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Natal dispersal and exploratory forays through atypical habitat in the mountain-bound snow leopard

Örjan Johansson[1,2] | **Justine Shanti Alexander**[2,3] | **Purevjav Lkhagvajav**[4] | **Charudutt Mishra**[1,5] | **Gustaf Samelius**[2,6]

[1]Grimsö Wildlife Research Station, Swedish University of Agricultural Sciences, Uppsala, Sweden

[2]Snow Leopard Trust, Seattle, Washington, USA

[3]Department of Ecology and Evolution, University of Lausanne, Lausanne, Switzerland

[4]Snow Leopard Conservation Foundation, Ulan Baatar, Mongolia

[5]Nature Conservation Foundation, Mysore, India

[6]Nordens Ark, Hunnebostrand, Sweden

Correspondence
Örjan Johansson
Email: orjan.johansson@slu.se

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Understanding how landscapes affect animal movements is key to effective conservation and management (Rudnick et al., 2012; Zeller et al., 2012). Movement defines animal home ranges, where animals generally access resources such as food and mates, and also their dispersal and exploratory forays. These movements are important for individual survival and fitness through genetic exchange within and between populations and for colonization of unoccupied habitats (Baguette et al., 2013; MacArthur & Wilson, 1967). Dispersal and exploratory movements typically occur when young animals leave their natal range and establish more permanent home ranges (Greenwood, 1980; Howard, 1960). In mammals, natal dispersal of males is usually more frequent and happens over greater distances compared with that of females (Clobert et al., 2001; Greenwood, 1980).

Landscape permeability affects an animal's ability to move through the environment. Landscape permeability is controlled by habitat characteristics and social factors that reduce access to food or security, consequently reducing survival (Zeller et al., 2012). In heterogenous landscapes, home ranges tend to be composed of habitats that offer relatively less resistance, while areas outside of the home range may impede movements to varying degrees due to hostile landscape characteristics or the presence of predators or territorial conspecifics (Jackson et al., 2016; Rudnick et al., 2012). Understanding the landscape features that affect movement ability can help identify dispersal corridors, assess connectivity between populations and habitat patches (Jackson et al., 2016; Zeller et al., 2018), and be used for effective metapopulation management.

In elusive species ranging over large areas, like the snow leopard (*Panthera uncia*), metapopulation genetic structure and habitat modeling can be used to infer barriers to movement (e.g., Hacker et al., 2022; Riordan et al., 2016). These must be supplemented with observations of individual animals, difficult as they are to obtain, in order to reliably interpret models on connectivity and permeability.

Snow leopards are apex predators adapted to mountain ecosystems, and live across South and Central Asian high mountains. Knowledge of the species biology is limited, including their dispersal behavior and barriers. Snow leopard distribution has largely been described through elevation and terrain models where flat areas are characterized as unsuitable habitats (Li et al., 2020; McCarthy et al., 2016; Riordan et al., 2016).

We examined the individual movement behavior of three subadult snow leopards (defined as snow leopards estimated to be <3 years old, traveling independently of their mothers) to assess whether they are restricted to mountainous routes or are able to navigate the resistance offered by relatively large flat areas between mountains during their dispersal. Our study was conducted in the Altai mountain massifs interspersed across a flat steppe landscape (Figure 1). The mountains represented islands of suitable habitat within the metaphorical sea of nonhabitat formed by steppes (MacArthur & Wilson, 1967; McCarthy et al., 2016). We show that these snow leopards traveled relatively large distances over flat areas of the steppe (average displacement between GPS locations taken at 5-h intervals on the steppe was 6.4 km compared with the average of 1.0 km for subadults in the mountains; Johansson et al., 2022; Figure 1, Table 1). Furthermore, the snow leopards appeared to cross the steppe aiming toward distant mountains that were visible from their departure points where they had left their natal mountainous habitat. We hypothesize that the decision of young snow leopards to venture into the steppe depends on whether the destination mountains are visible from the area of departure, and are relatively independent of the intervening distance (Figure 1).

