

Circadian Activity in Yellow Ground Squirrels *Spermophilus fulvus* Licht. (Sciuridae): A Pilot Instrumental Study

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Abstract—Most of the information on animal circadian activity is based on laboratory data. To obtain information from a natural population, we conducted for the first time an instrumental study of daily activity in yellow ground squirrels, which are large hibernating rodents. Eight individuals were fitted with glued-on radio transmitters that contained accelerometers and light sensors in summer 2021. Our data showed that yellow ground squirrels left their burrows only during daytime; the squirrels rested when they entered their burrows. As hibernation approached, the duration of aboveground activity decreased. In contrast to similar species with two peaks of activity, the aboveground activity of yellow ground squirrels was single-phased. Most likely, prolonged hibernation and, therefore, time deficiency motivated yellow ground squirrels to use daylight hours as effectively as possible.

Keywords: daily activity, radio transmitters, ground squirrels, yellow ground squirrel

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INTRODUCTION

Features of daily activity in animals are among the key characteristics of the biology of species. They are closely related to the ecological properties of the species: ways of searching for food, use of space, habitat characteristics, etc. At the same time, key physiological processes in the animal body are subject to diurnal cycles: the sleep–wake cycle; the activity of the cardiovascular, endocrine, and digestive systems; body temperature, etc. (Froy, 2007; Refinetti, 2019). Mammals are known to exhibit a wide variety of circadian activity patterns, including various 24-hour rhythms (day, night, 24 hours), as well as a short-term rhythm of activity; it has been shown for many species that the synchronization of these rhythms is implemented in accordance with the intensity of illumination (Ashby, 1972). At the same time, the variability of diurnal activity patterns within a species can be very significant and determined by sex (Schmidt, 1999; Everts et al., 2004; Vieira et al., 2010), physical condition, stage of the reproductive cycle (Clutton-Brock et al., 1982; Kenagy and Hoyt, 1989), environmental conditions (Rashitov, 2018; Podolski et al., 2013; Allen et al., 2018), etc.

Study of the daily activity regime of animals was traditionally limited to laboratory studies, which were often carried out under unnatural lighting conditions. Until recently, instrumental methods for recording activity were used only for a small number of species

and in conditions of captivity (e.g., Daan and Aschoff, 1975; Bartness and Albers, 2000; Refinetti, 2019). In the wild, information about daily changes in animal activity has been limited to data obtained from visual observations, which are especially unreliable in the case of small, secretive, and wary animal species. This state of affairs hindered the acquisition of relevant data from a wide range of species and the conduct of comparative analysis. In recent years, the rapid development of technology has made it possible to take the study of animal activity rhythms to a new level: representatives of different species began to be equipped with a variety of sensors, including in the wild. The advent of powerful computing equipment made it possible to develop approaches to the analysis of large amounts of information received from such recorders. However, instrumental studies in nature are still extremely rare.

Winter-sleeping mammals, which spend a significant part of the year in a state of profound inhibition of life processes, are of particular interest from the point of view of studying circadian rhythms. This interest is related to the fact that the mechanisms of regulation of hibernation-related processes (including the cycles of awakening during hibernation) may have a common nature with the mechanisms of regulation of diurnal activity cycles (Heller and Ruby, 2004; Malan, 2010). Ground squirrels (gophers, marmots) are a group of burrowing hibernating rodents that lead a diurnal life-

style (Shilova, 2000; Dobson, 1984; Armitage, 1986; Waterman, 2007). They are a traditional model group in behavioral ecology, since the wide variety of social systems and reproductive strategies in these rodents is combined with relatively small morphological, physiological, and ecological differences between the species. This makes it possible to study the evolution of various traits in mammals using the model of this group of species (Shilova, 2000, 2004; Vasilieva and Tchabovsky, 2017).

The burrowing lifestyle divides the activity of ground squirrels into two components: in the burrow and on the ground surface, which determines the specifics of studying the activity in these animals. On the one hand, this makes it possible to use a simplified approach to the study of the activity: an animal located on the ground surface can automatically be considered active, while an animal that is underground is considered inactive (see, for example, Bronson, 1962; Hut et al., 1999; Long et al., 2005). On the other hand, there are obvious methodological difficulties in obtaining information about an animal from a burrow, especially in the wild. To date, instrumental studies of diurnal activity patterns have been carried out only for a few species of ground squirrels, primarily on the European ground squirrel (*Spermophilus citellus*) (Hut et al., 1999) and parka squirrel (*Uroditellus parryi*) (Long et al., 2005, 2007; Chmura et al., 2020), in which the ratio of aboveground and underground activity was studied using light-sensitive sensors.

The yellow ground squirrel (*Spermophilus fulvus* Licht., 1823) is the largest of ground squirrels; males can reach a mass of 2 kg before hibernation (*Mlekopitayushchie...*, 1969; Vasilieva et al., 2009). This species inhabits dry steppes, semi-deserts, and deserts and is characterized by extremely long winter hibernation, up to nine months (Shilova, 2000; Vasilieva and Tchabovsky, 2017). With such a short period of active aboveground life, one can expect the presence of specific features of the daily activity regime in this species. However, until now, information about this species has been extremely limited; there is only information obtained during visual observations, indicating that these are strictly diurnal animals (Orlov, 1925; *Materialy...*, 1929; Ognev, 1947). Some authors argue that aboveground activity (i.e., staying outside the burrow during the day) in the yellow ground squirrel is two-phase: yellow ground squirrels stay on the ground surface in the morning and evening, while they do not leave their burrows in the middle of the day (Orlov, 1925; Ognev, 1947; *Mlekopitayushchie...*, 1969; Rosso-limo et al., 2004).

In this work, we undertook for the first time an instrumental study of the daily activity of the yellow ground squirrel in the wild using light-sensitive sensors and accelerometers with the purpose of obtaining information about the daily dynamics of staying on the ground surface and locomotor activity of yellow

ground squirrels during the period of preparation for hibernation.

