WILDLIFE BIOLOGY

Research article

Red pandas on the move: weather and disturbance effects on habitat specialists

Damber Bista[1], Greg S. Baxter[1], Nicholas J. Hudson[2], Sonam Tashi Lama[3], Janno Weerman[4] and Peter J. Murray[1,5,6]

[1]University of Southern Queensland, Institute for Life Sciences and the Environment, Toowoomba, QLD, Australia
[2]The University of Queensland, School of Agriculture and Food Sustainability, Gatton, QLD, Australia
[3]Red Panda Network, Baluwatar, Kathmandu, Nepal
[4]Royal Rotterdam Zoological & Botanical Gardens, Postbus, Rotterdam, the Netherlands.
[5]University of Southern Queensland, School of Agriculture and Environmental Science, Toowoomba, QLD, Australia.
[6]The University of Queensland, School of Veterinary Science, Gatton, QLD, Australia

Correspondence: Damber Bista (damb.2007@gmail.com)

Wildlife Biology
2024: e01384
doi: 10.1002/wlb3.01384
Subject Editor: Scott Newey
Editor-in-Chief: Ilse Storch
Accepted 16 October 2024

Challenging weather events can make winters harsh for habitat and diet specialists. They may also incur high energetic costs due to reduced availability of food resources and elevated predation risk. Using GPS satellite collars we tracked the movement of the red panda *Ailurus fulgens* in the Himalayas, and evaluated the effects of weather and disturbances on their movement patterns and habitat use. We also analyzed the nutritional content of their key diet plant species. The mean daily distance travelled by red pandas was 748 ± 40 m (median 573 m), with no detectable effect of weather conditions and snow age. However, males travelled further than females when there was snow on the ground ($\beta = 410.5$, $p < 0.02$). Red pandas moved between 2528 and 3250 m during the study period with the mean elevation 2857 ± 107 m when snow was on the ground and 2816 ± 99 m without snow. A group of disturbances such as distance to settlements, herding stations, and roads, and geo-physical variables affected their habitat use when the forest was covered with snow as they occupied areas away from human settlements ($\beta = 0.36$, $p = 0.03$), exhibited affinity for high elevations ($\beta = 0.37$, $p = 0.02$), and avoided steep slope ($\beta = -0.21$, $p = 0.04$). These movement patterns suggest a risk aversion strategy with males' behaviour appearing to be driven by reproductive instincts. Additionally, the distribution of their major dietary vegetation varied across the elevation gradient, leading to differences in the nutritional content of the diet, which might also have some effects on habitat use. Overall we found that despite red pandas exhibiting risk aversion behaviour, challenging weather events like snowfall could exacerbate the adverse effects on these habitat specialists.

Keywords: *Ailurus fulgens*, elevational gradient, habitat use, movement ecology, risk avoidance, snowfall

NORDIC SOCIETY OIKOS
www.wildlifebiology.org

Introduction

Given the distinct seasonal variations in temperate regions, animals, particularly habitat and diet specialists, residing there are more likely to respond to climatic variables than in other regions (Droghini and Boutin 2018, Pedersen et al. 2021). These animals have high energy costs in winter due to adverse weather events such as snowfall (Parker et al. 1984), reduced availability of food resources (Korslund and Steen 2006), and elevated predation risk (Huggard 1993). Therefore, winters are likely to be challenging for wildlife inhabiting such habitats. To cope with winter environmental conditions, wildlife may alter movement, activity, and behaviour (Schmidt et al. 2016, Droghini and Boutin 2018, Pedersen et al. 2021, Johansson et al. 2022), shift their ranges (Pedersen et al. 2021), and modify pelage patterns (Mills et al. 2018). Human presence is escalating in most wildlife habitats which is likely to affect the responses of animals to their environment (Doherty et al. 2021) as they attempt to adapt to optimize their survival, and failure to cope with harsh weather and disturbances could be fatal.

Some animals are well adapted to living in the cold. They may have high metabolic rates (Clarke et al. 2010, Fei et al. 2017), become less active to minimize their energy loss (Richard et al. 2014), and move to lower elevations to avoid snowfall (Pedersen et al. 2021). Wildlife prefers to occupy less disturbed areas having higher availability and quality of food resources (Schmidt et al. 2016, Pedersen et al. 2021). They move faster when they feel threatened and stressed while moving across unfavourable habitats (Fahrig 2007, Tucker et al. 2018). However, they may have to compromise and be forced to use less suitable habitats where human disturbances could be high and/or with poor availability and quality of food sources. However, most studies to date have reported their response to a particular variable, with limited research considering the combined effects of multiple factors. Habitat specialists respond quickly if the changes are not in their favour (Pfeifer et al. 2017, Tucker et al. 2018). Amongst the several factors influencing habitat use and movement patterns (Fig. 1), this study attempts to examine the responses to three factors simultaneously: weather, disturbance, and nutrition of a habitat and diet specialist, the red panda *Ailurus fulgens*.

Red pandas inhabit temperate forests with an abundance of bamboo in the understory in the eastern Himalayas (Glatston et al. 2015). They are diet specialists as over 95% of their diet is comprised of bamboo leaves and shoots (Bista et al. 2022b) choosing berries and leaves of other vegetation to supplement their diet (Yonzon and Hunter 1991,

