### **ORIGINAL PAPER**



# Long-distance dispersal of wolves in the Dauria ecoregion

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### **Abstract**

Using remote tracking (GPS+GSM module) we documented long-distance natal dispersals of two yearling wolves (*Canis lupus*) from The Daursky State Nature Biosphere Reserve, Russia. From the arithmetic center of natal home ranges the collared male and female traveled the straight-line natal dispersal distance of 280 km and 332.8 km, over 82 days and 34 days, respectively. Minimum distances of the entire tracking period were 3090.7 km (male) and 2056.7 km (female); the estimated actual travel distance of the entire tracking period was 9849 km and 4530 km, respectively. The travel speed of the wolves varied between phases (pre-dispersal, dispersal, and post-dispersal) and movement patterns (directional, nondirectional, and cluster). The mean travel speed of both wolves was the highest during dispersing (34.6 and 39.5 km/day), calculated as a minimum distance. It was one of the highest dispersal speeds among reported. The highest hourly mean travel speed was during pre-dispersing at dawn, moving directly (the male,  $5.77 \pm 4.25$  km/h; the female,  $4.09 \pm 2.44$  km/h). During pre-dispersing forays they returned several times to their home territories. During dispersal, yearlings crossed at least 5 territories of other packs. Wolves explored the steppe and forest-steppe in less modified habitats of the Russian part of the Dauria ecoregion and in the human-dominated Chinese part of the ecoregion.

Keywords Canis lupus · Long-range movement · Daursky State Nature Biosphere Reserve · Wolf

## Introduction

Dispersal is the primary way that maturing young gray wolves (*Canis lupus lupus*) potentially colonize new areas and maintain population genetic diversity (Fuller et al. 2003). Different aspects of gray wolf dispersal have been studied extensively in North America (Gese and Mech 1991; Boyd and Pleischer 1999; Fuller et al. 2003; Mech and Boitani 2003; Musiani et al. 2007; Treves

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et al. 2009; Jimenez et al. 2017) and in Europe (Wabakken et al. 2001, 2007; Linnell et al. 2005; Kojola et al. 2006; Blanco and Cortes 2007; Ciucci et al. 2009; Andersen et al. 2015; Byrne et al. 2018), but very limited information is available for North-East Asia, except of fragmented information from wolf dispersal research in China (Duan et al. 2016) and in the Gobi in Mongolia (Kaczensky et al. 2008; Joly et al. 2019). Wolves have been documented to disperse up to 1000 km with at least 3471 km traversed over 271 days (Wabakken et al. 2007), but more commonly 100–150 km from their natal pack (Linnell et al. 2005; Treves et al. 2009). Although some adults also disperse, in general wolves disperse when 1–2 years old (yearling; Gese and Mech 1991; Linnell et al. 2005; Blanco and Cortes 2007; Treves et al. 2009).

As part of a larger study of wolf activity, movements and food base within the Russian part of the Dauria ecoregion, we documented cases of long-range dispersal by GPS-collared yearling male and female wolves, occurring in the steppe zone of Central Asia. Here we provide a detailed account of this observation, in particular, the distances and speed of the pre-dispersal, dispersal, and after-dispersal phases and provide comments on the potential avenues of future research.