MATERIALS AND METHODS

Object and Place of Study

We collected data during the preparation of yellow ground squirrels for hibernation in June–July 2021 as part of a long-term study of a wild colony of yellow ground squirrels (*Spermophilus fulvus orlovii* Ogn. 1937) in the vicinity of the village of Dyakovka in the Krasnokutskii district of Saratov oblast (50°43'88" N, 46°46'04" E). In this colony, individual marking of yellow ground squirrels has been carried out since 2001. As a result, the age, origin, and main events of the annual cycle are known for almost all individuals.

Yellow ground squirrels were caught with the help of mesh traps of an original design and loops with radio transmitters, which, when triggered, instantly transmitted a warning signal over the radio channel. When caught, yellow ground squirrels were marked with subcutaneous veterinary microchips and with a black dye (urzola) for visual recognition. A detailed description of the capture and marking of yellow ground squirrels can be found in previously published studies (Vasilieva et al., 2009, 2014; Vasilieva and Tchabovsky, 2014, 2015).

Development and Use of Radio Transmitters for the Yellow Ground Squirrel

The yellow ground squirrel is a solitary species, which is still an object of hunting today (Shilova et al., 2015). Perhaps this partly determines the extreme caution of these animals, which was especially noted by researchers at the beginning of the 20th century (*Materialy...*, 1929). Catching yellow ground squirrels is extremely time-consuming: for some individuals, the installation of an almost invisible loop made of a thin cable with a touch sensor serves as a reason not to leave the burrow for a day. As a result, most yellow ground squirrels can be caught no more than twice during the entire season of activity (i.e., per year). Meanwhile, yellow ground squirrels are characterized by sharp changes in body weight throughout the annual cycle: from the moment they emerge from hibernation to the time of its onset, the animals increase their body weight by 1.5–2 times, and after the first exit from burrows and until the moment they enter hibernation, the young animals increase their weight by 4–5 times or more (Vasilieva et al., 2009). Thus, the use of collars as a physical basis for any tracking devices and recorders for this species is unacceptable: a collar worn on an animal can lead to suffocation during a rapid increase in body weight, and it may be impossible to catch the animal and remove the device in time. In addition, a collar used in the conditions of thorny steppe vegetation can lead to violation of the integrity of the skin, inflammation, and irrita-

tion in the case of thorny seeds getting under the collar (Williams et al., 2014). To avoid these unfortunate scenarios, we have developed a safe way to mount tracking devices on yellow ground squirrels. This study used for the first time radio transmitters of an original design, which had been specially developed for the yellow ground squirrel in the laboratory of population ecology of the Severtsov Institute of Ecology and Evolution. Small-sized transmitters weighing 12 g (0.8%–2.5% of the animal weight) were packed in shrink film and fixed on the back skin of yellow ground squirrels using Perma-Type Surgical Cement (Perma Type Company, United States). After molting, the radio transmitters spontaneously separated from the skin of the animals, and not a single individual had irritation or damage at the place where the transmitters had been attached to the skin. The molted individuals did not have visual signs that a transmitter had previously been attached to them.

The radio transmitters were equipped with light sensors, which recorded every ten minutes where the animal was located—in the burrow or on the ground surface; they also recorded the exact time of entry and exit from the burrow. In addition, the radio transmitters were equipped with accelerometers that recorded every ten minutes the fraction of the previous ten minutes that the animal had been in motion. These readings were composed of five-second slices: every five seconds, a transmitter stored “1” if the animal was moving (movement was recorded at acceleration ≥ 0.19 g at least along one of the three axes of the accelerometer) and “0” if it was motionless (acceleration was < 0.19 g), and “units” were summed up every ten minutes.

The data from the radio transmitters were transmitted over a radio channel to two radio receivers (434 MHz civil radio bands were used) located in the trees. For 2021, data (40310 records) were received using radio transmitters from four males (one adult and three young animals) and four females (one adult and three young animals) during the period from June 21 to July 30.

Data Analysis

To assess changes in yellow ground squirrel activity as hibernation approaches, we used the following variables obtained for each individual for each day of observations: (1) the time of the beginning of daytime activity (the time of the first exit from the burrow in the morning); (2) the duration of daily activity, which is the difference in time from the first exit from the burrow in the morning to the last record of the individual on the surface; (3) the exact time spent on the surface during the day, which is calculated as the duration of daily activity minus the total time spent in the burrow during the day (from the first exit from the burrow in the morning to the last record on the surface); (4) the time of the end of daily activity (time of the last record on the surface in the evening).

To analyze the daily dynamics of aboveground and locomotor activity, we used two variables: (1) staying in the burrow/on the surface throughout the day, which is a sequence of zeros and units received at a frequency of once every ten minutes based on the readings of a light sensor. Units corresponded to being on the surface, and zeros corresponded to being in the burrow. The moments of each exit from the burrow were marked with additional units; therefore, in fact, the records were somewhat more frequent than once every ten minutes. (2) The level of locomotor activity during the day, which means that, for the same time points as the readings of aboveground activity, the proportion of time in motion from the time elapsed since the previous record was noted; this proportion ranged from 0 (complete immobility) to 1 (continuous movement).

The days of capture of the animals, the days of entering hibernation, and the days of death from an attack by predators (one young male was killed by a booted eagle, the other was killed by a dog) were excluded from the analysis.

Data analysis was carried out in the R 4.1.0 environment (R Development Core Team, 2021). First of all, we described the general pattern of daytime activity of animals and analyzed how the time of the beginning and end of daytime activity and the duration of daytime activity of animals changed depending on the calendar date. We also tested the extent to which yellow ground squirrels were at rest when being in the burrow compared to being on the surface to assess the validity of the approach in which the animal on the ground surface is considered active and the animal in the burrow is considered inactive (Hut et al., 1999; Long et al., 2005). To do this, we studied how the level of locomotor activity of yellow ground squirrels changed during the transition between the burrow and the ground surface. To separate the effects of the diurnal rhythm and burrowing as such, we constructed two models: one for all measurements during the day, and the other for measurements only from the moment of the first exit of each animal from the burrow in the morning to the last entering into the burrow in the evening. To solve all these problems, we built linear mixed effects models in the *nlme* package (Pinheiro et al., 2022), with the number of the individual being included in all models as a random factor.