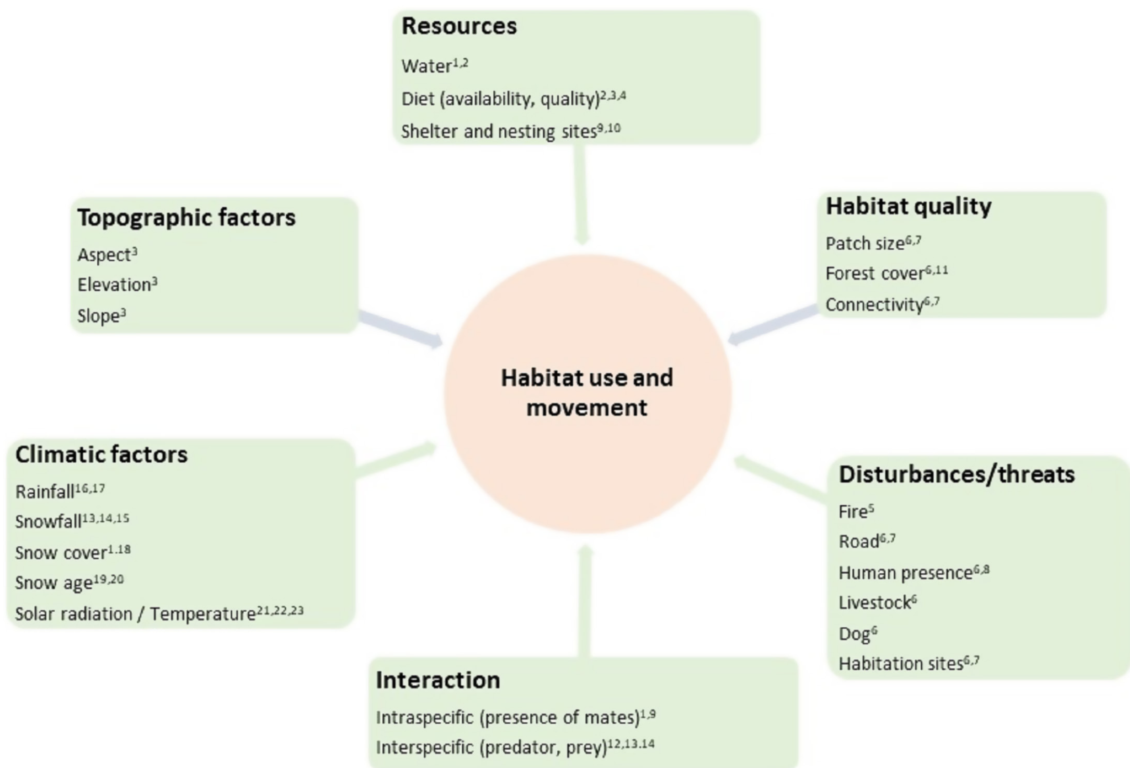

Figure 1. Conceptual framework showing factors affecting the habitat use and movement patterns of wildlife includingred pandas. These factors could influence these patterns both positively and/or negatively. [1]Yonzon (1989a); [2]Pradhan et al. (2001); [3]Bista et al. (2023); [4]Bista et al. (2019); [5]Thapa et al. (2018); [6]Bista et al. (2021a); [7]Bista et al. (2021b); [8]Doherty et al. (2021); [9]Bista et al. (2022a); [10]Sarmento and Berger (2020); [11]Acharya et al. (2018); [12]Tablado et al. (2014); [13]Droghini and Boutin (2018); [14]Homolka and Heroldová (2003); [15]Schmidt et al. (2016); [16]Elliot et al. (2014); [17]McMillan et al. (2022); [18]Pedersen et al. (2021); [19]Sheppard et al. (2021); [20]Murray and Boutin (1991); [21]Fei et al. (2017); [22]Liu et al. (2016).

Pradhan et al. 2001, Panthi et al. 2015). They maintain a territory using scent marking from their anal glands, urine and faeces (Conover and Gittleman 1989, Wood et al. 2003). Red pandas are polygynous as a male overlaps the territory of more than one female (Yonzon 1989, Bista et al. 2022a). They are forced to share their habitat with humans in most of their range, where local people rely on red panda habitat for firewood, livestock herding, and many other activities (Glatston et al. 2015, Thapa et al. 2018). Human encroachment is increasing in red panda ranges, which is further aggravating pressure on their habitat (Dalui et al. 2020, Hu et al. 2020). Being a habitat specialist, red pandas are likely to respond to any significant change in their environment no matter what the cause.

Many studies have reported red pandas' responses to human-induced disturbances (Yonzon et al. 1991, Yonzon and Hunter 1991, Acharya et al. 2018). They stay away from human settlements, avoid roads, and prefer less disturbed habitat patches (Bista et al. 2021a, b). All these studies have overlooked the effect of weather events on red pandas, even though understanding their role is critical as habitat specialists like red pandas are susceptible to changes in their environment. Our study addresses this gap by examining the effects of weather and human-induced factors, which will be vital for predicting how climate change may affect this species. Besides, the findings of this research will provide a baseline for future studies and offer valuable insights for conservation strategies, particularly in the context of climate variability.

Red pandas are adapted to an arboreal life in montane habitats, and as they spend most of their time in trees, unusual weather events like snowfall are likely to have adverse effects on their movement on the ground (Yonzon 1989). Furthermore, the cost of thermoregulation is high in winter due to reduced availability and quality of food sources (Fei et al. 2017). We therefore set two a priori hypotheses: 1) red pandas reduce their travel distance and speed during challenging weather events, such as snowfall; and 2) they occupy lower elevations to avoid snow even if this requires adapting to a less suitable diet and facing more disturbances.

Material and methods

Study area

The study was carried out in the Ilam and Panchthar districts in eastern Nepal (27°03′36″N, 87°59′24″E, Fig. 2), which ranges between sub-tropical and temperate climate zones. This area borders Singalila National Park in India to the east. The mean annual temperature is 13.1°C with precipitation of 2590 mm (Bista et al. 2021b). There are four distinct seasons in their range: winter (December–February), pre-monsoon (March–May), monsoon (June–September), post-monsoon (October–November), where the area may receive snowfall from December to April (Bista 2022). The study area harbours sub-tropical and broad-leaved mixed and deciduous forests with an abundance of bamboo in the understorey. Livestock herding is common with some herders following transhumance herding by moving their livestock to low elevations during the winter. Hence this area represents a human-dominated landscape with several settlements, roads, and livestock herding sheds distributed throughout the red panda habitat. Most of the human settlements are in the lower elevation compared to livestock herding sheds, while roads traverse throughout.

Data collection and processing

We captured and collared 10 red pandas including four males and six females, in 2019, with GPS satellite collars following a standard operating procedure (Bista et al. 2021d). These collars were set with 12 fixes daily (one fix every two hours) transferred remotely every 24 hours. To minimize telemetry error, we retained successful GPS fixes with a dilution of precision < 5 (Tahsin et al. 2015). Additionally, we omitted locations that were beyond our study area between 2000 and 3636 m. We excluded dates having less than 50% of fixes, i.e. 6 records of an individual to minimize the error in daily distance measurements and included those fixes with a 2-hour interval of each animal.

We included ten covariates comprising weather (precipitation, snow cover, snow age, solar radiation and temperature), disturbances (distance to herding shed, road, and settlement), and geophysical variables (elevation and slope, Table 1). Given the short period required for snow to melt in the study area, we collected data for seven days before, and after a snowfall event, and recorded weather data during winter. We collected daily rainfall and snowfall data from 1 December 2019 to 31 March 2020. We categorised the precipitation into rainfall, snowfall, and clear day. A day was classified as rainy if it had rained within the preceding 24 hours, and similarly for snowfall and clear days. Snowfall days were counted even if accompanied by rain. We categorised snow cover into two categories: yes (present) or no (absent), and snow age into three groups: no snow, fresh snow (hereafter fresh) and old snow (hereafter old). Snow that accumulated within the past 24 hours was classified as fresh. The GPS collars had in-built recorders for recording ambient temperature and we used those readings in our analyses.

We obtained the digital elevation model (DEM, shuttle radar topography mission, 1 arc-second) of the study area from the USGS and retrieved the slope and solar radiation of the used location. We recorded the location of herding stations and settlements during the field survey and obtained the road layer from the open street map. The Euclidean distance between these features and the location of red panda was measured.

We collected the leaves of bamboo species found within red panda habitat, specifically *Yushania maling* and *Thamnocalamus aristatus*. Additionally, we collected fruits of other red panda diet species including wild kiwi *Actinidia callosa*, sorbus *Sorbus cuspidate*, and *Magnolia cathcartii*. These samples were sent to the Nepal Environmental and Scientific Services (NESS) laboratory for detailed analyses of their nutritional content.

