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SEASONAL VARIATION OF SPACE USE IN *SPERMOPHILUS FULVUS* (SCIURIDAE): INSIGHTS FROM TELEMETRY STUDY

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Investigation of animal spatial use is crucial for both fundamental understanding of life history and ecology of the species, and for addressing applied issues in population management and the conservation of threatened species. Acquiring precise data on movements remains technically challenging for mammals with specific lifestyles, particularly for secretive, burrowing, or subterranean taxa. Here, we present the first study of spatial use in *Spermophilus fulvus* (hereinafter – yellow ground squirrel), a large rodent exhibiting an extremely prolonged period of summer – winter hibernation. We collected data in March–August 2019–2023 in a wild population located in the Dyakovsky Forest National Park (Saratov Region, Russia). Movements of yellow ground squirrels were recorded using Global Positioning System tracking devices. Additionally, for the first time in a rodent hibernator, we have tested a method of attaching GPS-trackers to the skin using surgical glue, which proved to be completely safe for the animals, including those species that exhibit pronounced fluctuations in body mass during their annual cycles. During the mating season in spring, males travelled for long distances in search for estrous females, whereas females remained in the vicinity of their hibernacula. Males traversed several kilometres per day and made excursions well beyond the settlement boundary, visiting and mating with many females, employing a competitive mate-searching strategy. The observed patterns of mating system are consistent with scramble competition polygyny involving promiscuity and multiple paternity in the yellow ground squirrel. Male movements were reduced on cold or rainy days, which imposed a risk of reproductive failure for females, which might remain unmated, if they came to estrus under unfavourable weather conditions. In summer, during the last weeks before hibernation, individuals of all sex-age classes occupied relatively small home ranges. Due to the process of natal dispersal, young males covered greater daily distances than other individuals did; nevertheless, dispersal occurred over short distances: unlike males during the mating season, dispersing juveniles did not leave the boundaries of the settlement. The results demonstrate the restructuring of spatial use from the mating period through to hibernation in the yellow ground squirrel, and contribute to our understanding of population processes in ground squirrels.

Key words: competitive mate search, daily distance, GPS-tracker, hibernating rodents, home range, mating strategies, yellow ground squirrel

Introduction

Spatial-use strategies of animals are fundamental ecological traits, shaped by abiotic environmental factors, life-cycle characteristics, foraging and mating strategies, and predator and competitor avoidance (Williams et al., 2014; Schweiger & Frey, 2021). These relationships are crucial for animal adaptation to habitat changes and reproductive success (Owen-Smith et al., 2010; Edelhoff et al., 2016; Gür, 2022), rendering investigation of animal movements essential for understanding of population processes and life-history evolution.

With XXI-century technological advances, telemetry and other instrumental tracking methods providing accumulation of high-quality spatial data have become widely accessible in zoological studies. These facilitate continuous, accurate monitoring of individual movements and spatial-use strategies for various taxa. The advent of data-processing equipment has enabled quantitative analyses of huge telemetry datasets (Halle & Weinert, 2000; Bradley & Dowler, 2019). However, telemetry methods have initially been developed for a limited subset of species, whereas some mammalian groups remain poorly studied, partly due to technical challenges posed by their life histories, e.g. fossorial or subterranean species.

Hibernating mammals represent a special focal group in behavioural ecology, as their main life-history processes including reproduction, growth, and dispersal, occur during a brief period of aboveground activity (Choromanski-Norris et al., 1986; Shilova, 2000, 2004). The transition between mating season and pre-hibernational fattening involves morphological, physiological, and behavioural changes.

The tribe Marmotini Pocock, 1923 (ground squirrels) includes burrowing diurnal rodents, which may be considered traditional model taxa in behavioural ecology. Despite similar morphological, physiological, and ecological traits across species, they display high diversity in social systems and reproductive strategies (Shilova, 2000, 2004). Many species undergo prolonged obligate hibernation as part of their annual cycle (Ortmann & Heldmaier, 2000; Armitage, 2017). To date, telemetry has been applied to only a few Marmotini species, largely due to the combined challenges of burrowing lifestyle and extended hibernation (Linn & Key, 1996; Kachamakova & Koshev, 2021; Poessel et al., 2023).

Spermophilus fulvus Lichtenstein, 1823 (hereinafter – yellow ground squirrel) is the largest Palearctic Marmotini species (Ognev, 1947; Rossolimo et al., 2004), with body mass reaching up to 2 kg (Vasilieva et al., 2009). It inhabits deserts, semi-deserts, and dry steppes of Central Asia, Iran, China, and Russia (Sludskii, 1969; Titov et al., 2017). In Southern Russia, it inhabits dry steppes on sandy soils (Shilova et al., 2015). Yellow ground squirrel lives solitarily. Its individuals usually use multiple separate burrows. Its summer–winter hibernation span may exceed nine months (Sludskii, 1969). After emergence from hibernation in March–early April, females become estrous and mate within the first few days (Vasilieva et al., 2024b). Juveniles usually leave natal burrows by late May, and two weeks later they begin to disperse (Vasilieva et al., 2024a). Adults immerge into hibernation in June–July and juveniles in July–early August (Vasilieva et al., 2024a). Despite its large body size, the yellow ground squirrel exhibits a «fast» life-history strategy with high juvenile mortality, fast growth, and maturation (they start to reproduce as yearlings), leading to a short lifespan compared with similar species. The yellow ground squirrel is folivorous and feeds primarily on fresh green vegetation. Under such conditions, we might expect rapid behavioural reorganisation throughout the period of aboveground activity. In southern Russia, the yellow ground squirrel lives at low population densities (Vasilieva et al., 2024a). There is a concern that it is undergoing declines in some parts of its range (see Lissovsky et al., 2019). At present, the yellow ground squirrel forms mixed hybridised populations with *Spermophillus major* Pallas, 1779, which may threaten the preservation of «pure» colonies of the species at the northern border of its range (Shilova et al., 2015; Titov et al., 2023). The yellow ground squirrel is listed in several regional Red Data Books of Russia, including the Red Data Book of the Saratov Region (Lissovsky et al., 2019).

Existing data on the spatial ecology of the yellow ground squirrel are fragmentary and largely derived from early XX-century visual observations (Orlov, 1925), yet valid data about space use are in high demand for population management and conservation projects. Telemetry has not been previously employed to study its movement patterns. In this study, based on telemetry data from free-living animals from the Dyakovsky Forest National Park, we aimed to (1) compare spatial use by yellow ground squirrels during the breeding season versus the pre-hibernation period; and (2) examine how sex, age class, and external environmental factors influence spatial-use patterns. This research constitutes the first pilot investigation of movement ecology in the yellow ground squirrel in the wild using Global Positioning System (GPS) telemetry.