To visualize the daily dynamics of the aboveground activity of animals (staying in the burrow/on the ground surface), we used the activity package (Rowcliffe, M. and Rowcliffe, M.M., 2022) in the R environment. To plot the curves, the frequency distributions of records of each animal on the ground surface were obtained (at the same time, data on whether the animal was in a burrow or on the surface were received at a constant frequency throughout the day). In addition, we used the *overlap* package (Ridout and Linkie, 2009; Meredith et al., 2021) and the Wald test from the

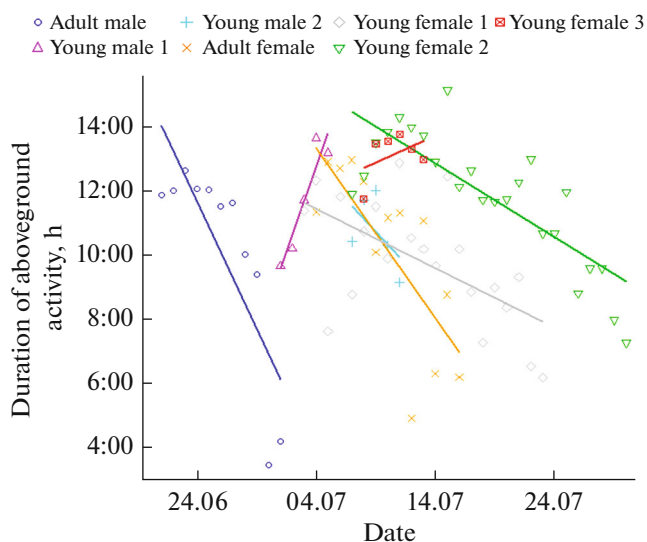


Fig. 1. Change in the duration of aboveground activity (in hours) depending on the calendar date in the yellow ground squirrel during the period of preparation for hibernation. Different colors represent different individuals. The duration of aboveground activity decreased significantly (linear models of mixed effects, $p < 0.05$).

activity package to compare quantitatively the daily dynamics of aboveground activity of males and females (we only performed this comparison for young animals), as well as adult and young animals. In order to visualize the changes in the mode of aboveground activity as hibernation approached, those individuals that were traced up to hibernation ($N = 4$) were compared as regards the daily dynamics of activity in the last seven days before hibernation (i.e., immediately before hibernation) and in the period of 8–14 days before hibernation. We considered the results of statistical tests to be significant at $p < 0.05$.

RESULTS

General Characteristics of Daily Activity

All yellow ground squirrels were active strictly during the daytime; not a single ground squirrel left the burrow in the dark. On average, yellow ground squirrels left their burrows at $6:16 \pm 1:49$ in the morning and went into their burrows at $17:07 \pm 1:22$, while sunrise on these days was before 4:00, and sunset was at about 20:00 (time is indicated everywhere according to Moscow time). Thus, on average, the duration of daily ground activity for yellow ground squirrels was $10:51 \pm 2:22$ h, of which the animals, on average, spent on the surface about $67 \pm 13\%$ of the time, and the rest of the day was spent by them in burrows. The activity budget of yellow ground squirrel depended on the calendar date: the later the date, the later the yellow ground squirrels left their burrows in the morning (mixed effects model, the individual number was

added to this and subsequent models as a random factor; $B = 0.50 \pm 0.14$, $t = 3.5$, $p = 0.0007$) and the earlier they went into their burrows in the evening ($B = -0.71 \pm 0.14$, $t = -5.1$, $p < 0.0001$). Thus, the duration of daytime aboveground activity decreased as hibernation approached ($B = -0.87 \pm 0.13$, $t = -6.7$, $p < 0.0001$, Fig. 1). Meanwhile, the exact time spent on the ground surface (minus the time that the animal spent in the burrow during the day) decreased even somewhat faster than the duration of aboveground activity ($B = -0.83 \pm 0.09$, $t = -9.0$, $p < 0.0001$).

Correspondence of the Budget of Aboveground and Locomotor Activity

The level of locomotor activity strongly depended on whether the yellow ground squirrel was in the burrow or on the surface: the locomotor activity on the surface was many times higher than in the burrow ($B = 1.46 \pm 0.01$, $t = 99.7$, $p < 0.0001$). On average, out of each ten-minute interval spent on the surface, the yellow ground squirrel moved 5.3 ± 2.9 min (median = 5.3 min/10 min), while in the burrow the time in motion averaged 1.2 ± 1.7 min/10 min (median = 0.6 min/10 min). At the same time, yellow ground squirrels staying in the burrow were almost immobile at night (time in motion was 0.1 ± 0.2 min/10 min, median = 0.05 min/10 min). When going into the burrow in the daytime, yellow ground squirrels sharply reduced their locomotor activity compared to the level of mobility when they were on the surface ($B = 1.14 \pm 0.02$, $t = 48.3$, $p < 0.0001$). Thus, the aboveground activity budget can be used in this study as an estimate of the locomotor activity budget.

Daily Variability of Aboveground Activity

Using the *activity* package, we built graphs of the probability of finding yellow ground squirrels on the ground surface depending on the time of day (Fig. 2). First, these graphs show a large variability in the activity budget between individuals: some individuals had a peak of aboveground activity in the evening; others, in the morning; and some, in the middle of the day. Only one adult male (Fig. 2a) maintained two-phase aboveground activity: in the middle of the day, it was mainly in the burrow. The remaining yellow ground squirrels, including an adult female (Fig. 2b), were active throughout the day, and their activity can be called single-phase.

