion (AICc) (Burnham & Anderson 2002), and averaged models if more than 1 model was within an ΔAICc value of 2 (Burnham et al. 2011). We checked model diagnostics for the assumption of normality and homoscedasticity.

2.3. Conspecific interactions

We examined both static and dynamic interactions among red pandas. The static interaction, also known as home-range overlap, considers joint space use between 2 individuals and completely ignores the temporal aspect (Kernohan et al. 2001). Conversely, dynamic interaction refers to interdependency in the movement of 2 individuals (Doncaster 1990). We estimated home-range overlap based on the Bhattacharya coefficient (BC) (Bhattacharyya 1943) for evaluating static interaction (Long et al. 2014, Winner et al. 2018). The BC value ranges from 0 to 1, where 0 indicates no shared space and 1 indicates completely overlapping home ranges (Winner et al. 2018). We analysed the pairwise overlap on annual and seasonal scales. We considered 3 dyad groups: male–male, male–female and female–female. We included subadults in overlap estimations when they were settled in a new area after dispersing from their mothers. Because our data had a non-parametric distribution, we examined the difference in home-range overlap between pairs of overlapping dyads using a Kruskal-Wallis rank sum test.

We estimated the proximity rate (Prox) and dynamic interaction index for examining dynamic interactions (Long et al. 2014). The Prox measures the proportion of simultaneous fixes at which 2 individuals approached each other under a specified distance threshold (Bertrand et al. 1996). This index is sensitive to proximity, whereas the dynamic interaction index provides better insight into displacement and direction (Joo et al. 2018) and is an indicator of attraction and avoidance between individuals. We used the Prox to examine whether 2 overlapping red pandas avoided simultaneous use of the same space. Territorial and solitary mammals avoid approaching each other unless it is for some valid biological purposes, such as mating or territory defence (Macdonald

1983, Elbroch & Quigley 2017). Therefore, we considered 2 h as the time threshold for determining simultaneous fixes between 2 individuals. Furthermore, we assumed 100 m as the distance threshold to consider 2 individuals to be in proximity to each other, as red pandas are likely to see each other at 100 m distance in the montane forest. This index ranges from 0 to 1, with 0 indicating avoidance and values close to 1 indicating attraction.

For individuals that shared home range simultaneously, we calculated the dynamic interaction index. This metric gives the cohesion in animal movement with respect to direction and distance (Long & Nelson 2013). It results in 3 indices: dynamic interaction in direction (DI_θ), dynamic interaction in displacement (DI_d) and overall dynamic interaction (DI). The value of DI and DI_θ ranges from −1 to 1, while DI_d lies between 0 and 1. Negative values refer to opposing movements and positive values show cohesive movements, while 0 indicates random movement.

2.4. Recursion

We investigated recursion by estimating 4 recursive metrics: residence time (cumulative amount of time spent in a location), revisits (total number of visits to a previously visited site), return time (total time elapsed between successive visits to a site) and time spent during each visit at a site using the 'recurse' package (Bracis et al. 2018). We defined each location as an area with a 60 m radius which was based on average step length. We considered a 2 h interval as time threshold between 2 successive revisits.

We examined the differences in recursion variables across age and sex classes using the Wilcoxon rank sum test (W). We also checked the correlation of revisit frequency with residence time, return time and time spent inside each location. We used LMMs to examine the variation of each recursion parameters across season, age and sex classes with animal as the random intercept. All analyses were carried out in R (R Core Team 2020).

3. RESULTS

3.1. Home range

We recorded median (interquartile range, IQR) annual home range of red pandas as 1.41 km² (range: 0.39–6.72 km², IQR: 0.63–2.79 km²). The best-fit model included only sex as the predictor of home

range size (marginal R^2 = 0.67, conditional R^2 = 0.8, Table 2). Males had a larger average annual home range (1.73 km^2 [IQR 1.35–3.2 km^2]) than females (0.94 km^2 [0.48–2.64 km^2]), which was more pronounced in the birthing season (4.59 km^2 [3.23–5.94 km^2]), β = 0.89, p < 0.003, Fig. 1; Fig. S3). Conversely, females had a relatively larger home range size in the mating season (0.75 km^2 [0.55–2.98 km^2]), with the smallest range during the cub-rearing season (0.24 km^2 [0.2–0.29 km^2]). In comparison to the AKDEc, the MCP method at 95% isopleth resulted in