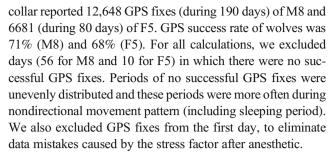


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# Materials and methods

The study area is located in the southeast of Zabaikalsky Krai, Russia, at the border with Mongolia (Dornod Aimag), China (Hulunbuir Province), and specifically within the Daursky State Nature Biosphere Reserve (Daursky Reserve), the part of the Chinese-Mongolian-Russian Dauria International Protected Area (DIPA), where wolves were collared (49°-51°N, 114°-120°E; Fig. 1). The study area represents the main steppe and forest-steppe ecosystems of the Dauria ecoregion. Wolf is the largest species in order Carnivora (Kirilyuk et al. 2013). Within the Russian and Mongolian parts of the region, Mongolian gazelle (Procapra gutturosa Pallas, 1777), Siberian Roe Deer (Capreolus pygargus Pallas, 1771), Tolai Hare (*Lepus tolai* Pallas, 1778), and Mongolian marmot (Marmota sibirica Radde, 1862) represent the main wild prey available to wolves (Kirilyuk et al. 2019). The density of wolf and wild prey within the Daursky Reserve is relatively higher than within the surrounding territories, due to good habitat conditions and the presence of well-managed reserves (Kirilyuk et al. 2019). During 2015-2019 in the Daursky Reserve and in the adjacent territories, we investigated collared wolves' home ranges (Kirilyuk et al. 2019), which reflected the approximate territories of most packs. At least 5 packs are transboundary; their home ranges cover territories in Russia and in Mongolia (Fig. 1). The study area supports approximately 5 wolf packs. Mean size of the wolves' home range was  $832 \pm 79.05 \text{ km}^2$  (100% minimum convex polygons (MCP)); the core area was  $30.2 \pm 8.8 \text{ km}^2$  (50% FK, Kernel method; Kirilyuk et al. 2019). According to the results of a winter route census conducted in 2018 by the Daursky Reserve, there were about 44 individuals. The study area is an important agricultural region where livestock raising prevails.

We used a remote tracking to study wolves' movement patterns. We tracked and captured a male wolf (M8) in February 2017 and a female wolf (F5) in January 2018. We immobilized the wolves from a jeep, following a chase method described for Asiatic wild asses by Walzer et al. (2007). Both wolves were anesthetized with xylazine (2%) at a dose of approximately 0.07–0.12 ml/kg (Kirilyuk et al. 2019). Wolves were aged by tooth wear and by body size (Gipson et al. 2000) and examined to determine their physical condition. We fit the wolves with a GPS collar (500-g; GPS + GSM modules ET-318 of Globalsat; Kirilyuk et al. 2019). We programmed the collar to collect date, time, and a GPS location (latitude and longitude; WGS 84) every 10 min and annually transmit data remotely through the Global System for Mobile Communications (GSM). In the absence of GSM net, the collar stored data on the internal memory for 3-5 days. We projected wolves' locations and analyzed data in NextGIS QGIS 17.7.0, determining that inaccuracy of GPS position was negligible at the scale of our analysis (inaccuracy of GPS position, 10 m, 2D RMS; www.globalsat.ru). The GPS



We defined natal dispersal as the dispersal of an animal from a natal home range to the place where it reproduces or would have reproduced if it had survived or found a mate (Greenwood 1980) and dispersal distance as the distance between the arithmetic center of the natal home range, or the capture site, and a newly established home range center, the mortality site or the last location while dispersing (Blanco and Cortes 2007). We considered a wolf to be dispersed from its natal home range once it moved consistently outside the territory boundaries (Kojola et al. 2006). Before leaving a natal home range, some wolves made pre-dispersal forays or spent time in the periphery of their natal home range (Messier 1985; Blanco and Cortes 2007). We did not include the pre-dispersal period in the calculation of dispersal distance. To define dispersal phases, we plotted cumulative net displacement (Euclidean distance, km) from the release site to each GPS fix received each day (around 1 h of midnight) (Fig. 1).