Between 2008 and 2022, we captured 30 adult and five subadult snow leopards and equipped them with GPS collars (North Star, Vectronic GPS Plus, and Vectronic Vertex Lite) in the Tost Mountains (43° N, 100° E) (see Johansson et al., 2013 for details on capture and immobilization). Collars were programmed to acquire a GPS fix every 5 h and uplink them via Globalstar or Iridium satellite communication. GPS locations of the 30 adult snow leopards followed the mountain contours closely with only 12 of 53,828 GPS locations located on the steppe. Young snow leopards separate from their mothers and begin traveling independently at 20–22 months of age (Johansson et al., 2021). The five subadult snow leopards, including three females (named F2, F11, and F13) and two males (M9 and M17), were collared prior to their separation from their GPS-collared mothers, or during the separation phase.

Of the five young individuals collared, a female (F11) did not leave the Tost Mountains and settled just east of her natal range, while a male (M17) dispersed east along the mountains and hills. One male (M9) dispersed across the steppe to a neighboring mountain range, while two females (F2 and F13) made significant exploratory forays across the steppe. For the three individuals who traveled across the steppe (M9, F2 and F13), we visited the sites of their last GPS locations prior to venturing out on the steppe and determined that in all cases there were mountains visible in the travel direction of the foray or dispersal (Figure 1).

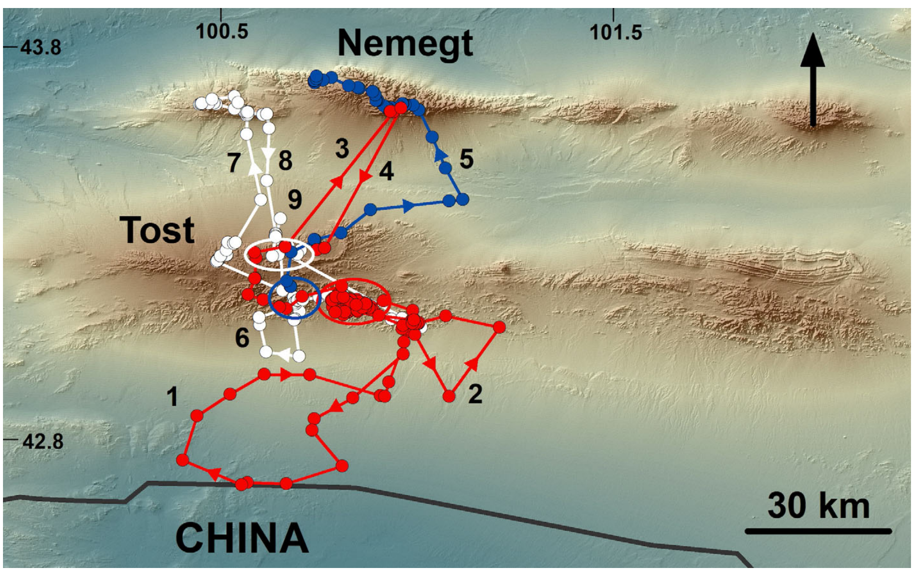

FIGURE 1 Exploratory forays and dispersal of three subadult snow leopards showing GPS locations (small circles) and travel routes for each excursion (F2 = red, M9 = blue, F13 = white), numbers correspond to the excursion numbers in Table 1. The natal ranges of the three snow leopards are illustrated (open ovals). There are two parallel fences along the border (black line) between China and Mongolia.

TABLE 1 Dispersals and exploratory forays of three young snow leopards.

Snow leopard	Excursion no.	Duration of excursion (h)	Cumulative distance (km)	Straight line distance (km)	Distance from mountain (km)	Displacement (km/5 h)
F2	1	115	156.9	…	44.9	6.8
F2	2	≤96	42.3	…	19.3	2.2
F2	3	≤93	…	41.8	…	…
F2	4	≤115	…	30.6	…	…
M9	5	35	48.7	32.7		7.0
F13	6	25	26.4	…	10.1	5.3
F13	7	20	36.3	34.2	…	9.1
F13	8	15	35.9	35.6	…	12.0
F13	9	30	16.2	…	7.4	2.7

Note: Excursion no. corresponds to the numbers in Figure 1. Cumulative distance is the distance between GPS locations along the path the snow leopard traveled, Straight line distance is the Euclidean distance from the mountain range the snow leopard left to the mountain range it reached after crossing the steppe, Distance from mountain shows the Euclidean distance between the GPS-location furthest away from the closest mountain for forays where the snow leopard returned instead of crossing to a new mountain range, Displacement shows the average distance moved between GPS locations on steppe (5 h intervals), the average displacement for subadult snow leopards in mountains is 1.0 km/5 h (Johansson et al., 2022).