An analysis of the overlap between the timing of aboveground activity in adult and young animals in the *overlap* package showed that young animals were active somewhat longer during the day, while they spend more time on the surface in the morning compared to adults (Wald test, $p = 0.005$, Fig. 3a). When comparing the budgets of males and females (only young individuals), we did not reveal any differences between them ($p = 0.2$, Fig. 3b). Finally, we compared

the aboveground activity budget before hibernation and 7–14 days before hibernation: the duration of aboveground activity decreased as hibernation approached ($p = 0.047$, Fig. 3c), which is consistent with the results of linear models.

DISCUSSION

This work is the first instrumental study of the activity budget of the yellow ground squirrel, during which reliable data on the daily cycle of this species during the period of preparation for hibernation were obtained. Early studies describing the daily activity budget of the yellow ground squirrel relied on visual observations of individuals that were not marked for individual recognition (*Mlekopitayushchie...*, 1969); in some studies, researchers closed the entrances to the ground squirrel burrows and judged the budget of the aboveground activity of the animals by the time when the ground squirrels opened them again (*Materialy...*, 1929). These methods may not be reliable enough for shy and cautious animals such as yellow ground squirrels, and it is also difficult to estimate the exact time of all entries and exits in burrows with such approaches. Our approach excludes the need for the presence of an observer at the colony, the error of observers, etc., and provides a high accuracy of the entry/exit time estimate. Of course, the sample in our work is extremely small, and this research can be considered a pilot study; however, we can at least qualitatively draw a number of conclusions.

Our data support early observations that yellow ground squirrels are strictly diurnal animals. Not a single individual left the burrow before sunrise or after sunset, which is consistent with other studies on the yellow ground squirrel, which mention that yellow ground squirrels almost do not appear on the surface before 6:00 or after 18:00 (Orlov, 1925; *Materialy...*, 1929; *Mlekopitayushchie...*, 1969) and generally corresponds to data on other ground squirrel species (Shilova, 2000).

In other studies on ground squirrels, the relationship between aboveground and locomotor activity is supposed implicitly without instrumental validation (Hut et al., 1999; Long et al., 2005). In the course of this study, using a combination of accelerometers and light sensors, we have checked whether such an approach is legitimate for the yellow ground squirrel. We have shown that almost all the locomotor activity of yellow ground squirrels during the day occurred at the time when the animals were on the ground surface. At night, yellow ground squirrels were almost completely motionless in their burrows; but even in the daytime, when going into the burrow, the animals reduced their locomotor activity several times, although it could be expected that yellow ground squirrels would intensively clear burrows during the period of preparation for hibernation. Probably, the most active burrowing activity in yellow ground squir-

rels falls on another phase of the annual cycle, which did not fall into the period that we analyzed in this study. Thus, it can be argued that yellow ground squirrels are at rest in the burrow and the stay of the animal on the ground surface can be used as an indicator of locomotor activity. At the very least, this pattern is characteristic of yellow ground squirrels in the last weeks before hibernation.

In our study, the high variability of activity patterns between individuals is striking: the maximum ground activity could occur in the morning, evening, or afternoon; it could be more than one, as in the adult male (see Fig. 2). This feature had also been observed earlier: E.I. Orlov (1925) wrote about ground squirrels that lived in the environs of the village of Dyakovka in 1924: “each of them has favorite moments of exit from burrows”; similarly, in the round-tailed ground squirrel (*Xerospermophilus tereticaudus*), different individuals showed consistent differences in the time of onset of diurnal activity (Drabek, 1973). Our data are not enough to study the individual characteristics of the aboveground activity budget, but the available data suggest the existence of various behavioral strategies for the distribution of activity during the day within the population, which requires additional data from natural populations.

Several studies on the yellow ground squirrel note that the aboveground activity in this species is usually two-phase at the height of summer: the animals are on the surface in the morning and evening hours, and in the middle of the day both adult and young animals go into their burrows (Orlov, 1925; *Mlekopitayushchie...*, 1969). For example, on Barsakelmes Island (Kazakhstan), a break in the aboveground activity of yellow ground squirrels during the day lasted from 10:00 to 16:00 in June (*Mlekopitayushchie...*, 1969). However, some authors indicate that the yellow ground squirrel may have one peak of aboveground activity during the day (Orlov, 1925; *Materialy...*, 1929), which is not quite common for ground squirrels.

Two-phase aboveground activity in mid-summer, during which animals rest in burrows during the day, has been described for many other gophers and marmots (e.g., Bronson, 1962; Drabek, 1973; Shubin, 1988; Armitage, 1991; Katona et al., 2002), as well as for other species of diurnal rodents (Bacigalupe et al., 2003). In diurnal rodents, a decrease in the aboveground activity during the day is associated with adaptability to life in habitats with high daytime air temperatures; i.e., burrowing in the middle of the day in these species is a kind of behavioral thermoregulation that protects the animals from overheating (*Mlekopitayushchie...*, 1969; Loehr and Risser, 1977; Vispo and Bakken, 1993; Váczi et al., 2006). During the observation period in our study, daytime temperatures reached 40°C in the shade (data from a temperature recorder located in the model area). However, in our sample, the two-phase pattern of the activity budget