Table 2. Candidate models describing red panda home range estimates as a function of the body mass, age (adult, sub-adult), sex (male, female) and season (birthing, cub-rearing, pre-mating, mating). Adult, female and birthing were used as references for age, sex and season, respectively. Models were fitted with each animal (n = 10) as the random intercept, and other variables as fixed factors, including interaction between sex and season. Model selection was based on the smallest corrected Akaike's information criterion (AICc)

Models	df	AICc	ΔAICc	Weight
Sex	4	15.9	0.00	0.80
Age + Sex	5	20	4.17	0.10
Body_mass + Sex	5	21.5	5.69	0.05
Age + Body_mass + Sex	6	24.3	8.40	0.01
Age	4	25.2	9.38	0.01
Body_mass	4	26.4	10.53	0.00
Age + Body_mass	5	27.1	11.20	0.00
Season + Sex	7	29.4	13.51	0.00
Sex × Season + Age + Body_mass	12	59.2	43.38	0.00

smaller home ranges for males (median = 1.14 km^2), females (0.69 km^2), and all pandas combined (median = 0.93 km^2, V = 54, p < 0.008, Wilcoxon signed-rank test, Table S1).

Overall, red pandas used nearly one-fourth of the total home range as the core area on an annual scale (0.3 km^2 [0.07–2.24 km^2]). The averaged model included age, sex and body mass (Table S2). The core area increased with body mass (β = 1.21, p < 0.001), and males occupied a larger core area (0.48 km^2 [0.3–1.08 km^2]) than females across seasons (0.22 km^2 [0.1–0.3 km^2]), but the difference was not significant (p = 0.08, Table S3). However, sub-adults had a significantly larger core area (0.24 km^2 [0.05–0.89 km^2]) than adults (0.19 km^2 [0.03–2.25 km^2], β = 2.45, p = 0.005). The model diagnostics did not show any obvious deviations from normality and homoscedasticity.

3.2. Static interactions

Altogether, 13 pairs of red pandas, including 8 male–female, 1 male–male and 4 female–female, overlapped their home ranges (Fig. S4). The median annual overlap of all individuals was 0.47 (CI 0.19–0.61, range 0.06–0.76). The median overlap between male and female dyads was 0.55 (CI 0.23–0.62, range 0.08–0.85), while the female pairs overlapped ranges the least (median 0.16, CI 0.05–0.59, range 0.06–0.6). We observed 2 neighbouring males overlapping half of their home ranges (range 0.37–0.64). We also observed 1 male overlapping the home range of up to 4 females.
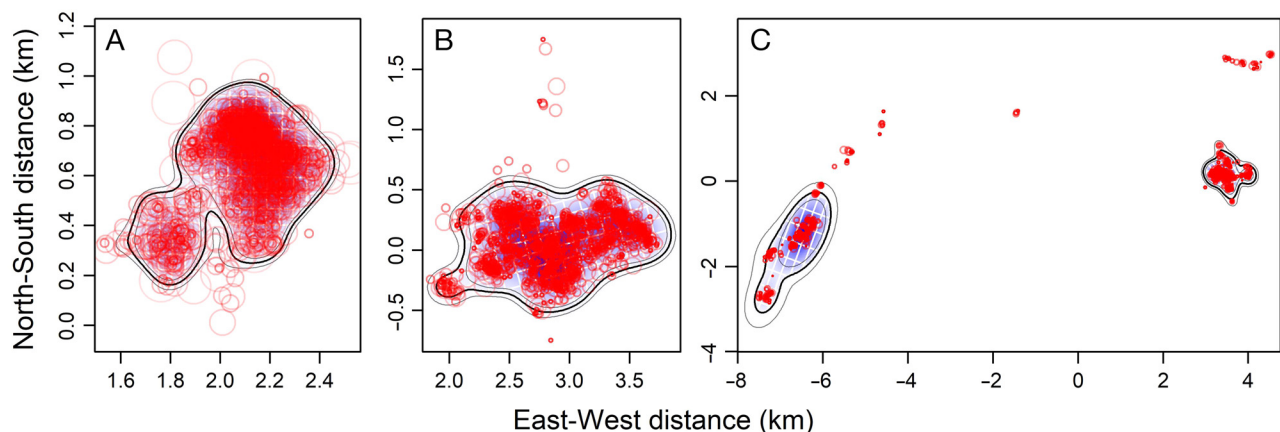

Fig. 1. Home ranges of red panda based on weighted and bias-corrected autocorrelated kernel density estimation: (A) range-resident female, (B) range-resident male and (C) dispersing sub-adult female. Zero distances along both axes represent the reference points located at the centre of the study area. Negative values along the x- and y-axes connote the distance west and south while positive values measure the distance east and north, respectively. The black line represents the point estimate of the 95% home range area. The inner and outer grey lines represent 95% confidence intervals. The red colour depicts the presence points of each individual and the purple grids connote the resolution of the density estimate.