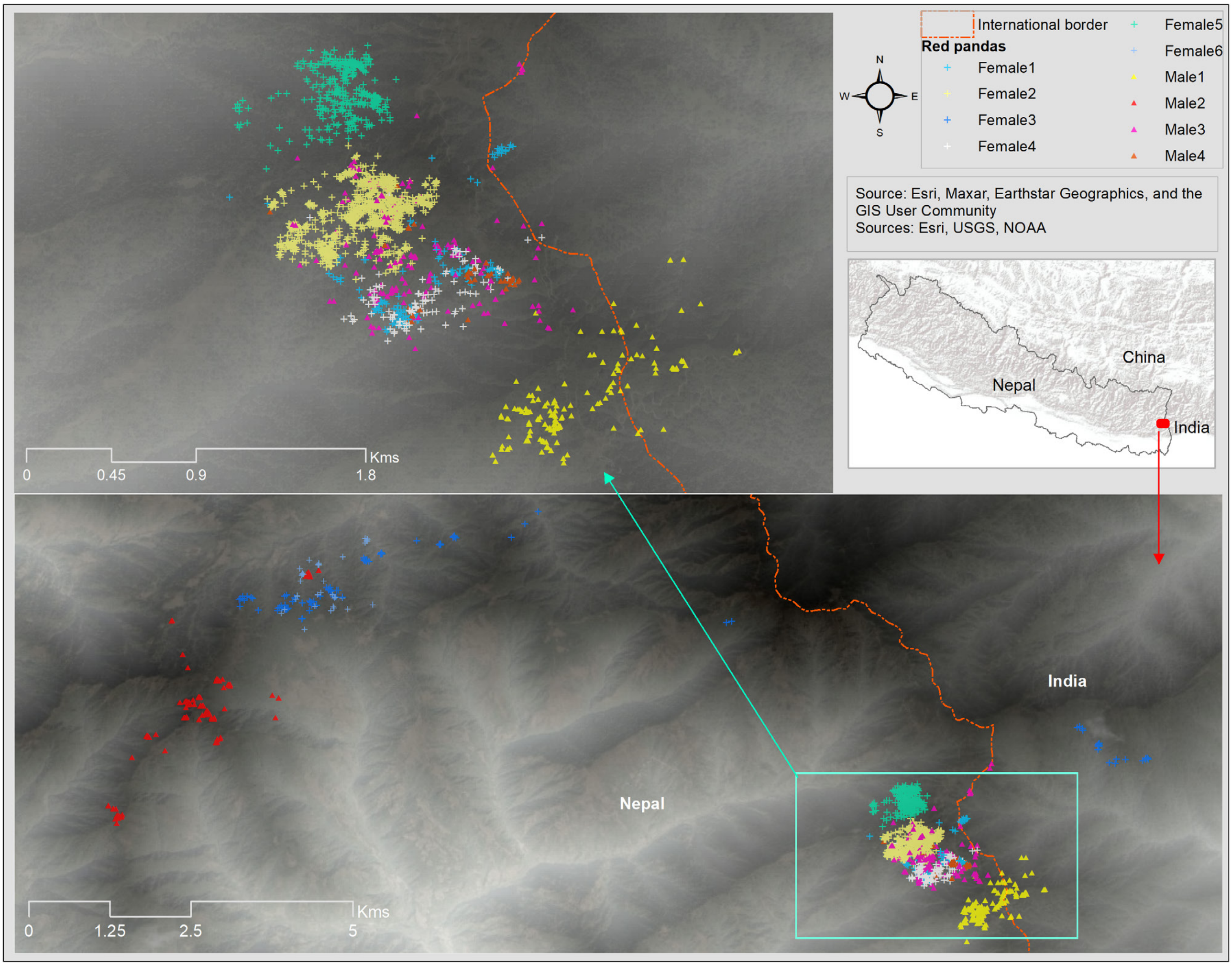

Figure 2. The inset shows the study area in eastern Nepal bordering India to the east. A total of 10 red pandas comprising six females and four males were monitored during the study period. GPS fixes of each study animal are highlighted with different colours, where + and Δ signs represent females and males respectively .

We estimated the water content of plant samples by oven-drying them at 70°C for 24 hours. For nutritional analysis, we used the Kjeldhal method for protein (978.04, AOAC 2016), Soxhlet-extraction for crude fat (2003.05, AOAC 2016), and the fitted glass crucible method for lignin content (978.10, AOAC 2016). We estimated cellulose and hemicellulose content from acid detergent fiber (ADF), acid detergent lignin (ADL) and neutral detergent fibre (NDF) using the method by Goering and Van Soest (1970). We calculated the cellulose percentage as the difference between ADF and ADL, while the hemicellulose percentage as the difference between NDF and ADF (Goering and Van Soest 1970).

Data analyses

We calculated step-length, speed and time lag using the 'move' package, ver. 4.2.4 (Kranstauber 2020). We used a linear mixed model (LMM) in 'lme4' package, ver. 1.1–35.1 (Bates et al. 2015) to examine the effects of weather events on the movement pattern of red pandas. Then we fitted the LMM with individual animals as a random intercept for weather effect on red panda movement with daily distance and speed as the response variables. We used the generalized linear mixed model to analyse the variables driving the habitat use of red pandas in response to snow cover on the forest floor by fitting individual animals as random intercept, while geophysical and disturbance variables were included as fixed factors. Initially we standardized all continuous variables and examined multicollinearity, and retained only those with a generalized variation inflation factor $GVIF^{1/2\ Xdf} \leq 2$ for further analyses (Fox and Monette 1992).

We selected the candidate model with the smallest corrected Akaike's information criteria (AICc) but we averaged models if more than one model was within 0–2 AICc (Burnham et al. 2011). We used one-way ANOVA to examine the differences in elevation and the nutritional content across various diet species. We used Kruskal–Wallis rank sum test, if their distribution was non-normal. Then, we used post-hoc tests: Tukey and Dunn tests to examine the pairwise differences for parametric and non-parametric data. We

Table 1. Description of covariates included in this study.

Variables	Description	Range
Sex	Sex of study animals.	Male, female
Distance	Sum of the 2-h step length of an individual in 24 h referred as daily distance unless and otherwise specified (m)	90–2880 m
Speed	Rate of change in distance per second of an individual (m sec^{-1})	0–0.62 m/s
Precipitation (precip)	Forms of precipitation events considered in 24 h. Snowfall was considered if both rain and snowfall occurred in 24 h	Snowfall, rainfall, clear (no precipitation)
Snow cover (snow_cov)	Forest floor condition whether it was covered with snow	Yes, no
Snow age (snow_age)	Age of snow considered based on accumulation within 24 h	Fresh, old
Temperature (temp)	Mean daily temperature (°C) recorded by the GPS collars. Mean temperature was 16.3 ± 3.5°C	–1–26°C
Distance to herding shed (herd_shed)	Euclidean distance between the presence record and the nearest cattle herding station (m)	90–5115 m
Distance to road (road)	Euclidean distance between the presence record and the nearest road (m). Source: www.openstreetmap.org	0–2616 m
Distance to human settlement (settel)	Euclidean distance between the presence record and outskirt of the nearest settlement (m)	30–3309 m
Elevation (elev)	–Elevation used by red pandas (m). Source: shuttle radar topography mission (SRTM, 1 arc-second), global digital elevation model (DEM) - https://earthexplorer.usgs.gov.	2430–3270 m
Slope	Slope used by red pandas (°). Source: SRTM, 1 arc-second DEM - https://earthexplorer.usgs.gov	3–51°
Solar radiation (solar)	Solar radiation received at the location used by red pandas. Source: SRTM, 1 arc-second DEM - https://earthexplorer.usgs.gov	0.3–303.2 KW m^{-2}

reported the mean (± SD) and median values of the daily distance and elevation traversed by red pandas. All analyses were carried out in R (www.r-project.org).