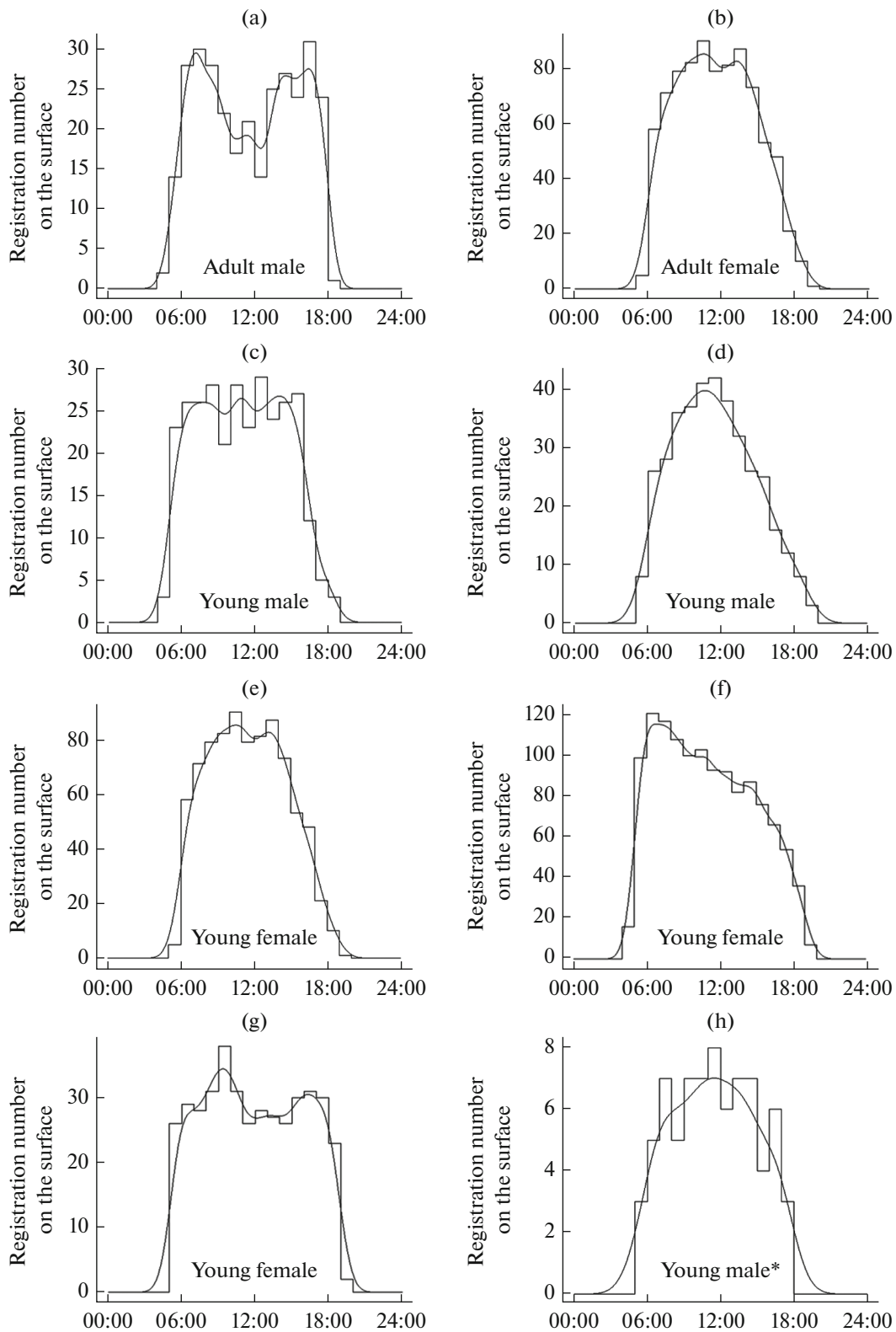


Fig. 2. Daily dynamics of yellow ground squirrels staying on the ground surface during the period of preparation for hibernation. The y-axis represents the number of records on the ground surface for each hour during the day. * The graph is based on only one day of operation of the radio transmitter (this individual was killed by a dog on the third day after capture).

was characteristic only of the adult male; the rest of the individuals, including the adult female, demonstrated single-phase aboveground activity, unlike other ground squirrel species. One of the reasons for such a discrepancy between our data and other studies may be that the aboveground activity budget in this species depends on age: there is evidence that young animals stay on the surface throughout the day, while adults are characterized by two-phase aboveground activity (*Mlekopitayushchie...*, 1969). According to our data, both young males and females stayed longer on the ground surface during the day compared to adult animals. It can be assumed that extremely long hibernation sets a strict time frame for young animals, which, from the moment they leave their burrows in May–June, must have time to increase their body weight by several times by the end of July in order to overwinter successfully, and some young animals also have time to disperse (Shilova et al., 2006; Vasilieva, 2011). Under such conditions, young animals stay on the ground surface for as long as possible during the day, including during the hottest hours. It was not entirely expected that there were no differences in the activity budgets between young males and females, since male ground squirrels are the dispersing sex, and females are prone to philopatry, and one could assume a longer duration of aboveground activity in males. In part, this may be due to the insufficient sample size; meanwhile, it is likely that young males and females, having the same aboveground activity budgets, use the time spent on the ground surface and space in different ways.

The decrease in the duration of stay on the ground surface as the moment of hibernation approached was not obviously associated with a reduction in daylight hours or with weather conditions, since this pattern was traced in different animals on different calendar dates, both in the second half of June and at the end of July. The data in this study are insufficient for a detailed analysis of these relationships, so we can only discuss these patterns at a qualitative level. It should be noted that two animals, in which no reduction in activity was detected, had a very short period of observation, and it can be assumed that activity in these shy animals can on the contrary increase in the first days after capture. A decrease in the duration of aboveground activity before hibernation has been described, for example, for the Colombian ground squirrel *Urocyonotellus columbianus* (Betts, 1976).