However, none of these dyads exhibited statistically significant differences in overlap (Kruskal-Wallis $\chi_2^2 = 2.5$, p = 0.3). The overlap between males and females in the pre-mating and mating seasons was relatively higher (median 0.34) than in other seasons, but this observation was not statistically significant (Kruskal-Wallis $\chi_3^2 = 2.11$, p = 0.5). The overlap between female pairs remained minimal throughout the year (Fig. 2).

Only 9 pairs, comprising 6 male–female, 2 female–female and 1 male–male dyad, overlapped their core area. However, the annual overlap of core area was minimal (median 0.09, range 0.05–0.74). A single male pair overlapped a large proportion of their core areas (0.46). The median core area overlap between males and females was 0.14 (range 0–0.74) while the females overlapped up to 0.03 (range 0–0.2) of their core areas, although these overlaps were not significant (Kruskal-Wallis $\chi_2^2 = 3.45$, p = 0.17) nor did the degree of overlap vary across seasons for core areas (Kruskal-Wallis $\chi_3^2 = 0.15$, p = 0.9).

3.3. Dynamic interactions

Amongst the 13 home-range overlapping pairs, only 6 were observed within 100 m distance at the 2 h threshold (Prox = 0.02–0.11, Fig. 3; Table S4). These 6 pairs included 4 male–female and 2 female–female dyads, but all of these dyads had low proximity statistics (range 0.01–0.11; Table S4). The male–female dyads had some level of attraction (DI = 0.02–0.03), although the low DI value shows that the attraction level was weak (Table S4). One sub-adult female shared her home range with 2 males and showed attraction towards one ($DI_\theta = 0.07$) and avoided the other ($DI_\theta = -0.01$). As expected, the individuals in 1 female–female dyad avoided each other after approaching within 100 m of each other (DI = −0.02, $DI_\theta = -0.05$, $DI_d = 0.57$).

We observed male M3 and female F2 together on 9 different occasions. They were seen together on 4 occasions during the mating season, between 30 December and 15 March, and on 5 occasions outside
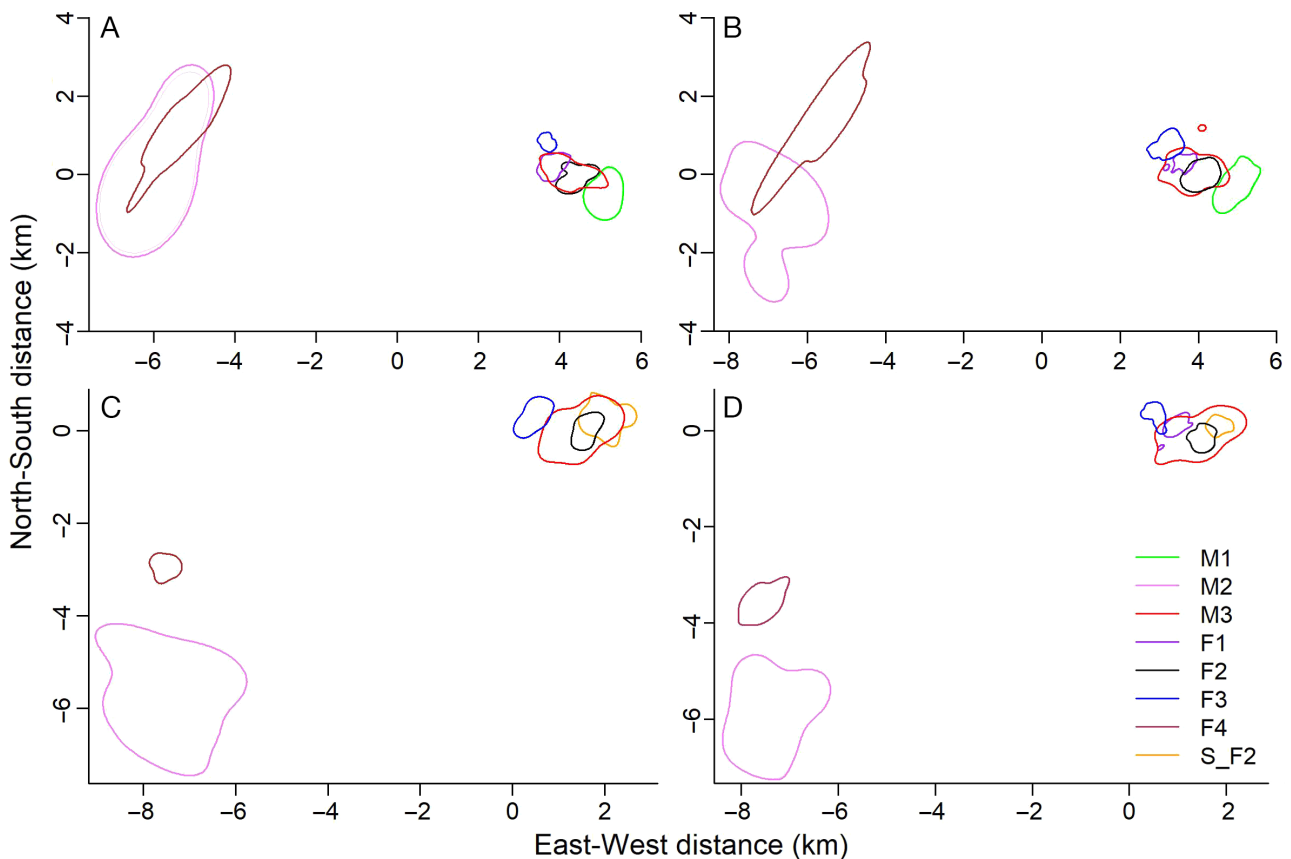