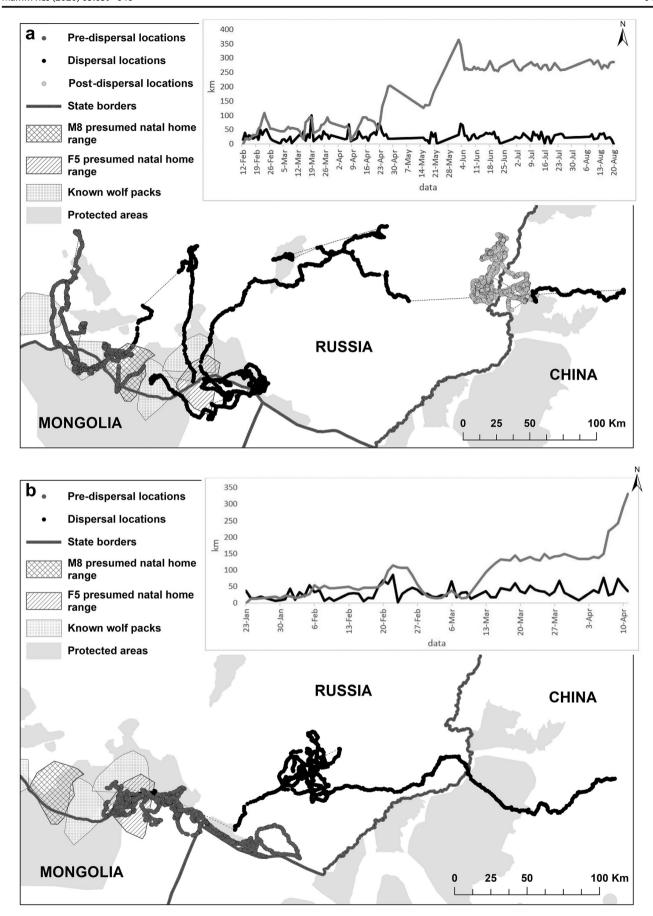
To classify movement patterns, we visually inspected the net displacement plot and the movement path. We identified 3 different movement patterns as follows: (1) directional, long-distance movement in more or less a single direction; (2) non-directional movements, short-distance movement in a zigzag pattern and recurrent use of the same general area; (3) cluster, home range—like movements, similar nondirectional movements, but more localized, reduced in extent, and for an extended period of time (Mech and Boitani 2003; Wabakken et al. 2007; Melnik et al. 2007). We considered cluster movement pattern as an indication of settlement (Gese and Mech 1991; Mech and Boitani 2003). We used Ripley's K Function with 90% confidence levels to exhibit statistically significant clustering of home range—like GPS locations.

We calculated two metrics to quantify the wolf's movement behavior in different phases (pre-dispersal, dispersal, and post-dispersal) and the time of day (day, dusk, night, and dawn). The first one is a minimum distance traveled daily by summing the distances between all successive GPS

Fig. 1 Global Positioning System (GPS) estimated long-distance dispersal paths of wolf M8 (a) and F5 (b) from Daursky State Nature Biosphere Reserve; territories of known wolf (*Canis lupus*) packs, 2015−2017. Wolf territories determined by 100% minimum convex polygons surrounding GPS telemetry fixes. Inset: minimum daily distance (black line) and cumulative net displacement (gray line) traveled by wolf M8 and F5 from the release site during their entire tracking period



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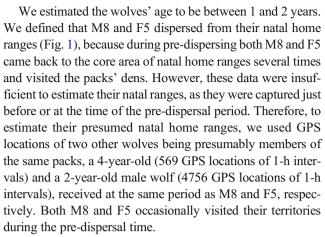
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locations received within each 24-h period (midnight–midnight). The second one is a travel speed (km/d; km/h), as the distance divided by the time between successive locations, which was then averaged. We classed the 4 time periods of the day as follows: dawn (1 h before to 2 h after sunrise), day (2 h after sunrise to 1 h before sunset), dusk (1 h before to 2 h after sunset), and night (2 h after sunset to 1 h before sunrise). We determined sunset and sunrise times for each 24-h tracking session (timewek.ru; Chavez and Gese 2006). For this analysis, we excluded 88 (M8) and 20 days (F5) with < 72 successful GPS fixes (50%). We used a one-way analysis of variance (ANOVA) to examine differences in travel speeds among determined phases and movement patterns.

We also attempted to estimate the actual movement distances covered by wolves. Despite of the fact that our collars were programmed for 10-min intervals, which potentially allowed to obtain the measurement of a nearly real movement, due to periods of gaps in obtaining fixes, this proved unachievable. Therefore, we extracted periods of uninterrupted consecutive fixes for each hour (n = 36) of the day and calculated the average distance at 10-min interval at each hour for an entire duration of observations (sample size, n = 760 for M8 and n = 720 for F5; confidence level, 99%; confidence interval, 4.54%). This allowed us to extrapolate the values of average movement distances for particular hours on the entire period of tracking. This way we were able to estimate the maximum approximation of the actual distance covered by wolves.