Material and Methods

Study area and object

Data were collected during spring (March–April) and summer (June–August) in 2019–2023 near the village of Dyakovka, Krasnokutsky District, Saratov Region, Russia (50.724444° N, 46.778888° E), within a natural population of *Spermophilus fulvus orlovii* Ognev, 1937. The model colony is located in Dyakovsky Forest National Park. Since 2001, long-term, individual-based monitoring has been conducted in this colony. Therefore the age, origin, and main life history events are known for most individuals.

Yellow ground squirrels were captured using wire-mesh traps and loops equipped with radio transmitters that emitted immediate warning signals upon activation. At the first capture, all individuals were marked with subcutaneous veterinary microchips (RFID tags, 1.4 × 8.0 mm, ISO

11784/11785 standard). Sex, body condition, and mass were recorded at each trapping, and individuals were marked with black hair dye for visual recognition. For detailed descriptions of capture and marking for the yellow ground squirrel, see: Vasilieva et al. (2009, 2014), Vasilieva & Tchabovsky (2014, 2015).

Telemetry in Spermophilus fulvus

This study represents the first field deployment of GPS-trackers designed by N.S. Vasiliev at the Population ecology laboratory of A.N. Severtsov Institute of Ecology and Evolution of the RAS (Russia) for yellow ground squirrels. The compact transmitters (30 × 20 × 8 mm), which weighed 12 g in 2019–2020 and up to 10 g in 2021–2023, were encased in transparent thermosetting film and had two antennas oriented toward the animal's tail. We glued them onto the shaved skin above the shoulder blades using Perma Type Surgical Cement (Perma Type Company, USA). Transmitter mass represented 0.7–2.2% of the animal body mass. Due to a rapid pre-hibernation increase in body mass and neck circumference (Vasilieva et al., 2009), collars are dangerous for yellow ground squirrels, posing a risk of suffocation and skin injuries (Williams et al., 2014). Skin attachment was perfectly safe for the yellow ground squirrels. Behavioural observations revealed no behavioural changes or signs of discomfort. After moulting, transmitters detached from the animals, and no traces of the tags were found afterwards.

Transmitters included GPS-modules to record surface location data, and light sensors that activated the GPS-module only when the animal was above ground. In 2019–2020, co-ordinates were registered hourly, while in 2021–2023, fixation intervals decreased to every 10 min. The tags registered additionally the location at every emergence from a burrow to precisely map burrows. Data were transmitted by a wireless module (Ebyte, China) using a radio channel (at 434 MHz) to two receivers mounted on trees.

In total, we equipped 37 individuals with transmitters, namely 19 males (14 adults, seven juveniles) and 18 females (12 adults, six juveniles). The dataset included approximately 500 transmitter-operational days and over 8000 location registrations. We validated the accuracy of co-ordinates using stationary transmitters placed on the ground within a colony and old burrows with known locations. The location error did not exceed ± 5 m, which was less compared to daily distances of yellow ground squirrels. We excluded from the analysis days of capturing, predation-related mortality, days of immergence into hibernation, and days of transmitter failure or loss.

All procedures were reviewed and approved by the Ethical Committee of A.N. Severtsov Institute of Ecology and Evolution of the RAS (protocols numbers are 2019-2020-31, 2021-44, 2022-44a, 2023-44b) and conformed to the Guidelines for the ethical treatment of nonhuman animals in behavioural research and teaching (ASAB/ABS, 2024) ADSnorecopa.no. At all stages of the study, including trapping, observations, visiting the colony, and telemetry, we minimised possible negative effects on the animals as much as possible.

Data analysis

We performed statistical analysis in R version 4.4.2 (R Core Team, 2024). Results were considered significant at $p < 0.05$. We used two main characteristics of yellow ground squirrels spatial-use: (1) individual home range area and (2) daily distance.

Based on Burt (1943), we defined the home range as an area used for daily routine activities, such as foraging, mating, and offspring care. We estimated the home range size using two standard methods. First of them is Minimum Convex Polygon (MCP, 100%), which constructs home range boundaries connecting the extreme location points (Mohr, 1947). MCP is suitable for small sample sizes but does not differentiate internal home range structure. The second method is the Fixed-Kernel Density Estimation, where the local density of points determines the frequency distribution of the spatial-use functions (Worton, 1989). We constructed the 95% kernel for the general home-range contour, and the 50% kernel for the core area (Worton, 1995; Blundell et al., 2001).

Due to the low frequency of location registrations in 2019–2020 (one per hour) and an insufficient number of points, the kernel estimation was inappropriate for these data. At the same time, MCP and 95% kernel home-range areas from 2021–2023 were highly correlated ($r = 0.96$; $p < 0.0001$). Thus, we used MCP areas as an estimation of home range size in statistical analyses across all datasets of 2019–2023. In 2021–2023, we filtered registration to match the hourly interval. Home-range polygons were constructed using QGIS Desktop 3.34.3, and areas were calculated using the «Calculate Geometry» tool in square metres. We log-transformed MCP areas to meet assumptions of the normality. For visualisation and exploration of spatial-use structure using high-frequency data (10-min. intervals from 2021–2023 data), 95% and 50% kernel home-range analyses were preliminarily performed in the Home Range Analysis by Kernel Density Estimation tool in QGIS Desktop 3.34.3.

We used estimations of the yellow ground squirrels' home range areas as proxies of overall space use throughout the seasons. We calculated MCP areas for every individual separately for spring and summer. We investigated the effects of several factors on the area using analysis of variance (ANOVA): (1) sex; (2) age (adult vs. juvenile); and (3) season (spring = breeding period, summer = pre-hibernation). We considered animals as adults when they hibernated and survived at least one winter.

Daily distance was calculated as the summarised length of the polyline connecting all subsequent registrations within a single day (Garland, 1983) and was used as dynamic characteristics of daily movements. We modelled variation in daily distance by examining the effects of (1) sex; (2) age; (3) number of days since onset of mating season; (4) average daily temperature; (5) daily precipitation (weather data obtained from http://rp5.ru). We defined the start of mating season as the date of spring emergence of the first female within the colony in each year (Vasilieva & Tchabovsky, 2015). We used the number of days after the start of the mating season instead of the calendar data due to strong variation in the timing of spring emergence within the colony among the study years (dates: 27.03.2019, 15.03.2020, 05.04.2021, 28.03.2022, 20.03.2023). We fitted linear mixed-effect models (LMMs) using the nlme package (Pinheiro & Bates, 2023) with the daily distance as a response separately for each season, with individual identity fitted as a random factor in both models. Post-hoc pairwise comparisons were conducted via Tukey's honest significant difference test using the «emmeans» package (Lenth, 2025).

Results

In both spring and summer, the transmitters worked about two weeks for every individual (Table 1). In spring, the observation period covered the mating season and the early gestation weeks in females. In summer, the period of the transmitters' work corresponded to the final weeks before yellow ground squirrels entered hibernation.