F2 conducted four excursions onto the steppe from 23 March 2011 to 27 May 2011 (Table 1). On the first excursion she went south to the border between Mongolia and China, covering at least 60.3 km from the point where she left Tost until she reached the border (Figure 1, excursion 1). This border is equipped with two fences with a no-man's land between them. The fences are reported to act as an absolute barrier for other wildlife such as Khulan (*Equus hemionus*) and Mongolian gazelles (*Procapra gutturosa*) (Ito et al., 2013; Linnell et al., 2016). This seems to be the case for snow leopards as well. F2 moved along the fence for at least 9.7 km and possibly up to 40 km before turning back toward the Tost Mountains again (Figure 1).

F2 made another excursion into the steppe south of Tost before, returning once again (Figure 1, excursion 2). Thereafter she traveled to the northern edge of Tost from where she crossed at least 41.8 km of the steppe into the Nemegt mountain range, where she remained for up to 8 days after which she returned to Tost (Figure 1, excursions 3 and 4). The GPS-location acquisition rate had deteriorated after the first excursion, preventing us from determining detailed information about her movement path, how much time she spent on the steppe and whether she made forays also when in Nemegt. Shortly after returning to Tost, the collar's prescheduled release mechanism was activated. We lost contact with F2 after that and her fate is unknown.

M9 left his natal range on 18 April 2012. Two days later, he dispersed across the steppe to Nemegt, where he established a permanent home range (Figure 1, excursion 5). Camera trap data confirmed that he remained there until at least 2015.

F13 was collared ~10 km south of her natal range on 19 April 2019. She made four excursions into the steppe. On the first excursion, she ventured south of Tost on 23 April and returned to Tost on 24 April (Figure 1, excursion 6). Similar to F2, she then turned north, and on 28 June she crossed at least 36.3 km of steppe to reach Nemegt, from where she returned to Tost on 6 July (Figure 1, excursions 7 and 8). The day after, on 7 July, she once again headed north, but returned to Tost on 9 July (Figure 1, excursion 9). Both of the excursions where she ventured north onto the steppe started from her natal range. She eventually settled in a partially overlapping home range on the eastern side of her natal range. Our camera trap data revealed that she reproduced in 2020.

Studies on connectivity and landscape-level conservation planning for snow leopards have used theoretical models based on habitat suitability (Li et al., 2020; Riordan et al., 2016) and relatedness among populations (Hacker et al., 2022). Riordan et al. (2016) suggested that the maximum lifetime dispersal ability of snow leopards is between 50 and 100 km in unfavorable habitats while Hacker et al. (2022) showed that populations in Mongolia and China were genetically separated, suggesting that the steppe landscape between these populations formed a substantial barrier between the populations. In contrast, the three dispersing individuals in our study traveled significant distances across the steppe, where each of them covered a minimum of 40 km. F2 traveled a distance of at least 84 km, first south and then alongside the border fence, before she turned back toward Tost, covering a total distance of at least 157 km on the steppe (Figure 1, excursion 1). It appears as if the route that F2 attempted to follow aligns with the least-cost path identified by Li et al. (2020) connecting the mountains in southern Mongolia with the Qilian Shan in China. Our observations show that, while snow leopards do not establish home ranges in flat areas, dispersing snow leopards are able to cross large stretches of steppe landscapes, suggesting that they offer less resistance than previously assumed. We hypothesize that although snow leopards could be more vulnerable to predation, for example, by wolves (*Canis lupus*) in flat areas, permeability is not dictated by the extent of flat steppes, but, rather that the barriers might include physical ones such as fences or psychological ones such as the lack of visible mountains that individual animals could aim to disperse to.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data supporting this research are sensitive and not available publicly. The snow leopard GPS-collar data are owned by Snow Leopard Trust (info@snowleopard.org) and are available to qualified researchers by requesting GPS locations from snow leopards with IDs F2, F11, F13, M9 and M17.

ORCID

Örjan Johansson https://orcid.org/0000-0002-9977-0405

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