## Results

Based on the net displacement plot, we identified 3 phases (Fig. 1). The pre-dispersal phase was determined when wolves made pre-dispersal forays or spent time in the periphery of their natal home range, came back to the core area of natal home ranges several times, and during which the mean net displacement was smaller than during the dispersal phase,  $45.9 (\pm 25 \text{ km})$  and  $42.7 (\pm 31 \text{ km})$  km for M8 and F5, respectively. The dispersal phase started once wolves moved consistently outside the territory boundaries; the onset of dispersing corresponded to a marked shift in daily movement behavior, with increases in both minimum distance traveled and net displacement, which increased to a mean of 113.5 (range 14-363.9 km) and 157.5 (range 16.6-332 km) km for M8 and F5, respectively. The post-dispersal phase started when wolves established a new home range (home range-like GPS locations), expressed in more localized movements, and for an extended period of time, net displacement did not increase and ranged from 255.2 to 294.5 km for M8. We did not define post-dispersal phase for F5, as she consistently moved in a directed manner away from a temporal "cluster" till the last location.



Male M8 was collared 10.3 km from the arithmetic center of his presumed natal home range (Fig. 1a). Based on the net displacement plot and visual inspection of the movement path (Fig. 1a), before M8 definitively left his natal home range on March 15, from February 12 to March 13 he made at least one short and one long pre-dispersal foray (10 and 110.7 km, a straight-line distance) crossing at least 2 other packs' territories (Fig. 1a). After leaving the natal home range, M8 traveled north, south, and south-east, also crossing well-known wolves' home ranges around or not far from his natal territories several times before moving in an eastern direction and to China (Fig. 1a). Male M8 dispersed until 05 June 2017 and then settled on a new territory, located at the border zone with majority of his home range in Russia. The last GPS collar signals were received at the northern part of M8's new home range, 10 km from the Chinese border. The straight-line natal dispersal distance between the male M8 natal home range and arithmetic center of the new established home range was 280 km (Fig. 1a). During the dispersal phase, the minimum distance traveled by the wolf was 1313.8 km; the minimum distance of the entire tracking period was 3090.7 km.

The straight-line natal dispersal distance of Female F5 was 332.8 km. She was collared at 20 km from the arithmetic center of her presumed natal home range (Fig. 1b). The minimum distance traveled of the entire tracking period was 2056.7 km, and the dispersal minimum distance was 946.2 km. Before F5 left her natal home range on March 9, she also made at least 3 long pre-dispersal forays with the following straight-line distances: 20.7, 122.7, and 24.3 km, crossing other packs' territories in different directions two times (Fig. 1b). While dispersing, F5 moved strictly in the north-eastern and eastern directions (Fig. 1b) and stayed in a temporal "cluster" in a period of 20 days. On April 6, she moved to the East. The last GPS collar signals of F5 were received from China (Hulunbuir Province), 101 km from the Russian border (Fig. 1b). We could not confirm whether male M8 and female F5 had died, were killed in their last location, or if this was the location where the collar powered off.



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The dispersal paths of M8 and F5 shifted between nondirectional and directional movement pattern periods with different travel speeds (Fig. 1, Table 1). M8 mean travel speed was the highest at the dispersal phase, moving directly, 48 km/ day (Table 1), but, in general, the mean wolf speed did not differ between phases (ANOVA,  $F_{2.99} = 2.64$ , P = 0.076). Directional travel speed of M8 was higher within both the pre-dispersal and the dispersal phase (ANOVA,  $F_{1.55}$  = 45.73, P = 0.000; Table 1) than during non-directional movements. The highest mean daily speed of F5 was during the predispersal phase, moving directly, 46.8 km/day (Table 1), but travel speed between the pre-dispersal and the dispersal phase did not differ (ANOVA,  $F_{1.57} = 2.69$ , P = 0.106). There was no significant difference between directional and nondirectional dispersal travel speed of F5 (ANOVA,  $F_{1,22} = 0.034$ , P = 0.855).

Diel activity patterns confirmed the preponderance of nocturnal activity; during the entire tracking period, the mean travel speed (km/1 h) was higher at dusk, night, and dawn than during the day (ANOVA,  $F_{3,404} = 26.3$ , P = 0.0001 for M8;  $F_{3,224} = 23.06$ , P = 0.0001 for F5; Table 1). While dispersing, the highest mean hourly travel speed of both M8 and F5 was also at dusk, night, and dawn (Table 1). Greatest distances traveled per hour were 12.75 km and 10.2 km (M8 and F5, respectively) and corresponded to movements at dawn.