During the mating season, males ranged extensively, covering areas greatly exceeding the boundaries of the focal colony (Table 1, Table 2, Fig. 1, Fig. 2A). In contrast, females remained close to their hibernacula, and their home-range areas were tens to hundreds of times smaller than those of males (Table 1, Table 2, Fig. 1, Fig. 2A). Male home ranges, including core areas, strongly overlapped (Fig. 2A).

Table 1. Characteristics of the space use by yellow ground squirrels of various sex and age groups across spring and summer in Dyakovsky Forest National Park (Russia)

Indicators	Adult males	Adult females	Juvenile males	Juvenile females
Transmitter registration duration in spring, days	10.8 ± 4.6 (n = 10)	16.1 ± 4.9 (n = 9)	–	–
Transmitter registration duration in summer, days	10.5 ± 3.7 (n = 6)	9.0 ± 5.7 (n = 5)	15.5 ± 11.2 (n = 7)	15.2 ± 6.9 (n = 6)
Home range area in spring (Kernel 95% method, m^2)**	241 213 ± 198 075 (n = 6)	18 101 ± 15 214 (n = 6)	–	–
Home range area in spring (Kernel 50% method, m^2)**	23 469 ± 18 450 (n = 6)	1836 ± 1797 (n = 6)	–	–
Home range area in summer (Kernel 95% method, m^2)**	10 970 ± 632 (n = 2)	15 288 ± 8742 (n = 3)	24 446 ± 10 715 (n = 6)	13 532 ± 6904 (n = 5)
Home range area in summer (Kernel 50% method, m^2)**	1093 ± 238 (n = 2)	2570 ± 857 (n = 3)	3106 ± 1475 (n = 6)	1791 ± 1361 (n = 5)
Mean daily distance in spring, m*	1850 ± 1381 (n = 10)	324 ± 275 (n = 9)	–	–
Mean daily distance in summer, m*	401 ± 260 (n = 6)	373 ± 181 (n = 4)	477 ± 216 (n = 7)	419 ± 188 (n = 6)

Note: * – based on registrations at 1-hour intervals; ** – based on registrations at 10-min. intervals. All values are presented as mean ± standard deviation, with the number of individuals indicated in parentheses (n)

Table 2. Effects of sex, age, and environmental conditions on home range structure and daily distance of yellow ground squirrels across spring and summer in Dyakovsky Forest National Park (Russia)

Dependent variables	Factors	
Home range area in both seasons, MCP method ($N_{individuals}$ = 30), ANOVA	**Sex**	**$F_{1,26}$ = 17.58; p < 0.001**
	Season	**$F_{1,26}$ = 11.05; p = 0.002**
	Sex × Season	**$F_{1,26}$ = 19.49; p < 0.001**
Home range area in summer, MCP method ($N_{individuals}$ = 25), ANOVA	Sex	$F_{1,20}$ = 0.003; p = 0.95
	Age	$F_{1,20}$ = 2.03; p = 0.17
	Sex × Age	$F_{1,20}$ = 0.13; p = 0.72
Daily distance in spring ($N_{individuals}$ = 20; $N_{observation}$ = 213), LMMs	**Number of days since onset of mating season**	**B = -0.01 ± 0.01; p = 0.045**
	Sex	**B = 1.13 ± 0.23; p < 0.001**
	Average daily temperature	**B = 0.03 ± 0.01; p = 0.009**
	Daily precipitation	**B = -0.12 ± 0.02; p < 0.001**
Daily distance in summer ($N_{individuals}$ = 25; $N_{observation}$ = 281), LMMs	**Number of days since onset of mating season**	**B = -0.04 ± 0.01; p < 0.001**
	Age	B = 0.35 ± 0.68; p = 0.61
	Sex	B = -1.15 ± 0.65; p = 0.09
	Sex × Age	**B = 1.7 ± 0.78; p = 0.03**
	Average daily temperature	**B = 0.03 ± 0.01; p = 0.038**
	Daily precipitation	**B = -0.04 ± 0.01; p = 0.003**

Note: Significant effects (p < 0.05) are highlighted in bold. Designations: MCP – Minimum Convex Polygon; LMMs – linear mixed-effect models; $N_{individuals}$ – number of individuals; $N_{observation}$ – number of observations.

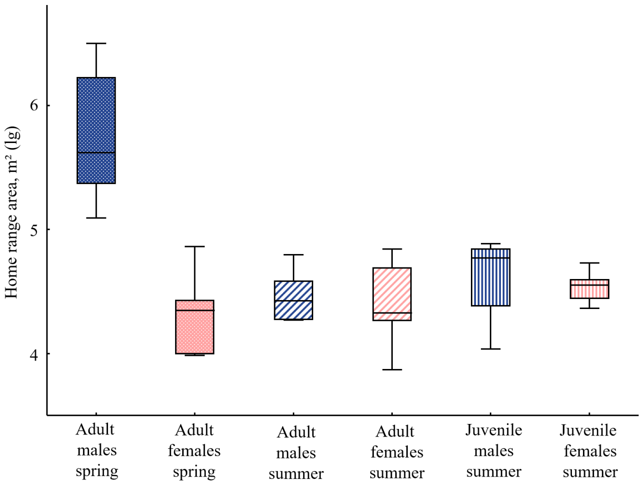

Fig. 1. Comparison of home range areas of the yellow ground squirrel constructed using the Minimum Convex Polygon method in Dyakovsky Forest National Park (Russia). The y-axis represents the decimal logarithm of the 1-m² area. The line within each box indicates the median (50% percentile). The top and bottom borders of the box represent the interquartile range (25% and 75% percentiles). The whiskers denote the range of the data. Blue colour – males, red colour – females; dotted boxes – spring data; hatched boxes – adults in summer; boxed with vertical lines – juveniles.

Daily distances of males were surprisingly high during the mating season period. Males often covered several kilometres per day, with the maximum record exceeding 12 km. Males frequently travelled beyond the focal colony and visited females in neighbouring colonies. Sometimes they went through unfavourable habitats, such as shrubs and groves of trees. Male routes showed that they visited the same locations (on all such sites, we found burrows of the yellow ground squirrel) and used the same rural roads during their movements (Fig. 2B). Daily distances for males in spring were significantly greater than daily distances for females, which distances typically remained less than 1 km (Table 1). The distances declined significantly as the breeding season progressed (Table 2). Weather had a strong effect on the yellow ground squirrel mobility. A lower mean daily temperature and increased precipitation corresponded to a reduced mobility in both males and females (Table 2). On rainy days, males restricted their movements to areas near winter burrows (Fig. 3). All long excursions exceeding 3 km were performed by males in days strictly without rain, and on all rainy days with precipitation higher than 7 mm, the male daily distances were shorter than 1 km.