Results

We recorded seven snowfall events and 20 rainfall events during the study period. After removing erroneous records, we had 1559 locations of eight red pandas available for analysis. The mean daily distance travelled by red pandas was 747 ± 588 m (median 573 m). They travelled further over 24 hours during snowfall (984 ± 791 m, median 802 m) compared to clear (774 ± 562 m, median 629 m) and rainy days (521 ± 472 m, median 376 m, Fig. 3A). Distances covered on the snow field (870 ± 673 m, median 662 m) were longer compared to days without snow on the ground (636 ± 475 m, median 497 m, Fig. 3B). Similarly, red pandas travelled longer distances on fresh snow (984 ± 791 m, median 802 m) compared to old snow (834 ± 633 m, median 643 m, Fig. 3C).

Red pandas moved between an elevation of 2528 and 3250 m during the study period. The mean elevation used on the snowfall day was 2880 ± 93 m (median 2878 m) which showed little variation compared to clear (2835 ± 91 m, median 2852 m) and rainy days (2825 ± 126 m, 2826 m, Fig. 3D). Similarly, the occupied elevation showed minimal variation with (2857 ± 107 m, median 2861 m) and without snow on the ground (2816 ± 99 m, median 2837 m, Fig. 3E). the elevation difference was negligible between the days with fresh (2880 ± 93 m, median 2878 m) and old snow on the ground (2853 ± 110 m, median 2859 m, Fig. 3F).

The additive effect of precipitation, sex of the panda, snow cover, temperature, and the interaction of sex with precipitation and snow cover explained the effect of weather on the distance travelled by red pandas (Table 2). Among these factors, only snow cover had a significant effect, with males travelling nearly double the distances travelled by females when the ground was covered with snow (males = 1264 ± 872 m, females = 662 ± 415 m, $\beta = 423.5$, $p = 0.02$ Fig. 4A, Supporting information).

On the other hand, the averaged model (the null model, and the model with snow cover), explained the effect on speed (Table 3), and only the influence of snow cover was significant for males ($\beta = 0.01$, $p < 0.001$, Fig. 4B).

Geo-physical parameters and disturbance variables explained the effects of red pandas' habitat use when snow was present (Table 4). They preferred high elevation ($\beta = 0.37$, $p = 0.03$, Fig. 4C), avoided steep terrain ($\beta = -0.21$, $p = 0.04$, Fig. 4D), and lived farther from human settlements ($\beta = 0.36$, $p = 0.03$, Fig. 4E). They further showed marginal affinity for solar radiation ($\beta = 0.22$, $p = 0.09$) and moved close to roads ($\beta = -0.33$, $p = 0.07$) when the forest floor was covered in snow.

There was a significant variation in the elevation of key diet vegetation ($F_2 = 22.5$, $p < 0.001$, Fig. 5A). The post-hoc test (Tukey) revealed that *T. aristatus* (2927 ± 104 m, median 2919 m) and fruiting trees (2919 ± 49 m, 2919 ± 49 m, median 2914 m) were found at higher elevations than *Y. maling* (2767 ± 124 m, median 2787 m, $p < 0.001$).

The nutritional content varied amongst the red panda diet species (Fig. 5B, Supporting information). While the percentage of the protein and crude fat content did not significantly differ between plant species, there were significant differences in cellulose (Kruskal–Wallis $X^2_2 = 11.07$, $p = 0.004$) and hemicellulose (Kruskal–Wallis $X^2_2 = 8.62$, $p = 0.01$) levels. The post-hoc (Dunn) test showed that both cellulose and hemicellulose were higher in the bamboo species compared to fruiting trees ($p < 0.05$). Similarly, lignin content varied

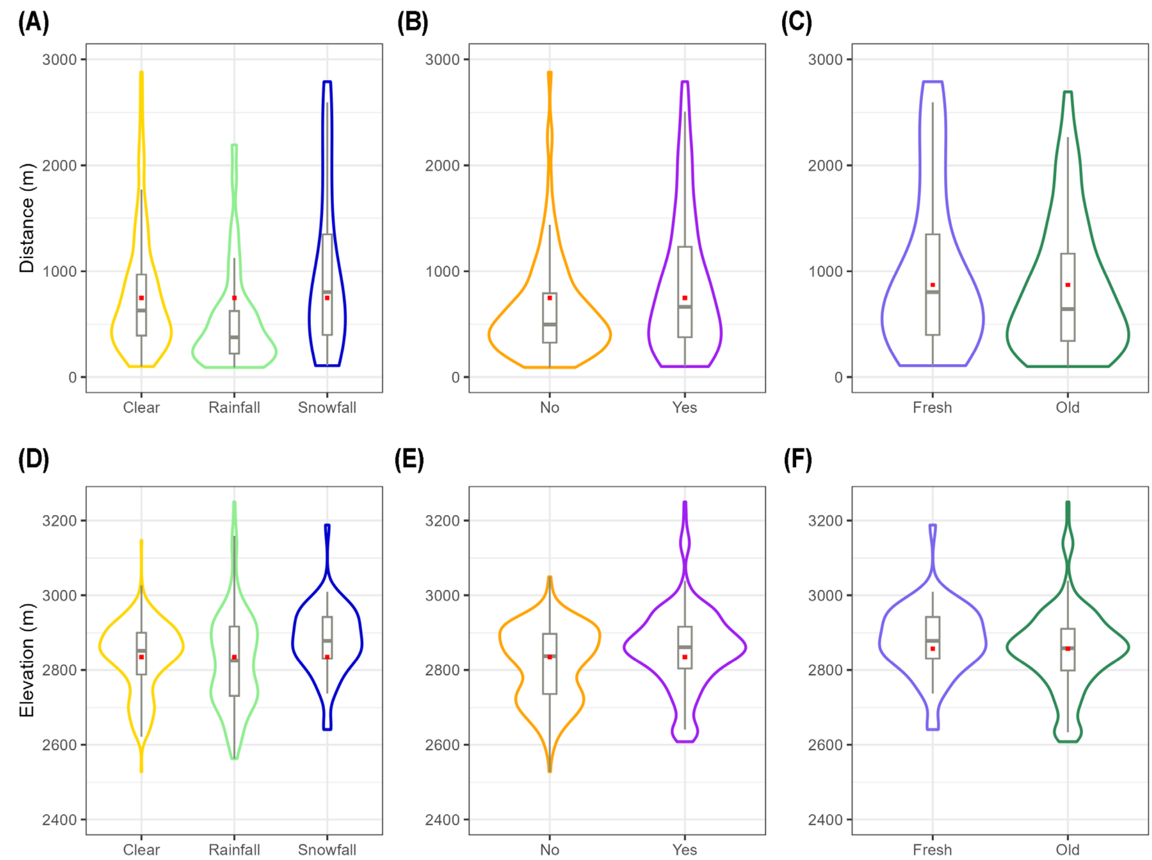

Figure 3. Violin plots show the distribution of raw data, where boxplots inside each violin plot represent the daily distance and elevation covered by red pandas. The red square indicates the mean while the horizontal line within the box represents the median. (A)–(C) Panels on the first row show the daily distance travelled in response to (A).Precipitation, (B) Forest floor snow cover, and (C) Snow age. Panels on the second row represent elevation covered in response to (D) Precipitation, (E) Forest floor snow cover, and (F) Snow age.