Fig. 2. Seasonal home range overlap among red pandas. The *x*- and *y*-axes correspond to distance (in km) along easting and northing, respectively (note different scales in panels). Zero values along both axes represent the reference points located at the centre of the study area. Colours represent home ranges of individual animals (n = 10; see Table 1) during (A) pre-mating, (B) mating, (C) birthing and (D) cub-rearing seasons
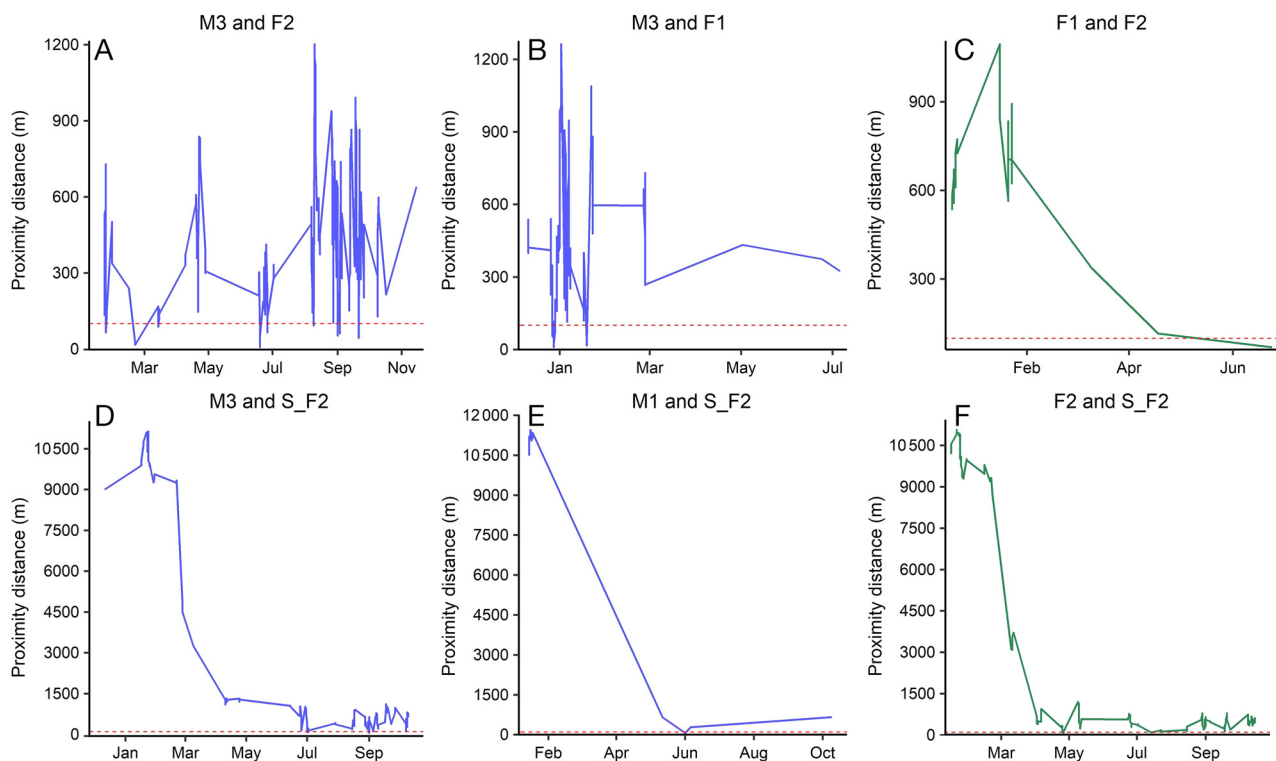
Fig. 3. Proximity plot of red panda dyads. Of 13 dyads, only 6 came close to each other (within 100 m) at the same time. (A,B, D,E) The blue line represents the proximity between male (M) and female (F) pairs, and (C,F) the green line represents proximity between female pairs. The x-axis represents the date, and the y-axis shows the distance between individuals in each dyad. The red dashed line is the 100 m threshold