It should be noted that it is not entirely clear how the yellow ground squirrel and other diurnal ground squirrels can synchronize the activity budget with the length of daylight hours. Such synchronization is inherent in mammals in general (Refinetti, 2019); however, our data and data on related ground squirrel species indicate that ground squirrels are never on the ground surface at dusk (Hut et al., 1999; Everts et al., 2004). Moreover, the use of light sensors suggests that they do not even approach the exit of the burrow during these periods to determine the times of sunset

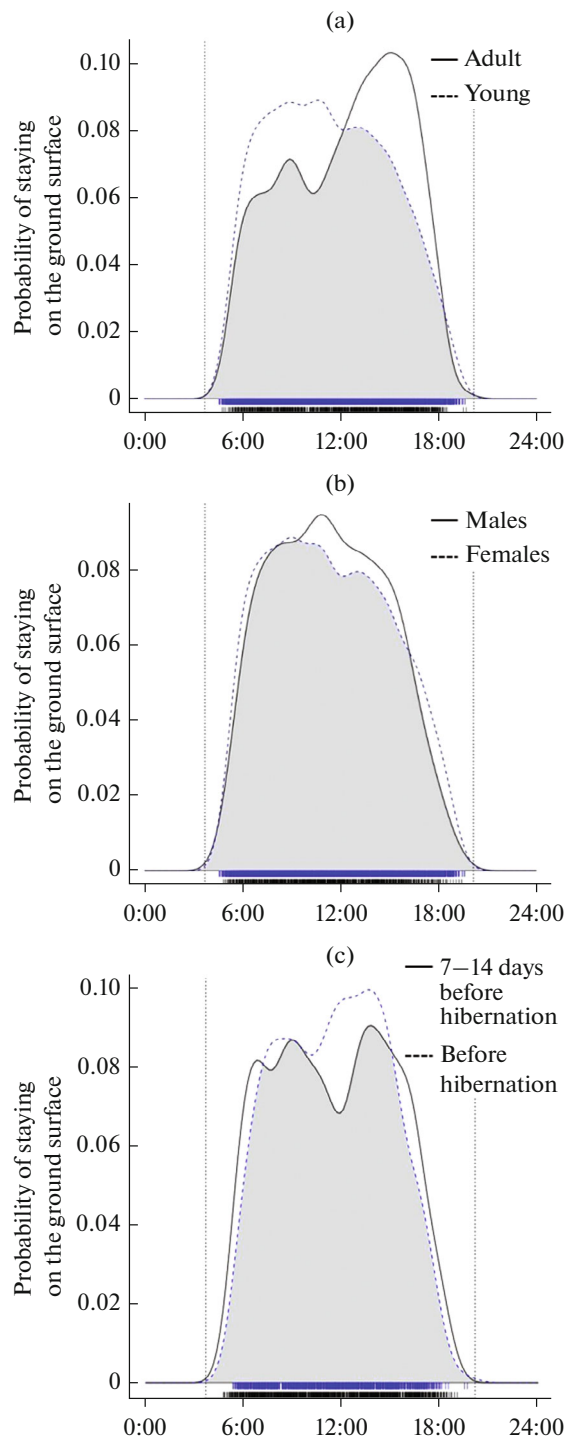


Fig. 3. Comparison of the daily dynamics of the stay of yellow ground squirrels on the surface (a) in adults and young individuals, (b) males and females, as well as (c) in the period of 7–14 days before hibernation and in the last week before hibernation. The differences are significant (Wald's test, $p < 0.05$) for (a) and (c); the curves correspond to the density functions built in the *overlap* package; the areas of overlap are shown in gray. At the bottom of the graphs, the exact moments of records are marked in black and blue (the blue color corresponds everywhere to dotted lines, and the black color corresponds to solid lines). The vertical dotted lines correspond to the average times of sunrise and sunset during the observation periods.

and sunrise and illumination, despite the fact that such behavior (“light sampling behavior”) is known for some mammalian species (De Coursey, 1986). It is known that significant changes in the hormonal status, blood biochemical parameters, etc., occur in other ground squirrel species as hibernation approaches (for example, Boonstra et al., 2011; Wilsterman et al., 2015). It is possible that gradual changes in the duration of aboveground activity in yellow ground squirrels can be associated to a greater extent with physiological rearrangements due to preparation for hibernation rather than with changes in external conditions.

CONCLUSIONS

Thus, we have obtained for the first time detailed data on the daily budget of the aboveground activity of the yellow ground squirrel. Despite the limited sample size, these data can be useful in planning studies of this species, including population censuses, population monitoring, etc. One of the results of this study—the absence of a pronounced decrease in the level of aboveground activity in the middle of the day—is consistent with the idea of the yellow ground squirrel as a species with a “fast” life cycle. Perhaps, under the conditions of extremely long hibernation and, accordingly, limited time for growth and weight gain, yellow ground squirrels (first of all, young animals) make the most of daylight hours for feeding, preparing burrows for winter, etc.; however, this assumption requires further study in nature.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflicts of interest.

Statement on the welfare of animals. All manipulations with animals were reviewed and approved by the Commission on Bioethics of the Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences (protocol nos. 31 dated March 11, 2019 and 44 dated March 29, 2021); the methods used were in accordance with the recommendations of the “Guidelines for the Treatment of Animals in Behavioral Research and Teaching (ASAB/ABS) (Buchanan et al., 2012).