ANOVA comparing adult individuals across spring and summer revealed significant effects of season, sex, and their interaction on the home range area (Table 2). Male home ranges during the mating season were significantly larger than those of females in spring and of all adults in summer (Tukey's test, p < 0.001). We did not detect any significant differences between female home ranges in spring, female home ranges in summer, and male home ranges in summer (Tukey's test, p > 0.05) (Table 1, Fig. 1). Spring home-range areas of males estimated using the 95% kernel method were about one-third of the size of areas obtained via MCP for the same individuals (Table 1). The 95% kernel areas were spatially fragmented in all males, comprising multiple discrete patches sometimes separated by several hundred metres (Fig. 2A). Females in spring and all individuals during the pre-hibernation period had compact home ranges without large gaps between fragments of the areas (Fig. 2A, Fig. 4A).

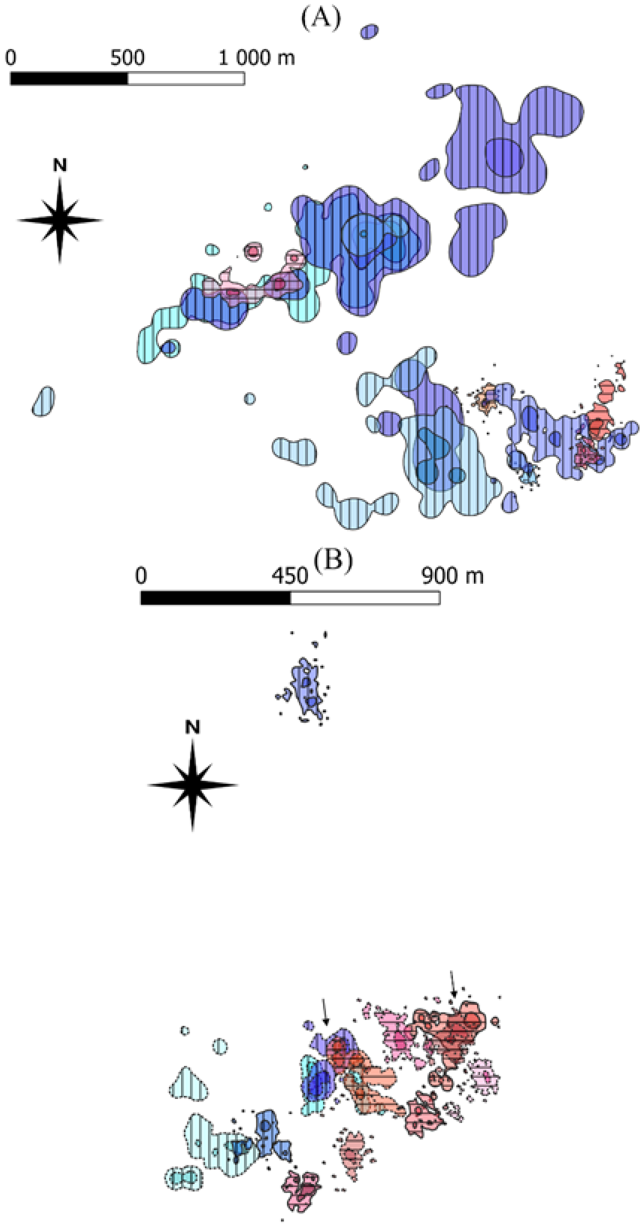

Fig. 2. Home ranges of the yellow ground squirrel in Dyakovsky Forest National Park (Russia), constructed using 95% and 50% kernel methods, for various sex and age groups in various seasons. Males are shown with shades of blue with vertical lines; females are shown with shades of red with horizontal lines; adults are denoted with solid contours, while juveniles with dashed contours. 95% kernel areas are large and semi-transparent; 50% kernel areas are smaller and darker. Scale 1 : 27247. Designations: A) Adult home ranges in spring: males (N = 5), females (N = 4); B) Adult and juvenile home ranges in summer: adult males (N = 2), adult females (N = 2), juvenile males (N = 3), juvenile females (N = 5); arrows indicate home range overlapping among related individuals.

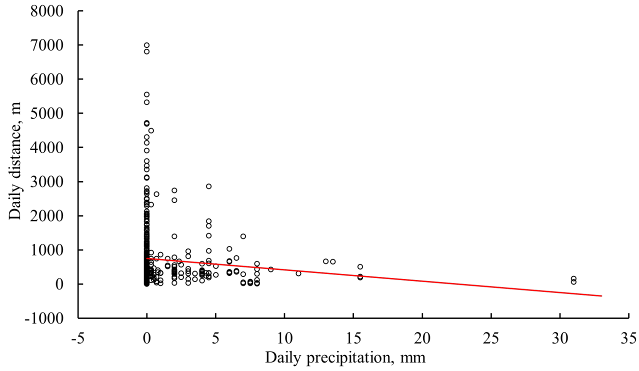

Fig. 3. Relationships between daily distance and daily precipitation for yellow ground squirrels during the mating season (r = -0.11; p = 0.01) in Dyakovsky Forest National Park (Russia). The x-axis represents daily precipitation in millimetres; the y-axis represents daily distances for every individual in metres.

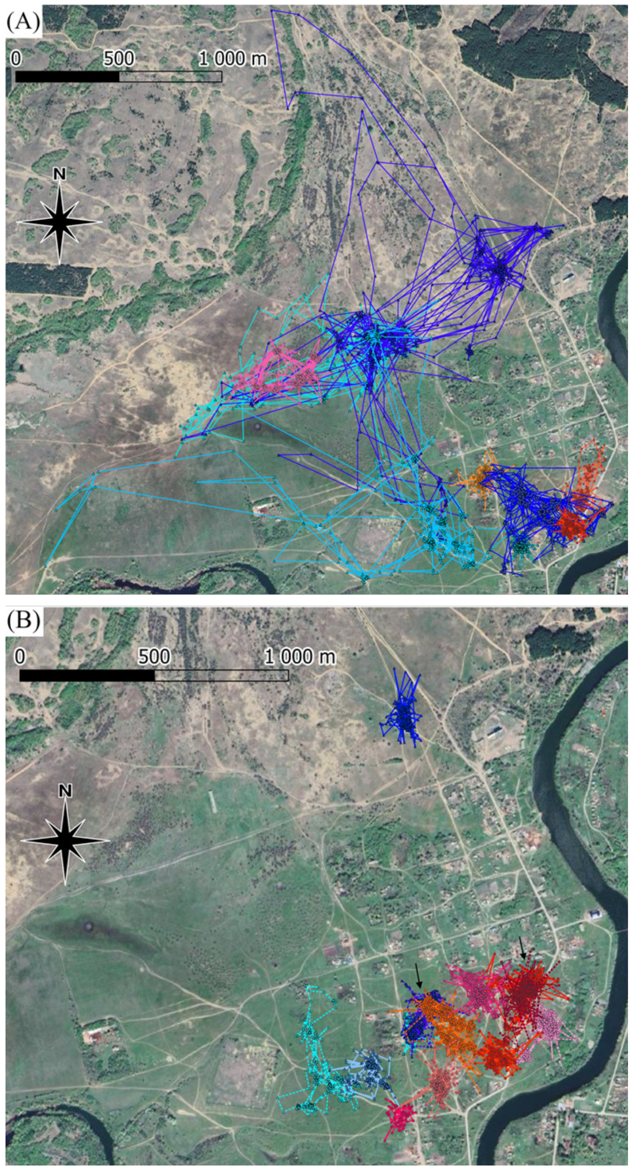

Fig. 4. Individual tracks of yellow ground squirrels for various sex and age groups during spring (A) and summer (B) observation periods in Dyakovsky Forest National Park (Russia). Males are denoted with shades of blue with triangular points; females are denoted with shades of red with circular points; solid lines – adults; dashed lines – juveniles. Scale: 1 : 27247. Arrows indicate route overlapping among related individuals.