between diet species (Kruskal–Wallis $X^2_2 = 7.9$, $p = 0.02$), with higher levels in fruiting trees and *Y. maling* than in *T. aristatus* ($p < 0.05$).

Discussion

Challenging weather events make winters harsh for wildlife inhabiting temperate regions, yet little is known about how habitat and diet specialists respond to such conditions. We investigated the fine-scale movement and habitat use of red pandas in response to weather and disturbance variables in a human-modified landscape. Our results unveiled the significant effects of snow cover on their daily distance and speed, with variations observed between sexes. Disturbances and geo-physical variables also influenced habitat use in the presence of snow on the ground, with red pandas occupying higher elevations and avoiding steep slopes and areas in proximity to human settlements. Risk aversion appeared as a key driver of habitat use in snow-covered forest with males being more responsive to weather changes, potentially due to reproductive instincts. While this is true, individual variation in movement patterns (marginal/conditional R^2 0.17/0.26) and habitat use (marginal/conditional R^2 0.06/0.41) was significantly high, likely due to differences in age, personality, reproductive status, and micro-habitat conditions.

There was no significant effect of weather conditions on the daily distance travelled by red pandas, which did not support our prediction that they would travel less distance during unusual weather events. Red panda average annual daily distance travelled was 756 m (Bista et al. 2021b), with individuals in this study covering more than 800 m per day

Table 2. Candidate models describing the climatic variables affecting the daily distance travelled by red pandas. [#] Precip = precipitation, Snow_cov = snow cover, Temp = temperature.

Models[#]	DF	Logik	AICc	ΔAICc	Weight
Precip + Sex + Snow_cov + Temp + Precip [Sex] + Snow_Cov [Sex]	11	−1623.49	3270.3	0	0.93
Precip + Sex + Snow_cov + Precip [Sex] + Snow_Cov [Sex]	10	−1627.21	3275.5	5.23	0.07
Precip + Sex + Snow_cov + Temp + Precip [Sex]	10	−1632.41	3285.9	15.63	0

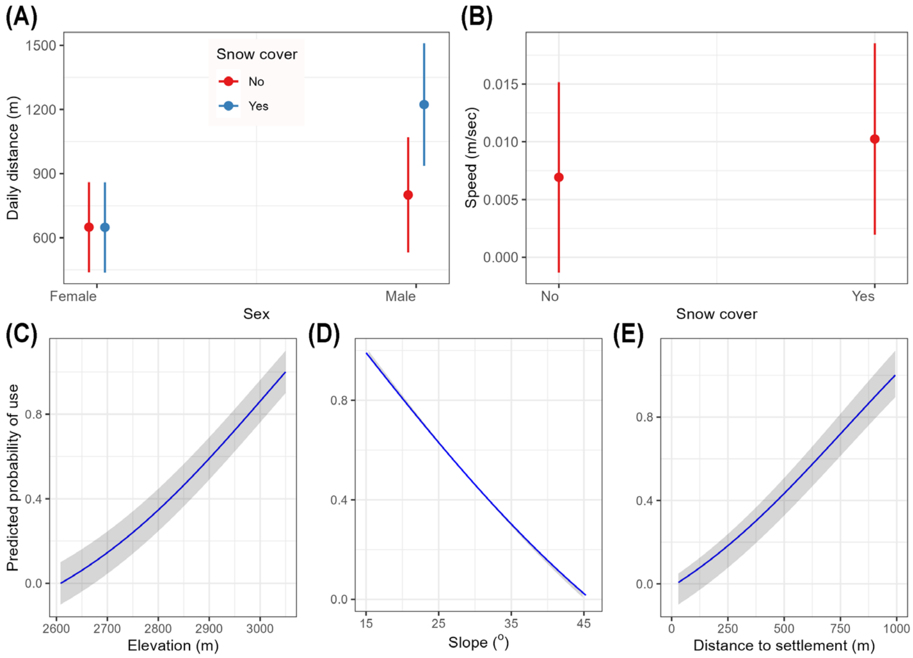

Figure 4. Predicted movement and habitat use patterns in response to snow cover. (A) Predicted distance of males and females in the presence and absence of snow cover on the forest floor. (B) Predicted speed in response to snow cover. Panels on the second row represent the predicted probability of habitat use in the presence of snow cover in response to (C) Elevation, (D) Slope, and (E) Distance to settlement. The circles on the first row connote the predicted values while lines on both sides show the 95% CI. Similarly, the blue line and grey ribbon on the second row show the trend line of the relative probability of habitat use and 95% CI respectively.

except during rainfall on snowfall days and when the ground was covered with fresh or old snow. Usually, red pandas are more active during the mating season (Bista et al. 2021b), which could be a reason for them covering long distances. Notably, males travelled longer distances than females during snowfall, likely due to their polygynous nature. The snowfall events overlapped with the mating season when males are more active than females (Yonzon and Hunter 1991, Bista et al. 2022a). Territory marking frequency of males is usually high during this time (Conover and Gittleman 1989, Zub et al. 2003). Additionally, rainfall and snowfall wash-off territory marks, with snowfall being more destructive as it completely covers the faecal pellets, which provoke males to (re)mark their territories to advertise their reproductive status and protect territories (Allen et al. 2016, Bista et al. 2022a). However, it appears that males have made a trade-off between reproductive effort and predation risk. The predation risk is high when there is snow on the ground as there are fewer obstacles and reduced camouflage compared to a snow-free forest cover. Predation risk is buffered to some extent after precipitation as predators struggle to detect prey due to high atmospheric pressure following rainfall and snowfall (Droghini and Boutin 2018). Nevertheless, males may experience stress while walking on the snow-covered forest floor, which is evidenced by their relatively higher speed (Fig. 4B).