REFERENCES

- Allen, M.L., Peterson, B., and Krofel, M., No respect for apex carnivores: distribution and activity patterns of honey badgers in the Serengeti, *Mamm. Biol.*, 2018, vol. 89, pp. 90–94.
- Armitage, K.B., Individual differences in the behavior of juvenile yellow-bellied marmots, *Behav. Ecol. Soc.*, 1986, vol. 18, pp. 419–424.
- Armitage, K.B., Social and population dynamics of yellow-bellied marmots: results from long-term research, *Annu. Rev. Ecol. Syst.*, 1991, vol. 22, pp. 379–407.
- Ashby, K.R., Patterns of daily activity in mammals, *Mamm. Rev.*, 1972, vol. 1, pp. 171–185.
- Bacigalupe, L.D., Rezende, E.L., Kenagy, G.J., and Bozinovic, F., Activity and space use by degus: a trade-off between thermal conditions and food availability?, *J. Mammal.*, 2003, vol. 84, pp. 311–318.
- Bartness, T.J. and Albers, H.E., Activity patterns and the biological clock in mammals, in *Activity Patterns in Small Mammals*, Berlin: Springer, 2000, pp. 23–47.
- Betts, B.J., Behaviour in a population of Columbian ground squirrels, *Spermophilus columbianus columbianus*, *Anim. Behav.*, 1976, vol. 24, pp. 652–680.
- Boonstra, R., Bradley, A.J., and Delehanty, B., Preparing for hibernation in ground squirrels: adrenal androgen production in summer linked to environmental severity in winter, *Funct. Ecol.*, 2011, vol. 25, pp. 1348–1359.
- Bronson, F.H., Daily and seasonal activity patterns in woodchucks, *J. Mammal.*, 1962, vol. 43, pp. 425–427.
- Buchanan, K., Burt de Perera, T., Carere, C., Carter, T., Hailey, A., Hubrecht, R., Jennings, D., Metcalfe, N., Pitcher, T., Peron, F., Sneddon, L., Sherwin, C., Talling, J., Thomas, R., and Thompson, M., Guidelines for the treatment of animals in behavioural research and teaching, *Anim. Behav.*, 2012, vol. 83, pp. 301–309.
- Chmura, H.E., Zhang, V.Y., Wilbur, S.M., Barnes, B.M., Buck, C.L., and Williams, C.T., Plasticity and repeatability of activity patterns in free-living arctic ground squirrels, *Anim. Behav.*, 2020, vol. 169, pp. 81–91.
- Clutton-Brock, T.H., Iason, G.R., Albon, S.D., and Guinness, F.E., Effects of lactation on feeding behaviour and habitat use in wild red deer hinds, *J. Zool.*, 1982, vol. 198, pp. 227–236.
- Daan, S. and Aschoff, J., Circadian rhythms of locomotor activity in captive birds and mammals: their variations with season and latitude, *Oecologia*, 1975, vol. 18, pp. 269–316.
- De Coursey, P.J., Light-sampling behavior in photoentrainment of a rodent circadian rhythm, *J. Comp. Physiol. A*, 1986, vol. 159, pp. 161–169.
- Dobson, F.S., Environmental influences on sciurid mating systems, in *The Biology of Ground-Dwelling Squirrels*, Murie, J.O., Michener, G.R., and Lincoln, L., Eds., Univ. Nebraska Press, 1984, pp. 227–249.
- Drabek, C.M., Home range and daily activity of the round-tailed ground squirrel, *Spermophilus tereticaudus neglectus*, *Am. Midl. Nat.*, 1973, vol. 89, pp. 287–293.

- Everts, L.G., Strijkstra, A.M., Hut, R.A., Hoffmann, I.E., and Millesi, E., Seasonal variation in daily activity patterns of free-ranging European ground squirrels (*Spermophilus citellus*), *Chronobiol. Int.*, 2004, vol. 21, pp. 57–71.
- Froy, O., The relationship between nutrition and circadian rhythms in mammals, *Front. Neuroendocrinol.*, 2007, vol. 28, pp. 61–71.
- Heller, H.C. and Ruby, N.F., Sleep and circadian rhythms in mammalian torpor, *Annu. Rev. Physiol.*, 2004, vol. 66, pp. 275–289.
- Hut, R.A., van Oort, B.E., and Daan, S., Natural entrainment without dawn and dusk: the case of the European ground squirrel (*Spermophilus citellus*), *J. Biol. Rhythms*, 1999, vol. 14, pp. 290–299.
- Katona, K., Vácz, O., and Altbácker, V., Topographic distribution and daily activity of the European ground squirrel population in Bugacpuszta, Hungary, *Acta Theriol.*, 2002, vol. 47, pp. 45–54.
- Kenagy, G.J. and Hoyt, D.F., Speed and time–energy budget for locomotion in golden-mantled ground squirrels, *Ecology*, 1989, vol. 70, pp. 1834–1839.
- Loehr, K.A. and Risser, A.C., Daily and seasonal activity patterns of the Belding ground squirrel in the Sierra Nevada, *J. Mammal.*, 1977, vol. 58, pp. 445–448.
- Long, R.A., Martin, T.J., and Barnes, B.M., Body temperature and activity patterns in free-living arctic ground squirrels, *J. Mammal.*, 2005, vol. 86, pp. 314–322.
- Long, R.A., Hut, R.A., and Barnes, B.M., Simultaneous collection of body temperature and activity data in burrowing mammals: a new technique, *J. Wildl. Manage.*, 2007, vol. 71, pp. 1375–1379.
- Malan, A., Is the torpor–arousal cycle of hibernation controlled by a non-temperature-compensated circadian clock?, *J. Biol. Rhythms*, 2010, vol. 25, pp. 166–175.
- Materialy k poznaniyu fauny nizhnego Povolzh'ya* (Materials for The Knowledge of the Fauna of the Lower Volga Region) Traut, I.I. and Orlov, E.I., Eds., Saratov: Izd. Otdela Primeneniya Nilov, 1929, no. 4.
- Meredith, M., Ridout, M., and Meredith, M.M., Package ‘overlap’. Estimates of coefficient of overlapping for animal activity patterns, 2021. <https://CRAN.R-project.org/package=overlap>.
- Mlekopitayushchie Kazakhstana* (Mammals of Kazakhstan), Sludskii, A.A., Ed., Alma-Ata: Nauka, 1969, vol. 1.
- Ognev, S.I., *Zveri SSSR i prilozhashchikh stran (zveri Vostochnoi Evropy i Severnoi Azii)* (Animals of the USSR and Adjacent Countries (Animals of Eastern Europe and North Asia)), Moscow: Akad. Nauk SSSR, 1947.
- Orlov, E.I., Yellow ground squirrel. Biological observations, *Vestn. Mikrobiol. Epidemiol.*, 1925, vol. 4, no. 1, pp. 58–66.
- Pinheiro, J., Bates, D.R., R Core Team. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-159, 2022. <https://CRAN.R-project.org/package=nlme>.
- Podolski, I., Belotti, E., Bufka, L., Reulen, H., and Heurich, M., Seasonal and daily activity patterns of free-living Eurasian lynx *Lynx lynx* in relation to availability of kills, *Wildl. Biol.*, 2013, vol. 19, pp. 69–77.
- R Core Team, R: A Language and Environment for Statistical Computing, Vienna (Austria): R Foundation for Statistical Computing, 2021. <https://www.R-project.org/>.
- Rashitov, S.S., Influence of diurnal activity of marmots on their fat accumulation, *Izv. Mezhdunar. Akad. Agrar. Obraz.*, 2018, no. 43, pp. 175–179.
- Refinetti, R., *Circadian Physiology*, CRC press, 2019.
- Ridout, M.S. and Linkie, M., Estimating overlap of daily activity patterns from camera trap data, *J. Agric. Biol. Environ. Stat.*, 2009, vol. 14, pp. 322–337.
- Rossolimo, O.L., Pavlinov, I.Ya., Kruskop, S.V., Lisovskii, A.A., Spasskaya, N.N., Borisenko, A.V., and Panyutina, A.A., *Raznoobrazie mlekopitayushchikh* (Diversity of Mammals), Rossolimo, O.L., Ed., Moscow: KMK, 2004.
- Rowcliffe, M. and Rowcliffe, M.M., Package ‘activity.’ Animal activity statistics R Package Version 1.3.2, 2022. <https://CRAN.R-project.org/package=activity>.
- Schmidt, K., Variation in daily activity of the free-living Eurasian lynx (*Lynx lynx*) in Białowieża Primeval Forest, Poland, *J. Zool.*, 1999, vol. 249, pp. 417–425.
- Shilova, S.A., Spatial and social organization of ground squirrels (genera *Spermophilus*, *Xerus*, and *Cynomys*) as a model of ecological and ethological research, *Usp. Sovrem. Biol.*, 2000, vol. 120, no. 6, pp. 559–572.
- Shilova, S.A., Ground squirrels, *Priroda* (Moscow, Russ. Fed.), 2004, no. 3, pp. 41–48.
- Shilova, S.A., Chabovskii, A.V., and Popov, B.C., Peculiarities of formation of settlements of the yellow ground squirrel (*Spermophilus fulvus* Licht., 1823) during dispersal to free territory, *Byull. Mosk. O-va Ispyt. Prir., Otd. Biol.*, 2006, vol. 111, no. 5, pp. 71–75.
- Shilova, S.A., Savinetskaya, L.E., and Chabovskii, A.V., Long-term and current population dynamics of the yellow ground squirrel (*Spermophilus fulvus*, Rodentia, Sciuridae) in the Eruslan sands of the Trans-Volga region, *Zool. Zh.*, 2015, vol. 94, no. 8, pp. 944–954.
- Shubin, V.I., Peculiarities of relationships in family groups of bobak, in *Ekologiya i povedenie mlekopitayushchikh Kazakhstana* (Ecology and Behavior of Mammals in Kazakhstan), Tr. Inst. Zool. Akad. Nauk Kaz. SSR, 1988, vol. 44, pp. 112–132.
- Vácz, O., Kooz, B., and Altbácker, V., Modified ambient temperature perception affects daily activity patterns in the European ground squirrel (*Spermophilus citellus*), *J. Mammal.*, 2006, vol. 87, pp. 54–59.
- Vasilieva, N.A., Factors affecting reproductive behavior and breeding success in the yellow ground squirrel (*Spermophilus fulvus*), *Extended Abstract of Cand. Sci. (Biol.) Dissertation*, Moscow: IPEE RAN, 2011.
- Vasilieva, N.A. and Tchabovsky, A.V., Timing is the only thing: reproduction in female yellow ground squirrels (*Spermophilus fulvus*), *Can. J. Zool.*, 2014, vol. 92, pp. 737–747.
- Vasilieva, N.A. and Tchabovsky, A.V., A shortage of males causes female reproductive failure in yellow ground squirrels, *Sci. Adv.*, 2015, vol. 1, no. 9, p. e1500401.