the mating season: in June, August and October. Further, we observed M3 with another adult female (F1) on 2 occasions during the mating season: 27–29 December and 19–20 January. We also observed a sub-adult female (S_F2) with 2 males: M3 (2 July, and 1 September) and M1 (1 June) and with 1 female: (F2; 26 April and 14 July). S_F2 and F2 lived within 120 m of each other for 9 d on a second occasion. We observed 2 other female dyads: F1–F2 and F1–F3, together on single occasions on 25 June and 10 November, respectively.

3.4. Recursion

The median number of revisits of red pandas to 1 activity centre was 13 (IQR 6–24, range 1–110, Fig. 4) where they spent 105 h (47–228 h) on an annual scale. The revisit frequency (median = 18 [IQR = 8–30]; Fig. S5A) and residence time (161 h [68–288 h]; Fig. S5C) of females were not statistically significantly different than those of males (revisit = 8 [4–13], residence time = 58 h [25–98 h]). The median return time of red pandas to one activity centre was 129 h (25–896 h), where they spent 7 h (3–23 h) during

each visit. Males took longer to visit the same location (222 h [62–576 h]) than females (104 h [10–609 h]; Fig. S5E), but they spent marginally less time inside that area (4 [1.5–11] h) than females (5 [2–15] h, $W = 21$, $p = 0.06$, Fig. S5G). Adults and sub-adults did not show variation in the number of revisits (Fig. S5B); however, residence time of sub-adults was high (Fig. S6D) and they took less time to return to a location (Fig. S5F) and spent more time there than adults (Fig. S5H), but these recursive movements were not significantly different from those of adults ($p > 0.05$). Residence time increased with increases in visit frequency ($r = 0.78$, $p = 0.007$), while the time spent inside each area during respective visits followed an opposite trend to the number of revisits ($r = -0.62$, $p = 0.05$). The return time also decreased with increases in revisit frequency, but the difference was not significant ($r = -0.27$, $p = 0.44$).

The number of revisits (Tables S5 & S6) and time spent at 1 location during each visit (Tables S7 & S8) did not vary across seasons. However, the residence time of females was higher during the pre-mating season than during the birthing season ($\beta_{17.7} = 208.7$, $p = 0.03$, Tables S9 & S10). Likewise, the return time of males was longer during the mating ($\beta_{15.8} = 182.2$, $p =$
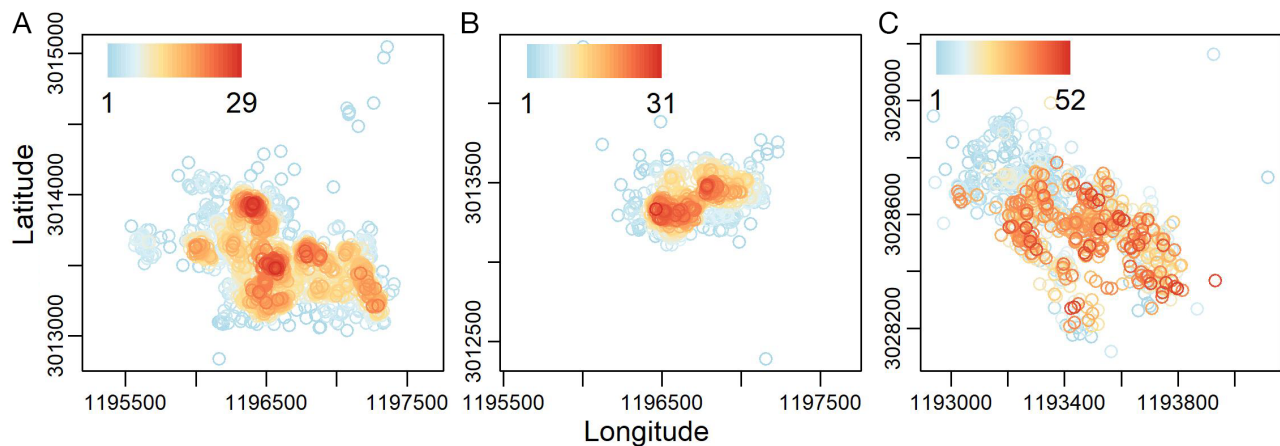
Fig. 4. Revisitation of locations by red pandas: (A) adult male, (B) adult female with cubs and (C) sub-adult female after settling in a new range (see Fig. S6 for all animals). The frequency of revisitation increases from blue to red. Latitude and longitude are expressed in UTM coordinates (m)