During the pre-hibernation period, the home-range size did not vary significantly with age or sex (Table 2). In summer, daily distances declined steadily as hibernation approached. Daily distances were slightly longer in males than in females, yet insignificantly (Table 2). Juvenile males travelled significantly farther than adult males (Tukey's test, $p < 0.001$). However, all summer movements (including those of juvenile males) remained within the focal colony (Fig. 4B). As in spring time, weather influenced mobility: a lower temperature and increased precipitation led to reduced travel distances (Table 2).

Discussion

The observed space use patterns of the yellow ground squirrel are partially consistent with other related studies. The high mobility of males during the breeding season and the relatively low mobility of females have been previously described in Vasilieva (2011) and Vasilieva & Tchabovsky (2018). However, the application of instrumental methods has yielded new insights. Home range sizes obtained through visual observations were underestimated, since the average home range of males in spring, based on telemetry data, exceeded 900 000 m^2, whereas visual observations indicated approximately 30 000–40 000 m^2 (Vasilieva et al., 2014). The camouflage colouration of the fur, using small hollows, deep tire tracks, and dense vegetation, made a running yellow ground squirrel almost invisible to the observer. So, long-distance movements (over 500 m) were detected only via telemetry. Traditional observational methods failed to record them, leading to their exclusion from analyses. This study has identified for the first time excursions of male yellow ground squirrels beyond the colony and visiting females in other colonies. These findings greatly contribute to the understanding of population genetic processes in the yellow ground squirrel and may have practical implications for population management.

Space use during the breeding season

During the breeding season, male yellow ground squirrels moved extensively, where the average home range of males was approximately twice the size of the model colony. Our data showed that the kernel density estimation method was unsuitable for the description of male home ranges in spring. The method assumes a two-dimensional normal distribution of animal locations (Worton, 1989), which does not correspond with the actual distribution of male registrations during the breeding season. This discrepancy is evident from the segmentation of male home ranges into separate polygons more than 1 km apart. Male home ranges overlapped as they visited the same female aggregations and travelled using the same rural roads during their movements (Fig. 2B). Notably, core areas of male home ranges could strongly overlap (Fig. 2A), such as some males lacked exclusive territories, except for their hibernacula. They traversed large distances daily in search of mates, including visiting females far beyond the model settlement boundaries. This space-use behaviour was described in other Rodentia species as competitive mate searching tactics during the breeding season (Alcock, 1980). In such species, males focus their efforts not on defending particular mates and/or territories, but on locating new receptive females, who typically mate with multiple males. Indeed, multiple paternity was described as common in *Spermophilus fulvus* litters (Batova et al., 2021). This strategy has also been described in other Marmotinae species, for example, in *Spermophilus tridecemlineatus* Mitchill, 1821 (Schwagmeyer & Woontner, 1986). Yet, such male strategies were typical for small-sized Marmotini species, whereas in species similar in body size to the yellow ground squirrel, males mostly defend a set of females or harems within their territory and form more or less strong male-female bonds (Armitage, 1981). We suggest that the mating system of the yellow ground squirrel was determined by the unique complex of life-history traits that could be named as «fast and solitary lifestyle» (Vasilieva et al., 2024b) in this desert-dwelling folivorous rodent.

Female yellow ground squirrels remained near their hibernacula during the breeding season and performed only short movements compared to males, similar to females in other hibernating Marmotini species (Michener & Locklear, 1990; Buck & Barnes, 1999). The prolonged hibernation period of the yellow ground squirrel constrains the time available for gestation and rearing offspring. Thus, estrus is brief, and pregnancy occurs shortly after emergence from hibernation (Vasilieva et al., 2024b). Consequently, females intensively forage near their hibernacula to accumulate resources for reproductive needs and to prepare for the subsequent hibernation, despite the risks associated with reduced mobility, which decreases their chances of encountering a mate

(Vasilieva & Tchabovsky, 2014, 2015). Similarly, females in other hibernating Marmotini species, such as *Urocitellus richardsonii* (Sabine, 1822) (Michener, 1998) and *Xerospermophilus mohavensis* (Merriam, 1889) (Harris & Leitner, 2004), begin to gain weight during the breeding season to accelerate offspring growth and prepare for hibernation.

Weather conditions significantly influenced the mobility of both males and females in spring, where a low temperature and increased precipitation reduced their activity. Decreased mobility during cold and rainy days has been documented in various Marmotini species (Everts et al., 2004; Chmura et al., 2020) and Rodentia group in general (Feliciano et al., 2002; Meynard et al., 2012; Maestri & Marinho, 2014). In this study, we discovered that on rainy days long-distance movements of male yellow ground squirrels were entirely suppressed. All excursions beyond the colony were performed during days without rain (with zero precipitation), and on all days with heavy rain or snow, males ceased their mate search. This fact suggests that it is highly disadvantageous for females, when their emergence from hibernation and the following estrus coincide with adverse weather conditions. Reduced male mobility on such days may diminish the female chances of encountering a mate and successful reproduction in the current year (Vasilieva & Tchabovsky, 2015).

Two to three weeks after the onset of the mating season, male activity began to gradually decrease, indicating the end of the breeding period. The timing of the mating season in yellow ground squirrels is determined by the timing of emergence from hibernation and the reproductive biology of females. Females within a colony typically emerge from hibernation during 15–20 days in March–April (Vasilieva & Tchabovsky, 2015), enter estrus shortly thereafter, and become pregnant. Five to seven days after spring emergence, females are no longer attractive to males (Vasilieva et al., 2024b). These observations align with the timing of activity of males in the present study, as in three weeks since the vernal emergence of the first female, they ceased long-distance movements, re-organised their activity budgets, and began to accumulate weight for the next hibernation. A valid decline in daily movement by males towards the end of the breeding season was previously documented only in a few Marmotini species, for example, in *Urocitellus richardsonii* (Michener & McLean, 1996).