- Vasilieva, N.A. and Tchabovsky, A.V., Making reproductive decisions in the context of a “fast” life cycle (on the example of the yellow ground squirrel *Spermophilus fulvus*), *Zh. Obshch. Biol.*, 2017, vol. 78, no. 1, pp. 3–14.
- Vasilieva, N.A., Savinetskaya, L.E., and Chabovskii, A.V., Large body size and a short period of ground activity do not prevent the rapid growth of the yellow ground squirrel *Spermophilus fulvus*, *Zool. Zh.*, 2009, vol. 88, no. 3, pp. 339–343.
- Vasilieva, N.A., Pavlova, E.V., Naidenko, S.V., and Tchabovsky, A.V., Age of maturation and behavioral tactics in male yellow ground squirrel *Spermophilus fulvus* during mating season, *Curr. Zool.*, 2014, vol. 60, pp. 700–711.
- Vieira, E.M., Baumgarten, L.C., Paise, G., and Becker, R.G., Seasonal patterns and influence of temperature on the daily activity of the diurnal neotropical rodent *Necromys lasiurus*, *Can. J. Zool.*, 2010, vol. 88, pp. 259–265.
- Vispo, C.R. and Bakken, G.S., The influence of thermal conditions on the surface activity of thirteen-lined ground squirrels, *Ecology*, 1993, vol. 74, pp. 377–389.
- Waterman, J.M., Male mating strategies in rodents, in *Rodent Societies: an Ecological and Evolutionary Perspective*, Sherman, P.W. and Wolff, J.O., Eds., Chicago: Univ. Chicago Press, 2007, pp. 27–41.
- Williams, C.T., Wilsterman, K., Kelley, A.D., Breton, A.R., Stark, H., Humphries, M.M., McAdam, A.G., Barnes, B.M., Boutin, S., and Buck, C.L., Light loggers reveal weather-driven changes in the daily activity patterns of arboreal and semifossorial rodents, *J. Mammal.*, 2014, vol. 95, pp. 1230–1239.
- Wilsterman, K., Buck, C.L., Barnes, B.M., and Williams, C.T., Energy regulation in context: free-living female arctic ground squirrels modulate the relationship between thyroid hormones and activity among life history stages, *Horm. Behav.*, 2015, vol. 75, pp. 111–119.

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