The average distance M8 covered during 10 min intervals between locations was  $0.36~\mathrm{km}\pm0.42~(SD)$  (range  $0.002-2.21~\mathrm{km/10}$  min), and for F5, it was  $0.4~\mathrm{km/10}$  min  $\pm0.43~(SD)$  (range  $0.003-1.79~\mathrm{km/10}$  min). Extrapolating these values to the entire time traveled (see Methods), we estimated that M8 and F5 covered 9849 km and 4530 km, respectively.

# Discussion

Our study contributed rare data on wolf dispersal in the steppe zone of Central Asia showing one of the highest estimates of wolf movements. The travel speed during dispersing of M8 and F5, calculated based on the minimum distance, was higher than of wolves studied in different landscapes of the forest zone (Linnell et al. 2005; Blanco and Cortes 2007; Wabakken et al. 2007; Treves et al. 2009; Byrne et al. 2018). We assume that the higher travel speed of wolves M8 and F5 can be explained by the comparatively "easier path" in the steppe landscape, where there are no significant obstacles to movement.

Our approach to estimate the actual distance traveled yielded travel distances of 9849 km and 4530 km for M8 and F5, respectively. However, we are aware that the method we applied, based on extrapolation of 10-min distances, may have provided biased results, because there were long-term periods with no successful GPS fixes. Despite, our estimates of actual distances could be somewhat overstated or

underestimated, we consider that this provides some indication as to how much longer the actual wolf travel distances can be compared with the minimum distances traveled between all subsequent GPS locations.

Cases of wolf movements found previously in southwest Mongolia are one of the longest reported annual movements by terrestrial mammals (Kaczensky et al. 2008; Joly et al. 2019). The two cases, studied in the Gobi, characterize the movement of wolves in conditions of extremely depleted populations under strong anthropogenic pressure (Kaczensky et al. 2008; Kirilyuk et al. 2019). Such movement characteristics are also in evidence at the northern extreme of the species' range in Alaska, where wide travels and a high daily speed of the pack were related to attempts to find and kill vulnerable prey, all of which are sparsely distributed in the region (Mech and Cluff 2011). In conversion to a month, the travel speed of our studied wolves was yet higher. Therefore, we can assume that in a year-long period yearlings could cover approximately the same or larger distance than wolves recorded in the Gobi. Such large distances are characteristic of the entire arid zone of Asia (Kaczensky et al. 2008; Joly et al. 2019) where winters are dry with a low snow cover.

The area from which the studied wolves began dispersing has the status of a protected area, and the additional protective effect of the interstate border. This area also has optimal habitats for the wolf, all-season food base, and has no significant limiting factors in winter. These contribute to the fact that the territory of the Daursky Reserve is densely occupied by wolf packs (Kirilyuk et al. 2019). In fact, during the entire period, M8 and F5 made numerous exploring pre-dispersal forays and dispersal routes, crossing at least five territories of other packs (Fig. 1). Sub-adults M8 and F5 may have been avoiding adults or other pack territories, moving along the pack's periphery, especially during pre-dispersal forays (Fig. 1), because subordinate status may make them particularly vulnerable to attack from conspecifics (Treves et al. 2009). In general, dispersers suffer a higher mortality than resident individuals (Messier 1985; Mech 1977; Blanco and Cortes 2007; Suvorov and Kirienko 2008), as well as mortalities also can be caused by other wolves (Mech et al. 1998). The area in China, in the direction of which the collared wolves moved, appears to have worse conditions than the Russian side due to human-dominated, fragmented landscapes with relatively low wild ungulate density (Yuan et al. 2008; Dou et al. 2014; Kirilyuk et al. 2019). During the entire tracking period, the highest mean hourly travel speed for both M8 and F5 was at dusk, night, and dawn, allowing the wolves to avoid people while traveling in areas intensively used by humans (Ciucci et al. 1997; Chavez and Gese 2006). Both wolves dispersed in the same direction, within about a year of each other and crossed the Russian-Chinese border at a distance of 30-40 km from each other. Observations of similar dispersal behavior are relatively rare (Kojola et al. 2006; Gable et al. 2019). We do not know