Space use during pre-hibernation period

During the summer pre-hibernation period, home ranges of adult males and females were equally small and exhibited minimal overlap, which was consistent with the solitary lifestyle of the yellow ground squirrel (Traut & Orlov, 1929; Ognev, 1947; Vasilieva et al., 2024a). By the start of the present study, juveniles had already become independent from their mothers, starting to disperse, and establish separate home ranges. In yellow ground squirrels, young females seem to exhibit philopatry, remaining close to their natal burrows, while males are more likely to disperse. It was reflected in the higher mobility of young males in the present study as compared with other individuals. Adult movements were primarily associated with foraging and preparing hibernacula, as successful foraging is critical for survival during hibernation (Armitage, 1981; Harris & Leitner, 2004).

Daily mobility decreased as hibernation approached. This trend was not evidently related to photoperiod shortening or weather conditions, as it occurred on different calendar dates for various individuals. For instance, adult males entered hibernation in June, adult females in late June – early July, and juveniles in late July to early August (Sludskii, 1969; Okulova et al., 2017; Vasilieva & Tchabovsky, 2018). Probably, the decrease in mobility prior to hibernation in yellow ground squirrels was not driven mostly by environmental conditions but triggered by internal physiological factors such as hormonal and blood biochemical parameters. For instance, pre-hibernation changes in steroid levels, which could affect the Marmotini species behaviour, have been documented in *Urocitellus columbianus* Ord, 1815 and *Urocitellus parryii* Rich, 1825 (Boonstra et al., 2011; Wilsterman et al., 2015).

The small sample size used in this study limited our ability to quantitatively analyse the overlap of home ranges and identify factors influencing this overlapping. However, qualitative observations indicated that home ranges of closely related individuals, such as a mother and its two female juveniles, or two juvenile males and a female from the same litter, overlapped more than those of unrelated individuals (Fig. 4A). This pattern suggests that the relatedness shapes spatial organisation in this species, similarly to other Marmotini species with matrilineal groups, represented by spatial aggregations of relative females (Holekamp & Sherman, 1989; Ims, 1989; Le Galliard et al., 2006).

The timing of our study partially coincided with the dispersal period of juvenile individuals, during which some juveniles may have been establishing new home ranges. Notably, no juvenile left the colony. All of them remained within the colony boundaries, selecting and digging hibernation burrows more or less near their natal area. This observation suggests that male spring excursions may play a more considerable role in gene flow between distant parts of the colony and between various colonies than it was previously recognised, since natal dispersal appeared to be too short-distance. Since our present sample size is small, future investigations are required. Our findings offer new insights into the potential role of male spring movements and juvenile dispersal in the population structure and gene flow of yellow ground squirrels. These results should be taken into account when planning conservation efforts and population management strategies, including reintroduction projects.

Conclusions

Our study demonstrates that the space-use strategies of yellow ground squirrels are shaped by their life-history characteristics, mostly by an extremely prolonged hibernation period, which imposes constraints on the timing of essential life processes. To our knowledge, this is the first telemetry study on the spatial use of Marmotinae species in Russia and one of the few in Eurasia. Our research is a pilot study, since our small sample size partially limits detailed analysis and conclusions. Yet it provides a roadmap for future research that should quantitatively elucidate factors governing spatial organisation and movement ecology in the yellow ground squirrel.

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References

Alcock J. 1980. Natural Selection and the Mating Systems of Solitary Bees. *American Scientist* 68(2): 146–153.

Armitage K.B. 1981. Sociality as a life-history tactic of ground squirrels. *Oecologia* 48(1): 36–49. DOI: 10.1007/BF00346986

Armitage K.B. 2017. Hibernation as a major determinant of life-history traits in marmots. *Journal of Mammalogy* 98(2): 321–331. DOI: 10.1093/jmammal/gyw159

Batova O.N., Vasilieva N.A., Titov S.V., Savinetskaya L.E., Tchabovsky A.V. 2021. Female polyandry dilutes inbreeding in a solitary fast-living hibernator. *Behavioral Ecology and Sociobiology* 75: 145. DOI: 10.1007/s00265-021-03086-1

Blundell G.M., Maier J.A.K., Debevec E.M. 2001. Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates. *Ecological Monographs* 71(3): 469–489. DOI: 10.1890/0012-9615(2001)071[0469:LHREOS]2.0.CO;2

Boonstra R., Bradley A.J., Delehanty B. 2011. Preparing for hibernation in ground squirrels: adrenal androgen production in summer linked to environmental severity in winter. *Functional Ecology* 25(6): 1348–1359. DOI: 10.1111/j.1365-2435.2011.01890.x

Bradley R.D., Dowler R.C. 2019. A century of mammal research: changes in research paradigms and emphases. *Journal of Mammalogy* 100(3): 719–732. DOI: 10.1093/jmammal/gyy147

Buck C.L., Barnes B.M. 1999. Annual Cycle of Body Composition and Hibernation in Free-Living Arctic Ground Squirrels. *Journal of Mammalogy* 80(2): 430–442. DOI: 10.2307/1383291

Burt W.H. 1943. Territoriality and Home Range Concepts as Applied to Mammals. *Journal of Mammalogy* 24(3): 346–352. DOI: 10.2307/1374834

Chmura H.E., Zhang V.Y., Wilbur S.M., Barnes B.M., Buck C.L., Williams C.T. 2020. Plasticity and repeatability of activity patterns in free-living Arctic ground squirrels. *Animal Behaviour* 169: 81–91. DOI: 10.1016/j.anbehav.2020.09.007

Choromanski-Norris J., Fritzell E.K., Sargeant A.B. 1986. Seasonal Activity Cycle and Weight Changes of the Franklin's Ground Squirrel. *American Midland Naturalist* 116(1): 101–107. DOI: 10.2307/2425941

Edelhoff H., Signer J., Balkenhol N. 2016. Path segmentation for beginners: An overview of current methods for detecting changes in animal movement patterns. *Movement Ecology* 4(1): 21. DOI: 10.1186/s40462-016-0086-5

Everts L.G., Strijkstra A.M., Hut R.A., Hoffmann I.E., Millesi E. 2004. Seasonal Variation in Daily Activity Patterns of Free-Ranging European Ground Squirrels (*Spermophilus citellus*). *Chronobiology International* 21(1): 57–71. DOI: 10.1081/CBI-120027982

Feliciano B.R., Fernandez F.A.S., Freitas D., Figueiredo M.S.L. 2002. Population dynamics of small rodents in a grassland between fragments of Atlantic Forest in southeastern Brazil. *Mammalian Biology* 67(5): 304–314. DOI: 10.1078/1616-5047-00045

Garland T. 1983. Scaling the Ecological Cost of Transport to Body Mass in Terrestrial Mammals. *American Naturalist* 121(4): 571–587. DOI: 10.1086/284084

Gür H. 2022. The future impact of climate and land-use changes on Anatolian ground squirrels under different scenarios. *Ecological Informatics* 70: 101693. DOI: 10.1016/j.ecoinf.2022.101693

Halle S., Weinert D. 2000. Measuring and Analysing Activity of Small Mammals in the Laboratory and in the Field. In: S. Halle, N.C. Stenseth (Eds.): *Activity Patterns in Small Mammals. Ecological Studies.* Vol. 141. Berlin, Heidelberg: Springer Berlin Heidelberg. P. 285–312. DOI: 10.1007/978-3-642-18264-8_18

Harris J.H., Leitner P. 2004. Home-Range Size and Use of Space by Adult Mohave Ground Squirrels, *Spermophilus mohavensis*. *Journal of Mammalogy* 85(3): 517–523. DOI: 10.1644/1383951

Holekamp K.E., Sherman P.W. 1989. Why Male Ground Squirrels Disperse: A multilevel analysis explains why only males leave home. *American Scientist* 77(3): 232–239.