0.01) and pre-mating seasons ($\beta_{15.7} = 280.2$, p < 0.001, Tables S11 & S12) than during the birthing season.

4. DISCUSSION

Our findings demonstrate that red panda space use patterns varied across spatial scales, with marginal fluctuations in seasonal home range sizes. The variation in home range size was determined by sex, while body mass and age influenced the core area, but individual-level variation also existed. As we were limited to the effects of morphometric factors on space use, we did not aim to estimate the effect of disturbance and habitat fragmentation. Our results further supported the solitary and territorial nature of red pandas, although males did share habitat with some females, and they came in proximity more often during the mating season. In addition, recursive movement revealed site fidelity in red pandas which varied across seasons.

Available studies show that the home range size of red pandas may vary substantially. Yonzon (1989) reported 5.12 km² (1.38–11.57 km²) as the average home range size in Langtang National Park, Nepal. Other studies based in China reported home ranges of the Chinese congener *Ailurus styani*, ranging between 0.94 and 3.4 km² (Johnson et al. 1988, Reid et al. 1991, Zhang et al. 2009). The random effect (variance = 0.9) shows that individual-level variation in home range was high in the present study. Therefore, our estimation is not surprising, although it is less than a quarter of the home range estimated in Nepal (Yonzon 1989).

The discrepancy in home range among studies may be due to differences in habitat quality, disturbances

(McLoughlin & Ferguson 2000, Jetz et al. 2004) and methods employed in their estimation (Kernohan et al. 2001). The data collection technique and home range estimation method used in our study varied from those used by Yonzon (1989) and in studies on *A. styani* (Johnson et al. 1988, Reid et al. 1991, Zhang et al. 2009). The morphometric variation and habitat requirements between the 2 species may also have contributed to the differences in home range size. Future studies on *A. styani* with GPS telemetry may confirm this conclusion. Furthermore, inclusion of the non-stationary phases in home range estimation results in large and unrealistic home ranges (Kay et al. 2017), which was not addressed in previous studies, with the exception of Yonzon (1989). However, the sample size and sampling resolution of our study is larger than those of previous studies, likely making our findings more representative than other estimations.

Our results support the land-tenure hypothesis in red pandas, as males had larger home ranges than females. This observation is in line with Yonzon (1989) and consistent with reports on *A. styani* (Reid et al. 1991, Zhang et al. 2009), which could be attributed to the polygynous mating system in red pandas (Wei et al. 2005). However, the range size of sub-adults did not vary from that of adults despite the variation in their body mass. Therefore, our results did not support the body mass hypothesis at the home range scale; rather, this was true for core areas. The size of the core area occupied by sub-adults was larger than that of adults, which could be attributed to inefficient use of resources due to limited experience in habitat utilization. Our findings are similar to the home range patterns of other diet specialists, such as koalas (0.78 km², Davies et al. 2013), Huon

tree kangaroos *Dendrolagus matschiei* (1.39 km^2, Porolak et al. 2014) and bamboo lemurs (*Prolemur* and *Hapalemur* spp., 0.15– 0.62 km^2, Tan 1999). In relation to body size, our findings also corroborate those of the giant panda, another species with a specialized bamboo diet (Hull et al. 2015), and racoons *Procyon lotor*, which are omnivores in the order Carnivora (Beasley et al. 2007). We suggest that the herbivorous diet is the major cause of the smaller range size in red pandas than in solitary carnivores of similar body size (Sandell 1989). Likewise, the results did not support our prediction of larger home ranges of males during the mating season. On the contrary, males had relatively larger home ranges during the birthing and cub-rearing seasons and smaller ranges during the mating season.