Contrary to expectations, our study did not support the hypothesis that red pandas move to lower elevations during challenging weather events. Despite the minimal differences in elevations used during such events, red pandas exhibited an affinity for higher elevations. This finding contradicts Yonzon (1989) who reported their movement towards low elevations during winter. Perhaps they don't find a mild snow event a large hindrance since they are well-adapted for cold environments. Their thick fur coat and low foot-load (20.7 ± 3.2 gm cm^{-2}), along with insulated footpads make it easier to walk on snow (Penczykowski et al. 2017, Bista et al. 2021d). These features could explain why they easily adapt to the snowfall. Additionally, activity patterns of captive red pandas was observed to be similar in winter and summer (Fei et al. 2017). However, they showed selectivity in habitat use in the presence of snow by avoiding slopes > 29° and staying away from human settlements.

The avoidance of areas close to human settlements, where human activities are high when the ground is covered with snow, may also have encouraged them to use high elevations, as these areas are mostly located at lower elevations. Poaching activity increases after snowfall in these areas (Rai unpubl.), as most wildlife move to lower elevations to escape the cold and their footprints on the snowfield make easier tracking for poachers. Similarly, the avoidance of high-slope areas in

Table 3. Candidate models describing the climatic variables affecting the speed of red pandas. # Snow_cov = snow cover.

Models#	DF	Logik	AICc	ΔAICc	Weight
Null model	3	2783.06	−5560.1	0	0.54
Snow_cov	4	2783.86	−5559.7	0.42	0.44
Sex	4	2780.30	−5552.6	7.53	0.01

Table 4. Candidate models describing the covariates affecting the habitat use when the ground is covered with snow. # Elev = elevation, Herd_shed = distance to herding shed, Settel = distance to settlement.

Models	DF	Logik	AICc	ΔAICc	Weight
Elev + Settel + Slope + Solar	6	−322.71	657.60	0	0.08
Elev + Road + Settel + Slope + Solar	7	−322.10	658.40	0.84	0.05
Elev + Settel + Slope	5	−324.15	658.40	0.85	0.05
Road + Settel + Slope + Solar	6	−323.36	658.90	1.30	0.04
Elev + Herd_shed + Settel + Slope + Solar	7	−322.44	659.10	1.52	0.04
Road + Settel + Slope	5	−324.70	659.50	1.95	0.03
Herd_shed + Road + Settel + Slope + Solar	7	−322.67	659.50	1.97	0.03
Elev + Settel + Sex + Slope + Solar	7	−322.70	659.60	2.04	0.03

the snow-covered forest could be related to high movement cost and inflated risk associated with such terrain (Dailey and Hobbs 1989, Hull et al. 2016). Interestingly, red pandas used areas close to roads which could be attributed to reduced vehicular movement on snow-covered roads.

Red pandas appeared to have used areas receiving high solar radiation to stay warm which is comparable with the habitat use patterns of giant panda (Hull et al. 2016). However, this is not sufficient to maintain their high metabolic rate in the winter which demands more energy. Consequently, red pandas must reduce activity levels or eat a more nutritious diet (Fei et al. 2017). A decline in the nutritional value of bamboo in winter further exerts pressure on their energy demand (Wei et al. 2000, Li et al. 2017), necessitating supplementary nutrition from other sources. Given their short alimentary tract, red pandas derive less energy from structural carbohydrates and rely more on dietary protein content (Nie et al. 2019). We found some diet plant species in the higher elevations had higher protein content, such as fruiting trees had higher protein content than the bamboo leaves at similar elevations. Bamboo leaves, in contrast have higher percentages of lignin, cellulose, and hemicellulose, which are difficult for the red panda to digest (Nie et al. 2019, Hu et al. 2024). However, availability of fruiting trees was relatively low compared to bamboo. Thus, red pandas might have occupied medium elevations where they can access both fruiting trees and bamboo more easily. Further studies are needed to get better insight into the effects of food resources on the movement ecology of red panda. Moreover, the narrow elevation range of the study area (2400–3600 m) limited the opportunity to explore movement patterns along a broader elevational gradient, which should be considered in future studies.

Predation avoidance might also have driven red pandas to occupy the narrow elevation range (2713–2984 m) and precluded them from moving to higher or lower elevations during unusual weather events. They share their habitat with many predators including *Catopuma temminckii*, *Martes flavigula*, *Neofelis nebulosa*, *Panthera pardus*, *Panthera tigris*, *Pardofelis marmorata*, *Prionailurus bengalensis*, *Prionodon pardicolor* and *Ursus thibetanus* (Bista et al. 2021c). The presence of these predators might have some influence on their movement patterns along the elevation gradient. Other prey species move to an area that has a lower predator density in winter (Tablado et al. 2014, Droghini and Boutin 2018). Most of the predators also move to lower elevations during snowfall (Homolka and Heroldová 2003). Therefore, we

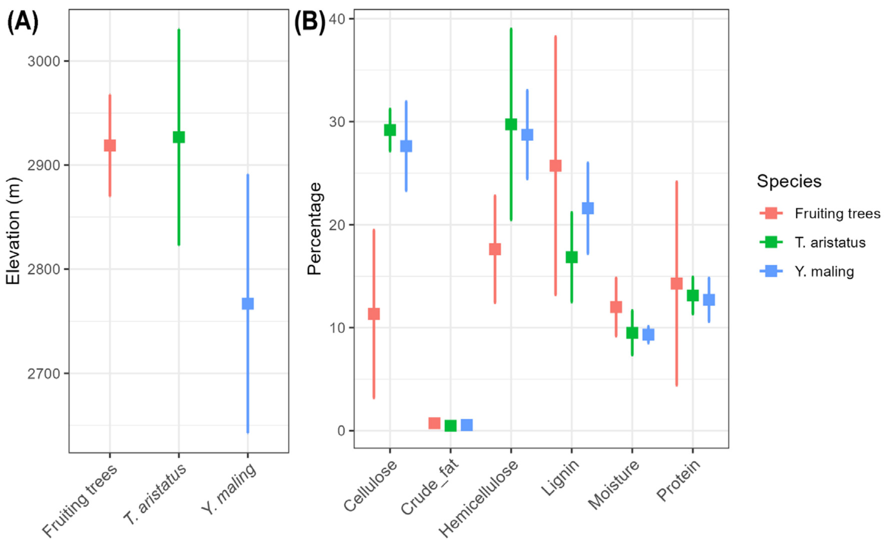

Figure 5. Distribution of the major diet species and the percentage of different nutritional contents. Two bamboo species (*T. aristatus*, *Y. maling*) and three fruiting trees (*S. cuspidate*, *A. collosa*, *M. cathcartii*) were included. Coloured boxes and lines represent mean values and standard deviation respectively. (A) Elevation of the diet species, (B) Nutritional contents of the diet species.

speculate that predation risk avoidance is another factor to discourage them from moving to lower elevations (Lima and Bednekoff 1999). However, we had a small sample size, with only seven records of predators during snowfall amongst 42 records from the camera trapping images. A long-term study with a larger sample size is needed to confirm these findings.