Table 1 Mean circadian travel speed (km/1 h), phases, and movement patterns' distances, mean travel speed (km/day) of wolves M8 and F5 in the Dauria ecoregion

| I able I IVICAII CIICAUIAII LIAV                     | mean cheanan haver speed (MIII/1 II), phases, and inovernent panerins | id movement pattern  |                     | an naver speed (MIII)   | lay) of wolves i     | uistanices, mean navel speed (nim nay) of worves into and 1.3 m ure Damia ecologion | na concin            |   |                |
|--|---|--|---------------------|---|----------------------|---|----------------------|---|----------------|
| M8<br>Phase/movement pattern                         | Date  | Minimum distance (km) <sup>a</sup>   | e (km) <sup>a</sup> |   | Travel spee $x$      | Travel speed $(km/day)^a$   | min                  | max   |                |
| Pre-dispersal<br>Directional                         | 12.02–14.03   | 540.7<br>250   |                     |   | 28.5<br>41.8         |   | 13<br>27.8           | 51.6<br>51.6  |                |
| Nondirect<br>Dispersal<br>Directional                | 15.03-04.06   | 290.7<br>1313.8<br>832.2   |                     |   | 22.4<br>34.6<br>48.9 |   | 13<br>10.6<br>25.6   | 33<br>100.4<br>100.4  |                |
| Nondirect<br>Post-dispersal Cluster<br>Entire period | 05.06–20.08<br>12.02–20.08.2017                                       | 481.6<br>1236<br>3090.7  |                     |   | 22.9<br>27.5<br>30.3 |   | 10.6<br>1.6<br>1.6   | 44.8<br>43.06<br>100.4  |                |
| Mean travel speed (km/1 h) <sup>a</sup><br>Phase     | Date  |  | <i>n</i> (h)        | $\begin{array}{c} \mathrm{Dusk} \\ x \pm \mathrm{SD} \end{array}$ | n (h)                | Night $x \pm SD$  | <i>n</i> (h)         | $\begin{array}{c} \text{Dawn} \\ x \pm \text{SD} \end{array}$ | <i>n</i> (h)   |
| Pre-dispersal<br>Directional                         | 12.02–14.03   | $1.71 \pm 1.25$<br>$2.48 \pm 1.6$  | 117                 | $1.06 \pm 1.28$<br>$1.5 \pm 1.7$                                  | 42                   | $1.44 \pm 0.93$ $1.81 \pm 0.99$   | 129                  | $2.93 \pm 3.16$<br>$5.77 \pm 4.25$                            | 13             |
| Nondirect<br>Dispersal<br>Directional                | 15.03–04.06   | $1.36 \pm 0.92$<br>$0.88 \pm 0.98$<br>$1.27 \pm 1.2$                         | 82<br>283<br>135    | $0.85 \pm 1.05$<br>$2.52 \pm 1.79$<br>$3.14 \pm 2.1$              | 29<br>97<br>46       | $1.29 \pm 0.89$<br>$2.15 \pm 1.88$<br>$3.22 \pm 2.28$                               | 89<br>244<br>108     | $1.62 \pm 1.26$<br>$3.61 \pm 2.46$<br>$4.07 \pm 2.28$         | 84 84<br>84 24 |
| Nondirect.<br>Post-dispersal                         | 05.06–20.08   | $0.56 \pm 0.61$<br>$0.39 \pm 0.57$   | 148<br>414          | $2.02 \pm 1.3$<br>$2.11 \pm 1.15$                                 | 51<br>122            | $1.28 \pm 0.78$<br>$2.58 \pm 1.16$  | 136<br>235           | $3.21 \pm 2.6$<br>$2.10 \pm 1.69$                             | 42<br>102      |
| Cluster<br>Entire period                             | 12.02–20.08   | $0.82\pm1.0$   | 814                 | $2.07\pm1.52$   | 261                  | $2.21\pm1.49$   | 809                  | $2.81 \pm 2.4$  | 227            |
| F5<br>Phase/movement pattern                         | Date  | Minimum distance (km) <sup>a</sup>   | e (km) <sup>a</sup> |   | Travel spee $x$      | Fravel speed $(km/day)^a$   | min                  | max   |                |
| Pre-dispersal<br>Directional                         | 23.01–08.03   | 1110.5<br>701.5  |                     |   | 33.6<br>46.8         |   | 3.04                 | 86.1<br>86.1  |                |
| Nondirect.<br>Dispersal<br>Directional               | 09.03-11.04   | 409<br>946.2<br>401.7  |                     |   | 20.4<br>39.5<br>40.1 |   | 3.04<br>17.2<br>17.2 | 36.8<br>77.01<br>77.01  |                |
| Cluster<br>Entire period                             | 23.01–11.04.2018  | 544.5<br>2056.7  |                     |   | 38.9<br>34.5         |   | 23.3<br>3.04         | 66.9<br>86.1  |                |
| Mean travel speed (km/1 h) <sup>a</sup><br>Phase     | Date  | $\begin{array}{c} \operatorname{Day} \\ x \pm \operatorname{SD} \end{array}$ | <i>n</i> (h)        | $\begin{array}{c} \mathrm{Dusk} \\ x \pm \mathrm{SD} \end{array}$ | <i>n</i> (h)         | Night $x \pm SD$  | <i>n</i> (h)         | $\begin{array}{c} \text{Dawn} \\ x \pm \text{SD} \end{array}$ | <i>n</i> (h)   |
| Pre-dispersal<br>Directional                         | 23.01–08.03   | $1.42 \pm 0.97$<br>$1.9 \pm 1.14$  | 197                 | $3.15 \pm 1.89$<br>$3.79 \pm 1.7$                                 | 39                   | $1.15 \pm 1.29$<br>$1.81 \pm 1.62$  | 235                  | $3.63 \pm 2.09$<br>$4.09 \pm 2.44$                            | 32             |
| Nondirect<br>Dispersal<br>Directional                | 09.03–11.04   | $1.05 \pm 0.63$<br>$0.25 \pm 0.3$<br>$0.24 \pm 0.38$                         | 104<br>143<br>66    | $2.64 \pm 1.92$<br>$3.55 \pm 1.5$<br>$3.98 \pm 1.77$              | 54 46<br>77 46       | $0.64 \pm 0.62$<br>$3.03 \pm 1.67$<br>$3.25 \pm 2.2$                                | 128<br>174<br>67     | $3.25 \pm 1.74$<br>$3.25 \pm 2.19$<br>$2.75 \pm 1.62$         | 38<br>17       |
| Cluster<br>Entire period                             | 23.01–11.04   | $0.26 \pm 0.27$<br>$0.95 \pm 0.96$   | 77<br>340           | $3.25 \pm 1.33$<br>$3.32 \pm 1.7$                                 | 37<br>149            | $2.58 \pm 1.24$<br>$1.93 \pm 1.7$   | 107<br>409           | $3.57 \pm 2.49$<br>$3.48 \pm 2.12$                            | 30             |
|  |   |  |                     |   |                      |   |                      |   |                |