Males are expected to increase their home range to find mating partners and increase their breeding success in the mating season (Yonzon 1989, Clutton-Brock 2016). A large home range also facilitates meeting their energy requirements (Larter & Gates 1994), as the mating season is characterised by cold temperatures and less availability of quality food resources. However, we found that the males occupied a relatively smaller range during the mating season. Nevertheless, the movement rate of males was high in that season, which reflects their increased effort to find mating partners and deter competing males (Bista et al. 2021b). Patrolling a large home range inflates the energetic cost of movement (Jetz et al. 2004, Tucker et al. 2014), and animals may be reluctant to increase the range size if the cost of expanding the home range is not compensated by energy gains (McLoughlin & Ferguson 2000). This was further supported by higher overlap in home ranges between males and females in mating and pre-mating seasons than in other seasons, suggesting that males adopted this strategy to meet their energy requirements by decreasing their territoriality and focussing on core areas where they could find females.

Conversely, the availability of food resources is high in the birthing and cub-rearing seasons, as the study area receives high rainfall during these times (Pradhan et al. 2001). For that reason, males covered a large area in these seasons, with minimal cost expended on securing their energy requirements. We speculate that the males utilize this opportunity to expand their home range, resulting in a larger range after the mating season.

Dispersers occupy vacant space and establish their territory with the onset of the birthing season. This might encourage males to occupy such space to keep male dispersers out and allow female dispersers in. This was evident in our study, as one sub-adult female settled in an unoccupied area which was later overlapped by an adult male in the birthing season. These observations show that the distribution of females is not the only determinant of spatial organization of males. Males also invest in territory maintenance and range expansion if the adjoining areas are unoccupied outside the mating season. The short return time of males to a given location in the birthing and cub-rearing seasons further bolsters the territory-maintenance hypothesis during these seasons. Similar observations of territory maintenance outside the mating season have been reported in mustelids (Erlinge & Sandell 1986) and procyonids (Gehrt & Fritzell 1998). These observations also suggest that home ranges of females would be relatively larger in areas with low productivity, and males would be less likely to overlap many female home ranges due to the high energetic cost of maintaining their territory (Fisher & Owens 2000). Therefore, we hypothesize that home range size of red pandas may be larger in areas with degraded habitat and lower precipitation.

Seasonal home ranges of females partly matched our prediction, as their range size was larger in the mating season, but they occupied a smaller range in the cub-rearing season. This variation could be explained by the resource-distribution hypothesis (Larter & Gates 1994, Gehrt & Fritzell 1998). Females must accumulate body-energy reserves to prepare themselves for the upcoming breeding cycle (Beck et al. 2003). We observed red pandas feeding on fruits of Himalayan whitebeam (*Sorbus* sp.) and wild kiwi *Actinidia collosa* to supplement their diet in the winter. However, these fruiting trees are randomly scattered throughout the forest, which forces these animals to roam over a large area. In addition, females are reluctant to take risks especially when they are with their cubs (Sergio et al. 2007), but as the cubs disperse with the onset of the following mating season, females are less risk averse (Brown et al. 1999, Sergio et al. 2007). This behaviour would have further contributed to females covering a larger area in the mating season (van Beest et al. 2016). The dispersal of female sub-adults may inflate their home range size, but we did not consider this phase in the home range estimation, as dispersers did not show stationary movement during the mating season. Conversely, the availability of high-quality food, especially bamboo, is high in the cub-rearing season in our study area, hence red pandas do not have to move over a large area to meet their energy requirements.

Our findings supported our prediction of spatial and temporal variation in overlap across sex classes. In general, red pandas overlapped a relatively larger proportion of home ranges than their core areas. The overlap between opposite sexes was high, while same-sex overlap varied between males and females. The females avoided same sex overlap, but we found a pair of males overlapping nearly half of their home range and core area. Our observation of the home range overlap between male–female dyads is consistent with previous studies (Yonzon 1989, Reid et al. 1991, Zhang et al. 2009). Variation in home-range overlap between males and females indicates shifts in activity areas across seasons. Such overlap was high in the pre-mating and mating seasons, which could be attributed to resource distribution (Larter & Gates 1994) and reproductive instinct (Clutton-Brock 2016). Nonetheless, we acknowledge the possibility of overlapping home ranges with non-collared individuals which was not captured in our study.

We observed some level of attraction between opposite sexes when they were in proximity to each other, but the frequency of meeting and attraction between them was lower outside the mating season. These observations of spatial and temporal interaction across sex classes suggest that red pandas are strictly territorial, and their interactions increase from the pre-mating season and peak in the mating season.

Territorial solitary males compete with each other to occupy the ranges of many females, resulting in high overlap in their ranges (Fisher & Owens 2000). However, we never observed neighbouring males together; rather they visited shared areas at different times. There was minimal overlap of the mating ranges between neighbouring males. This suggests that male pandas avoid physical aggression; rather, they use territorial marking to establish their territory. This could be attributed to their strategy to minimize the costs of territory maintenance as the physical confrontation may outweigh the benefit (Macdonald 1983, Elbroch & Quigley 2017). Further study is needed to understand the territory marking behaviour of red pandas in the wild.