Conclusions

Our findings revealed that red panda movement patterns during challenging weather events are influenced by the additive effects of weather, disturbances, and geo-physical variables, yet food resources might also have some effects. Contrary to expectations, red pandas did not show significant affinity for lower elevations in the presence of snow, which could be attributed to risk avoidance, and availability and quality of food resources. These findings have conservation implications for habitat specialists like red pandas, inhabiting human-dominated areas. Despite some limitations, such as narrow elevation range, small sample size, and short sampling period, our results bolster the importance of conserving large areas with abundant supplementary food resources. Such areas facilitate access to suitable foraging patches where red pandas will feel less stressed while traversing within their ranges. However, our results may not fully capture the movement patterns of red pandas inhabiting areas with minimal or no human disturbances. Therefore, future studies should consider addressing these limitations and prioritize locations with no or minimal disturbances having broader elevational gradients to better understand the response to weather events in more natural habitat.

Acknowledgements – We are thankful to the support from Department of Forests and Soil Conservation, and Department of National Parks and Wildlife Conservation, Government of Nepal, Divisional Forest Office, Ilam, Sandakpur Rural Municipality, The Mountain Organization, and Shree Deep Jyoti Youth Club. We acknowledge Ang Phuri Sherpa for his support to manage this project on the ground. We thank Purushottam Pandey, Sita Gurung, Ngima Sherpa, Gyajo Lama Bhote, Aadesh Khamdak, Kiran Rai, RPN's forest guardians and locals who assisted during the field experiment.

Funding – This study was funded by Rotterdam Zoo and The Red Panda Network.

Permits – This study was approved by the Animal Ethics committee of the University of Queensland (SAFS/133/19/NEPAL), and the technical committee of the Department of Forests and Soil Conservation, and Department of National Parks and Wildlife Conservation, Government of Nepal (DFSC-521/075/076 and DFSC-244/076/077).

Author contributions

Damber Bista: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (equal); Project administration (lead); Resources (equal); Visualization (lead); Writing - original draft (lead); Writing - review and editing (equal). **Greg S. Baxter:** Conceptualization (equal); Methodology (equal); Supervision (equal); Writing - review and editing (equal). **Nicholas J. Hudson:** Conceptualization (equal); Methodology (equal); Supervision (equal); Writing - review and editing (equal). **Sonam Tashi Lama:** Investigation (equal); Resources (equal); Writing - review and editing (equal). **Janno Weerman:** Investigation (equal); Resources (equal); Writing - review and editing (equal). **Peter J. Murray:** Conceptualization (equal); Methodology (equal); Supervision (equal); Writing - review and editing (equal)

Transparent peer review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/wlb3.01384.

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.cjsxksngd (Bista et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Acharya, K. P., Shrestha, S., Paudel, P. K., Sherpa, A. P., Jnawali, S. R., Acharya, S. and Bista, D. 2018. Pervasive human disturbance on habitats of endangered red panda *Ailurus fulgens* in the central Himalaya. – Global Ecol. Conserv. 15: e00420

Allen, M. L., Yovovich, V. and Wilmers, C. C. 2016. Evaluating the responses of a territorial solitary carnivore to potential mates and competitors. – Sci. Rep. 6: 27257

AOAC, G. 2016. Official methods of analysis of, 2nd edn. – AOAC International.

Bates, D., Mächler, M., Bolker, B. and Walker, S. 2015. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.

Bista, D. 2022. Disturbance and fragmentation impacts movement ecology of a habitat specialist: conservation implications for red pandas. – The University of Queensland, Australia.

Bista, D., Baxter, G. S., Hudson, N. J., Lama, S. T. and Murray, P. J. 2021a. Effect of disturbances and habitat fragmentation on an arboreal habitat specialist mammal using GPS telemetry: a case of the red panda. – Landsc. Ecol. 1–15.

Bista, D., Baxter, G. S., Hudson, N. J., Lama, S. T., Weerman, J. and Murray, P. J. 2021b. Movement and dispersal of a habitat specialist in human-dominated landscapes: a case study of the red panda. – Movem. Ecol. 9: 62

Bista, D., Lama, S. T., Shrestha, J., Rumba, Y. B., Weerman, J., Thapa, M., Acharya, H., Sherpa, A. P., Hudson, N. J., Baxter, G. S. and Murray, P. J. 2021c. First record of Bengal tiger, *Panthera tigris tigris* Linnaeus, 1758 (Felidae), in eastern Nepal. – Check List 17: 1249–1253.

Bista, D., Lama, S. T., Weerman, J., Sherpa, A. P., Pandey, P., Thapa, M. K., Acharya, H., Hudson, N. J., Baxter, G. S. and Murray, P. J. 2021d. Improved trapping and handling of an arboreal, montane mammal: red panda *Ailurus fulgens*. – Animals 11: 921

Bista, D., Baxter, G. S., Hudson, N. J., Lama, S. T., Weerman, J. and Murray, P. J. 2022a. Space use, interaction and recursion in a solitary specialized herbivore: a red panda case study. – Endang. Species Res. 47: 131–143

Bista, D., Bhattrai, B., Shrestha, S., Lama, S. T., Dhamala, M. K., Acharya, K. P., Jnawali, S. R., Bhatta, M., Das, A. N. and Sherpa, A. P. 2022b. Bamboo distribution in Nepal and its impact on red pandas. – In: Red panda. Elsevier, pp. 353–368.

Bista, D., Baxter, G. S., Hudson, N. J., Lama, S. T., Weerman, J. and Murray, P. J. 2024. – Dryad Digital Repository, https://doi.org/10.5061/dryad.cjsxksngd.

Burnham, K. P., Anderson, D. R. and Huyvaert, K. P. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. – Behav. Ecol. Sociobiol. 65: 23–35.

Clarke, A., Rothery, P. and Isaac, N. J. B. 2010. Scaling of basal metabolic rate with body mass and temperature in mammals. – J. Anim. Ecol. 79: 610–619.

Conover, G. K. and Gittleman, J. L. 1989. Scent-marking in captive red pandas (*Ailurus fulgens*). – Zoo Biol. 8: 193–205.

Dailey, T. V. and Hobbs, N. T. 1989. Travel in alpine terrain: energy expenditures for locomotion by mountain goats and bighorn sheep. – Can. J. Zool. 67: 2368–2375.

Dalui, S., Khatri, H., Singh, S. K., Basu, S., Ghosh, A., Mukherjee, T., Sharma, L. K., Singh, R., Chandra, K. and Thakur, M. 2020. Fine-scale landscape genetics unveiling contemporary asymmetric movement of red panda (*Ailurus fulgens*) in Kangchenjunga landscape, India. – Sci. Rep. 10: 15446.

Doherty, T. S., Hays, G. C. and Driscoll, D. A. 2021. Human disturbance causes widespread disruption of animal movement. – Nat. Ecol. Evol. 5: 513–519.

Droghini, A. and Boutin, S. 2018. The calm during the storm: snowfall events decrease the movement rates of grey wolves (*Canis lupus*). – PLoS One 13: e0205742.

Fahrig, L. 2007. Non-optimal animal movement in human-altered landscapes. – Funct. Ecol. 21: 1003–1015.

Fei, Y., Hou, R., Spotila, J. R., Paladino, F. V., Qi, D. and Zhang, Z. 2017. Metabolic rate of the red panda, *Ailurus fulgens*, a dietary bamboo specialist. – PLoS One 12: e0173274.