<sup>a</sup> Cumulative Euclidean distances summed of successive locations



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exactly what leads wolves from the same areas to disperse long distances in the same direction. We speculated that there could be habitat corridors, or this could be just a chance. More research is needed to detect and understand these patterns.

Our findings extend our knowledge of wolf dispersal capabilities and help explain how wolves disperse from protected areas to surrounding territories. Studied cases of transboundary dispersal of young wolves may indicate that through natal dispersal the wolf population in this ecoregion originates from the protected areas inhabited by an increasing stable group of wolves, such as the Dauria International Protected Area and its component part, the Daursky State Nature Biosphere Reserve. We presumed that young wolves dispersing from this area settle not only in adjacent or nearby areas bordering their natal territory (Kirilyuk et al. 2019) but also over many hundreds of kilometers, even in areas with worse habitat conditions, such as China. During dispersal, predators gradually explore the surrounding area, discovering vacant and suitable areas to inhabit, or an adoptable pack. This hypothesis requires long-term research to validate its claims.

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Authors' contributions All authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by Anastasia Kirilyuk and Vadim E. Kirilyuk. The first draft of the manuscript was written by Anastasia Kirilyuk and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Availability of data and material The data that support the findings of this study are available from The Daursky State Nature Biosphere Reserve, but restrictions apply to the availability of these data, which were used under license for the current study, and so are not publicly available. Data are however available from the authors upon reasonable request and with permission of the Daursky State Nature Biosphere Reserve.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The scientific council of Daursky State Nature Biosphere Reserve approved procedures of animal capturing and collaring.

Consent to participate Not applicable.

**Consent for publication** Not applicable.

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