Red pandas travelled long distances during the mating season, which indicates that they spend more time on the ground than in any other seasons (Bista et al. 2021b). As predation risk is relatively high on the ground, they may have selected the low lunar photoperiod, as the predation risk during darker nights is lower (Pratas-Santiago et al. 2017). Except in 1 case, we observed males and females together only in the low moonlight period (between 5 d before and 4 d after the new moon) during the mating season. Mating in winter ensures that the cubs are born in the monsoon season when food availability is high (Northrop & Czekala 2010). Our findings suggest that red pandas initiate their mating behaviour following the new moon in the winter solstice to maximize their breeding success.

Our data clearly show site fidelity in red pandas and support the prediction of having many activity centres within the home range. We found red pandas spending more time in sites that they visited more frequently. Similar behaviour has been observed in other mammals (English et al. 2014, Schloesing et al. 2020). We assume this behaviour was driven by the availability of high-quality habitat with an abundance of forage and resting sites that provide refuge from predators (Watts 1998, English et al. 2014, Merrill et al. 2020). Spending more time in familiar habitat also helps them to minimize energy loss in foraging and protection (Schloesing et al. 2020). This correlates with our observations that females spent long hours in certain habitat patches in the pre-mating season when they were with their dependent cubs, which would have minimized their movement cost and predation risk. Furthermore, resource-recovery rate appears to have influenced the recursive movement of the study animals (Berger-Tal & Bar-David 2015). For example, the return time of males to a location was longer in the mating and pre-mating seasons than in the other 2 seasons, which could be linked with the resource recovery cycle. The study area receives minimal precipitation and remains cold during these 2 seasons, while nearly 80% of total annual precipitation falls in birthing and cub-rearing seasons (Subba et al. 2019). This high variation in rainfall directly influences the availability and recovery of food resources, resulting in the variation in recursive movement across seasons.

Seasonal differences in recursive movement patterns further suggest a response to varying biological activities across seasons. For instance, the short-term return time occurring in 5–10 d also suggests a territory defense strategy. Red pandas mark their territory with chemicals, although scat piles are also believed to serve as territory marks (Bista et al. 2021a). This return time could be due to the decay rate of chemicals used for territory marking (Berger-Tal & Bar-David 2015). Additionally, animals occupy certain areas for refuge from predators and disturbances (Sarmento & Berger 2020). This could be important in human-dominated landscapes where the risk level varies on a temporal scale ranging from diel cycles to seasons. This behaviour would have some effect on the recur-

sive movement of red pandas, as our study area was greatly influenced by human activities. These observations demonstrate that certain areas within the home range possesses high ecological value. Red pandas remember such sites, repeatedly visit those areas and spend long periods there.

Our study has shown that space use, interactions and site fidelity of red pandas vary across seasons. Further, the data suggest that space use by female red pandas is driven by resource availability and distribution while the reproductive instinct instigates the space use pattern of males. These results may have wider implication for the conservation of solitary herbivores including, but not limited to, giant pandas, koalas and bamboo lemurs, such as the greater bamboo lemur *Prolemur simus* and the golden bamboo lemur *Hapalemur aureus*. Our findings have implications in designing future studies on resource use and presence–absence surveys. Population estimation of red pandas is challenging due to their elusive and solitary nature, low density and difficult topography of their montane habitat. Therefore, home range size estimated in this study can provide a strong base for population estimation of red pandas in a given habitat.

This study highlights the importance of conserving bamboo and other high-quality fruiting trees in biologically critical seasons. Furthermore, the cubs also separate from their mothers and disperse from their natal sites following the winter solstice. As increased disturbances may affect mating success and dispersal, we suggest regulating human activities for at least 4 mo following the winter solstice. Despite the small sample size, this study also offers insights into the conspecific interactions and the territorial nature of red pandas and suggests that some areas within their territories are visited repeatedly. However, we lack information on the characteristics of these revisited sites. Therefore, further research should focus on identifying such ecologically important areas. Evaluation of the role of habitat covariates, disturbances and fragmentation in space use patterns was beyond the scope of this study. Hence, our findings warrant further work to assess the effects of these factors on red panda space use patterns and site fidelity. Yet, importantly, this study suggests minimizing disturbances and emphasizes the importance of the conservation of ecologically critical sites within the habitat range of this habitat specialist.

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