Ims R.A. 1989. Kinship and Origin Effects on Dispersal and Space Sharing in *Clethrionomys Rufocanus*. *Ecology* 70(3): 607–616. DOI: 10.2307/1940212

Kachamakova M., Koshev Y. 2021. Post-release settlement and survival of endangered European ground squirrel after conservation reinforcement. *Journal for Nature Conservation* 63: 126048. DOI: 10.1016/j.jnc.2021.126048

Le Galliard J.F., Gundersen G., Andreassen H.P., Stenseth N.C. 2006. Natal dispersal, interactions among siblings and intrasexual competition. *Behavioral Ecology* 17(5): 733–740. DOI: 10.1093/beheco/arl002

Lenth R. 2025. *emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.11.1.* Available from https://CRAN.R-project.org/package=emmeans

Linn I., Key G. 1996. Use of space by the African Striped Ground Squirrel *Xerus erythropus*. *Mammal Review* 26(1): 9–26. DOI: 10.1111/j.1365-2907.1996.tb00144.x

Lissovsky A.A., Sheftel B.I., Saveljev A.P., Ermakov O.A., Kozlov Yu.A., Smirnov D.G., Stakheev V.V., Glazov D.M. 2019. *Mammals of Russia: species list and applied issues*. *Archives of Zoological Museum of Moscow State University* 56: 1–191. [In Russian]

Maestri R., Marinho J.R. 2014. Singing in the rain. Rainfall and moonlight affect daily activity patterns of rodents in a Neotropical forest. *Acta Theriologica* 59(3): 427–433. DOI: 10.1007/s13364-014-0177-x

Meynard C.N., Pillay N., Perrigault M., Caminade P., Ganem G. 2012. Evidence of environmental niche differentiation in the striped mouse (*Rhabdomys* sp.): inference from its current distribution in southern Africa. *Ecology and Evolution* 2(5): 1008–1023. DOI: 10.1002/ece3.219

Michener G.R. 1998. Sexual Differences in Reproductive Effort of Richardson's Ground Squirrels. *Journal of Mammalogy* 79(1): 1–19. DOI: 10.2307/1382838

Michener G.R., Locklear L. 1990. Differential Costs of Reproductive Effort for Male and Female Richardson's Ground Squirrels. *Ecology* 71(3): 855–868. DOI: 10.2307/1937357

Michener G.R., McLean I.G. 1996. Reproductive behaviour and operational sex ratio in Richardson's ground squirrels. *Animal Behaviour* 52(4): 743–758. DOI: 10.1006/anbe.1996.0219

Mohr C.O. 1947. Table of equivalent populations of North American small mammals. *The American Midland Naturalist* 37(1): 223–249. DOI: 10.2307/2421652

Ognev S.I. 1947. *Animals of the USSR and Adjacent Countries (Animals of Eastern Europe and North Asia)*. Moscow: AS USSR. 559 p. [In Russian]

Okulova N.M., Grazhdanov A.K., Neronov V.V. 2017. *Structure and dynamics of mammalian communities in Western Kazakhstan*. Moscow: KMK Scientific Press Ltd. 920 p. [In Russian]

Orlov E.I. 1925. Yellow ground squirrel. Biological observations. *Vestnik mikrobiologii i epidemiologii* 4(1): 58–66. [In Russian]

Ortmann S., Heldmaier G. 2000. Regulation of body temperature and energy requirements of hibernating Alpine marmots (*Marmota marmota*). *American Journal of Physiology* 278(3): 698–704. DOI: 10.1152/ajpregu.2000.278.3.R698

Owen-Smith N., Fryxell J.M., Merrill E.H. 2010. Foraging theory upscaled: the behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365(1550): 2267–2278. DOI: 10.1098/rstb.2010.0095

Pinheiro J., Bates D. 2023. *nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-164.* Available from https://CRAN.R-project.org/package=nlme

Poessel S.A., Leitner P., Inman R.D., Esque T.C., Katzner T.E. 2023. Demographic and environmental correlates of home ranges and long-distance movements of Mohave ground squirrels. *Journal of Mammalogy* 104(1): 104–114. DOI: 10.1093/jmammal/gyac082

R Core Team. 2024. *R: a language and environment for statistical computing*. Vienna (Austria): R Foundation for Statistical Computing. Available from https://www.R-project.org/

Rossolimo O.L., Pavlinov I.Ya., Kruskop S.V., Lisovskii A.A., Spasskaya N.N., Borisenko A.V., Panyutina A.A. 2004. *Diversity of Mammals*. Moscow: KMK Scientific Press Ltd. 366 p. [In Russian]

Schwagmeyer P.L., Woontner S.J. 1986. Scramble competition polygyny in thirteen-lined ground squirrels: the relative contributions of overt conflict and competitive mate searching. *Behavioral Ecology and Sociobiology* 19(5): 359–364. DOI: 10.1007/BF00295709

Schweiger B.R., Frey J.K. 2021. Weather determines daily activity pattern of an endemic chipmunk with predictions for climate change. *Climate Change Ecology* 2: 100027. DOI: 10.1016/j.ecochg.2021.100027

Shilova S.A. 2000. Spatial and Social Organization of Ground Squirrels (Genera *Spermophilus*, *Xerus*, and *Cynomys*) as a Model for Ecological-Ethological Studies. *Advances in Current Biology* 120(6): 559–572. [In Russian]

Shilova S.A. 2004. Ground squirrels. *Priroda* 3: 41–48. [In Russian]

Shilova S.A., Savinetskaya L.E., Tchabovskii A.V. 2015. Long-term and recent dynamics of the yellow souslik (*Spermophilus fulvus*, *Rodentia*, *Sciuridae*) population from Yeruslan sands of Transvolga region. *Zoologicheskii Zhurnal* 94(8): 944–954. DOI: 10.7868/S0044513415080140 [In Russian]

Sludskii A.A. (Ed.). 1969. *Mammals of Kazakhstan*. Vol. 1. Alma-Ata: Nauka. 455 p. [In Russian]