Fox, J. and Monette, G. 1992. Generalized collinearity diagnostics. – J. Am. Stat. Assoc. 87: 178–183.

Glatston, A., Wei, F., Than, Z. and Sherpa, A. P. 2015. *Ailurus fulgens* (errata version published in 2017). – The IUCN Red List.

Goering, H. K. and Van Soest, P. J. 1970. Forage fiber analyses: apparatus, reagents, procedures, and some applications. – Agricultural Research Service, US Department of Agriculture.

Homolka, M. and Heroldová, M. 2003. Impact of large herbivores on mountain forest stands in the Beskydy Mountains. – Forest Ecol. Manage. 181: 119–129.

Hu, Y., Thapa, A., Fan, H., Ma, T., Wu, Q., Ma, S., Zhang, D., Wang, B., Li, M., Yan, L. and Wei, F. 2020. Genomic evidence for two phylogenetic species and long-term population bottlenecks in red pandas. – Sci. Adv. 6: eaax5751.

Hu, Y., Hu, Y., Zhou, W. and Wei, F. 2024. Conservation genomics and metagenomics of giant and red pandas in the wild. – Annu. Rev. Anim. Biosci. 12: 69–89.

Huggard, D. J. 1993. Effect of snow depth on predation and scavenging by gray wolves. – J. Wildl. Manage. 57: 382–388.

Hull, V., Zhang, J., Huang, J., Zhou, S., Viña, A., Shortridge, A., Li, R., Liu, D., Xu, W., Ouyang, Z., Zhang, H. and Liu, J. 2016. Habitat use and selection by giant pandas. – PLoS One 11: e0162266.

Johansson, Ö., Mishra, C., Chapron, G., Samelius, G., Lkhagvajav, P., McCarthy, T. and Low, M. 2022. Seasonal variation in daily activity patterns of snow leopards and their prey. – Sci. Rep. 12: 21681.

Korslund, L. and Steen, H. 2006. Small rodent winter survival: snow conditions limit access to food resources. – J. Anim. Ecol. 75: 156–166.

Kranstauber, B. 2020. move: visualizing and analyzing animal track data. – R package ver. 4.0.6. – https://CRAN.R-project.org/package=move.

Latimer, G. 2016. Official methods of analysis of AOAC International. – AOAC International.

Li, Y., Swaisgood, R. R., Wei, W., Nie, Y., Hu, Y., Yang, X., Gu, X. and Zhang, Z. 2017. Withered on the stem: is bamboo a seasonally limiting resource for giant pandas? – Environ. Sci. Pollut. Res. Int. 24: 10537–10546.

Lima, S. L. and Bednekoff, P. A. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. – Am. Nat. 153: 649–659.

Mills, L. S., Bragina, E. V., Kumar, A. V., Zimova, M., Lafferty, D. J. R., Feltner, J., Davis, B. M., Hackländer, K., Alves, P. C., Good, J. M., Melo-Ferreira, J., Dietz, A., Abramov, A. V., Lopatina, N. and Fay, K. 2018. Winter color polymorphisms identify global hot spots for evolutionary rescue from climate change. – Science 359: 1033–1036.

Nie, Y., Wei, F., Zhou, W., Hu, Y., Senior, A. M., Wu, Q., Yan, L. and Raubenheimer, D. 2019. Giant pandas are macronutritional carnivores. – Curr. Biol. 29: 1677–1682.e2.

Panthi, S., Coogan, S. C., Aryal, A. and Raubenheimer, D. 2015. Diet and nutrient balance of red panda in Nepal. – Sci. Nat. 102: 1–4.

Parker, K. L., Robbins, C. T. and Hanley, T. A. 1984. Energy expenditures for locomotion by mule deer and elk. – J. Wildl. Manage. 48: 474–488.

Pedersen, S. H., Bentzen, T. W., Reinking, A. K., Liston, G. E., Elder, K., Lenart, E. A., Prichard, A. K. and Welker, J. M. 2021. Quantifying effects of snow depth on caribou winter range selection and movement in Arctic Alaska. – Movem. Ecol. 9: 48.

Penczykowski, R. M., Connolly, B. M. and Barton, B. T. 2017. Winter is changing: trophic interactions under altered snow regimes. – Food Webs 13: 80–91.

Pfeifer, M. et al. 2017. Creation of forest edges has a global impact on forest vertebrates. – Nature 551: 187–191.

Pradhan, S., Saha, G. K. and Khan, J. A. 2001. Ecology of the red panda *Ailurus fulgens* in the Singhalila National Park, Darjeeling, India. – Biol. Conserv. 98: 11–18.

Richard, J. H., Wilmshurst, J. and Côté, S. D. 2014. The effect of snow on space use of an alpine ungulate: recently fallen snow tells more than cumulative snow depth. – Can. J. Zool. 92: 1067–1074.

Schmidt, N. M., van Beest, F. M., Mosbacher, J. B., Stelvig, M., Hansen, L. H., Nabe-Nielsen, J. and Grondahl, C. 2016. Ungulate movement in an extreme seasonal environment: year-round movement patterns of high-arctic muskoxen. – Wildl. Biol. 22: wlb.00855.

Tablado, Z., Fauchald, P., Mabille, G., Stien, A. and Tveraa, T. 2014. Environmental variation as a driver of predator–prey interactions. – Ecosphere 5: 1–13.

Tahsin, M., Sultana, S., Reza, T., and Hossam-E-Haider, M. 2015. Analysis of DOP and its preciseness in GNSS position estimation. 2015 International Conference on Electrical Engineering and Information Communication Technology (ICEEICT), Bangladesh.

Thapa, A., Hu, Y. and Wei, F. 2018. The endangered red panda (*Ailurus fulgens*): ecology and conservation approaches across the entire range. – Biol. Conserv. 220: 112–121.

Tucker, M. A. et al. 2018. Moving in the Anthropocene: global reductions in terrestrial mammalian movements. – Science 359: 466–469.

Wei, F., Wang, Z., Feng, Z., Li, M. and Zhou, A. 2000. Seasonal energy utilization in bamboo by the red panda (*Ailurus fulgens*). – Zoo Biol. 19: 27–33.

Wood, W. F., Dragoo, G. A., Richard, M. J. and Dragoo, J. W. 2003. Long-chain fatty acids in the anal gland of the red panda, *Ailurus fulgens*. – Biochem. Syst. Ecol. 31: 1057–1060.

Yonzon, P. B. 1989. Ecology and conservation of the red panda in the Nepal Himalayas. – The Univ. of Maine, USA.

Yonzon, P. B. and Hunter, M. L. 1991. Conservation of the red panda *Ailurus fulgens*. – Biol. Conserv. 57: 1–11.

Yonzon, P., Royce, J. and Fox, J. 1991. Geographic information systems for assessing habitat and estimating population of red pandas in Langtang National Park, Nepal. – Ambio 20: 285–288.

Zub, K., Kowalczyk, J., Jedrzejewska, W., Theuerkauf, B., Schmidt, K. and Jedrzejewski, R. 2003. Wolf pack territory marking in the Bialowieza Primeval Forest (Poland). – Behaviour 140: 635–648.