Titov S.V., Kuzmin A.A., Zaks S.S., Chernyshova O.V. 2017. Species specificity of biotopic preferences as a factor in interspecific isolation in mammals (by the example of genus *Spermophilus*). *Russian Journal of Ecosystem Ecology* 2(4). DOI: 10.21685/2500-0578-2017-4-4 [In Russian]

Titov S.V., Kuzmin A.A., Chernyshova O.V., Kartavov N.A., Simakov M.D. 2023. Long-Term Dynamics of Spatial and Genetic Structure of a Narrow Hybrid Zone between Russet (*Spermophilus major* Pallas, 1778) and Yellow (*Spermophilus fulvus* Lichtenstein, 1823) Ground Squirrels. *Biology Bulletin* 50(4): 668–685. DOI: 10.1134/S1062359023606353

Traut I.I., Orlov E.I. (Eds.). 1929. *Materials for The Knowledge of the Fauna of the Lower Volga Region.* Vol. 4. Saratov: Otdel Primeneniya NILOV. 121 p. [In Russian]

Vasilieva N.A. 2011. *Factors affecting reproductive behavior and breeding success in the yellow ground squirrel (Spermophilus fulvus)*. PhD Thesis. Moscow. 196 p. [In Russian]

Vasilieva N.A., Tchabovsky A.V. 2014. Timing is the only thing: Reproduction in female yellow ground squirrels (*Spermophilus fulvus*). *Canadian Journal of Zoology* 92(8): 737–747. DOI: 10.1139/cjz-2014-0084

Vasilieva N.A., Tchabovsky A.V. 2015. A shortage of males causes female reproductive failure in yellow ground squirrels. *Science Advances* 1(9): e1500401. DOI: 10.1126/sciadv.1500401

Vasilieva N.A., Tchabovsky A.V. 2018. Reproductive Decisions in a “Fast-Living” Sciurid: A Case Study of the Yellow Ground Squirrel (*Spermophilus fulvus*). *Biology Bulletin Reviews* 8: 12–22. DOI: 10.1134/S2079086418010061

Vasilieva N.A., Savinetskaya L.E., Tchabovskii A.V. 2009. Large body size and short period of activity do not impede fast growth in the long-teeth ground squirrel (*Spermophilus fulvus*). *Zoologicheskii Zhurnal* 88(3): 339–343. [In Russian]

Vasilieva N.A., Pavlova E.V., Naidenko S.V., Tchabovsky A.V. 2014. Age of maturation and behavioral tactics in male yellow ground squirrel *Spermophilus fulvus* during mating season. *Current Zoology* 60(6): 700–711. DOI: 10.1093/czoolo/60.6.700

Vasilieva N.A., Savinetskaya L.E., Tchabovsky A.V. 2024a. Juvenile survival curves in a solitary ground squirrel with a prolonged hibernation: effects of individual characteristics, environment, and maternal investment. *Current Zoology* 70(1): 13–23. DOI: 10.1093/cz/zoac097

Vasilieva N.A., Tikhonova N.B., Savinetskaya L.E., Kuznetsova E.V. 2024b. Female hormonal profiles and vaginal cytology in a ground squirrel species with prolonged hibernation. *Mammalian Biology* 104(1): 55–67. DOI: 10.1007/s42991-023-00387-y

Williams C.T., Wilsterman K., Kelley A.D., Breton A.R., Stark H., Humphries M.M., McAdam A.G., Barnes B.M., Boutin S., Buck C.L. 2014. Light loggers reveal weather-driven changes in the daily activity patterns of arboreal and semifossorial rodents. *Journal of Mammalogy* 95(6): 1230–1239. DOI: 10.1644/14-MAMM-A-062

Wilsterman K., Buck C.L., Barnes B.M., Williams C.T. 2015. Energy regulation in context: Free-living female arctic ground squirrels modulate the relationship between thyroid hormones and activity among life history stages. *Hormones and Behavior* 75: 111–119. DOI: 10.1016/j.yhbeh.2015.09.003

Worton B.J. 1989. Kernel Methods for Estimating the Utilization Distribution in Home-Range Studies. *Ecology* 70(1): 164–168. DOI: 10.2307/1938423

Worton B.J. 1995. Using Monte Carlo Simulation to Evaluate Kernel-Based Home Range Estimators. *Journal of Wildlife Management* 59(4): 794–800. DOI: 10.2307/3801959

СЕЗОННЫЕ ИЗМЕНЕНИЯ ИСПОЛЬЗОВАНИЯ ПРОСТРАНСТВА У *SPERMOPHILUS FULVUS* (SCIURIDAE) НА ОСНОВЕ ДАННЫХ ТЕЛЕМЕТРИИ

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Сведения об использовании пространства животными имеют ключевое значение как для фундаментальных представлений о жизненном цикле вида, так и при решении прикладных задач менеджмента популяций и сохранения редких видов. Получение точных сведений о перемещениях некоторых видов до сих пор представляет сложную техническую задачу, в том числе, для скрытных, норных, подземных видов. Мы впервые провели исследование использования пространства у *Spermophilus fulvus* (далее – желтый суслик) – крупного грызуна с экстремально длительной зимней спячкой. Сбор данных проводили в марте – августе 2019–2023 гг. в природной популяции, которая располагается на территории национального парка «Дьяковский лес» (Саратовская область, Россия). Перемещения желтых сусликов регистрировали с помощью устройств спутникового слежения. Впервые для зимоспящих грызунов был опробован метод крепления устройства слежения на кожу с помощью медицинского клея. Он показал себя как полностью безопасный, в том числе, для животных с сильными колебаниями массы тела в течение годового цикла. Весной в период гона самцы широко перемещались в поисках рецептивных самок, самки держались около зимовочных нор. Самцы ежедневно проходили по несколько километров и совершали выходы далеко за пределы поселения, посещая рецептивных самок. Эти наблюдения согласуются с предположением о том, что самцы желтого суслика используют стратегию конкурентного поиска партнера. Выявленные закономерности подтверждают соответствие системы спаривания желтого суслика полигинии с прямой конкуренцией. Перемещения самцов сокращались в холодные и дождливые дни, что могло для самок создавать угрозу остаться холостыми, если они вступали в эструс в дни с плохой погодой. В течение последних недель перед спячкой желтые суслики всех половозрастных групп держались на небольших индивидуальных участках. В связи с процессами расселения молодые самцы проходили в день большее расстояние, чем другие особи, но расселение происходило на небольшие расстояния: в отличие от самцов в период гона, расселяющиеся детеныши не покидали границ поселения. Полученные результаты демонстрируют перестройки использования пространства от периода гона до спячки у желтого суслика и вносят вклад в понимание популяционных процессов у наземных беличьих.

Ключевые слова: GPS-трекер, желтый суслик, зимоспящие грызуны, репродуктивные стратегии, стратегия конкурентного поиска партнеров, суточный ход, участок обитания