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Juvenile survival curves in a solitary ground squirrel with a prolonged hibernation: effects of individual characteristics, environment, and maternal investment

Nina A. Vasilieva*, **Liudmila E Savinetskaya, and Andrey V. Tchabovsky**

A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow 119071, Russia

*Address correspondence to Nina A. Vasilieva. E-mail: ninavasilieva@gmail.com
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Abstract

Juvenile survival is a key life-history influence on population dynamics and adaptive evolution. We analyzed the effects of individual characteristics, early environment, and maternal investment on juvenile survival in a large solitary hibernating rodent—yellow ground squirrel *Spermophilus fulvus* using Cox mixed-effects models. Only 48% of weaned pups survived to dispersal and 17% survived to hibernation. Early life expectancy was primarily determined by individual characteristics and, to a lesser extent, by the early environment. The strongest and positive predictor of juvenile survival was body mass which crucially affected mortality immediately after weaning. Males suffered higher mortality than females after the onset of dispersal; however, the overall difference between sexes was partly masked by high rates of mortality in the first days after emergence in both sexes. Later emerged juveniles had lower life expectancy than the earliest pups. The overall effect of local juvenile density was positive. Prolonged lactation did not enhance juvenile survival: Pups nursed longer survived shorter than the young nursed for a shorter period. Our findings support the hypothesis that females of *S. fulvus* cannot effectively regulate maternal expenditures to mitigate the effects of unfavorable conditions on their offspring. The strategy to deal with seasonal time constraints on life history in female *S. fulvus* suggests an early termination of maternal care at the cost of juvenile quality and survival. This female reproductive strategy corresponds to a "fast-solitary" life of folivorous desert-dwelling *S. fulvus* and other solitary ground squirrels with prolonged hibernation.

Key words: early-life conditions, ground squirrels, hibernation, juvenile mortality, maternal investment, survival curves

Juvenile survival is an essential determinant of variation in individual fitness and population dynamics in living organisms (Dobson 1995; Altwegg et al. 2005; Abadi et al. 2017). Studying the effects of individual characteristics, environmental conditions, and parental care on early survival can help us to understand the intra- and interspecific variation in life-history traits including life expectancy, the pace of life, and lifetime reproductive success (Dobson and Oli 2007; Plard et al. 2015; Marshall et al. 2017; Ronget et al. 2018).

Key individual characteristics which affect survival may be universal or depend on the species' life history. One of the most universal characteristics that positively and strongly influence early survival in mammals is the body mass at weaning (Foltz et al. 1988; Clutton-Brock et al. 2001; Hall et al. 2001; Vasilieva and Tchabovsky 2020). Another individual-level predictor is sex (especially in species with marked sexual dimorphism in body size and dispersal—Solomon 2003; Zollner and Lima 2005; Gedir and Michener 2014). In mammals, young females normally survive better than males, because they are typically smaller (and therefore less vulnerable to reduced food availability and nutritional stress) and philopatric (Smith and Anderson 1998; Hall et al. 2001; Beauplet et al. 2005). In polytocous species, litter size is another important prognostic factor of survival. In larger

litters, juveniles are expected to suffer higher mortality due to lower body mass caused by the quality–quantity trade-off and a higher level of competition among littermates (Stearns 1989; Dani and Kodandaramaiah 2017). In a seasonal environment, juvenile survival often depends on the time of birth and weaning: It is important to be born and weaned early in the season to have sufficient time before winter (or other unfavorable periods), and early-born offspring often enjoy higher survival (Clutton-Brock et al. 1987; Smith and Anderson 1998; Kerr et al. 2007), especially in hibernators (Armitage et al. 1976). To understand which individual characteristics are most influential on early survival and how their effects are related to a species' life history, it is crucial to analyze them not separately but in combination.

The effects of individual characteristics on survival are modified by environmental conditions. In particular, population and local densities (Fowler 1987; Gaillard and Yoccoz 2003), predation (O'Donoghue 1994), habitat quality (Beauplet et al. 2005; Scornavacca et al. 2016), weather, and climatic factors (Fowler 1987; Buettner et al. 2007) can influence juvenile survival. The negative density effect reflects the increased competition for resources, and the negative impact of density on juvenile growth and survival is more pronounced at low than high food availability (Plaisir et al. 2022). On the other

hand, aggregation in space can reduce predation risk through the "group-size effect" allowing more time for foraging at the cost of reduced vigilance (Quenette 1990; Beauchamp et al. 2021). Predation is the main proximate cause of juvenile mortality in many species (O'Donoghue 1994), which can modulate and reinforce the effects of all other early-life conditions and juvenile characteristics on survival (Rieger 1996; Johnson et al., 2019).

Parental care and the size of maternal expenditure (in particular, gestation and lactation [GL] duration) can mitigate the negative effects of other factors and influence juvenile survival through variation in juvenile body mass (El Oksh et al. 1967; Gerber et al. 2021). Prolonged lactation as a major component of maternal effort can increase the weight gain and survival of young (Huber et al. 2001). In hibernating mammals, the brevity of the active season limits the amount of time available for all life processes and has a strong effect on lactation, gestation, and the development and maturation of young (Armitage 1981; Waterman 1996).

Ground-dwelling sciurids are burrowing hibernating diurnal rodents with a short active season and a well-ordered annual cycle, which typically reproduce once a year (Dobson 1984; Waterman 2007). They inhabit open landscapes and use the same burrow systems for long periods, making them one of the best model taxa for long-term individual-based studies and survival analysis. Due to the short growing season, it is crucial for ground squirrels to be born and weaned early, which increases their chances to survive to their first hibernation (Armitage et al. 1976; Michener 1985; Vasilieva and Tchabovsky 2014). Strong time constraints on growth and development determine various parameters of their life history such as maternal investment, dispersal rate, the time of maturation, and sociality level. In particular, prolonged hibernation may lead to delayed maturation of the young, their retention in the natal group, and extended maternal care beyond weaning (Armitage 1981, 1999) which can be viewed as a way to reduce juvenile mortality by slowing the life cycle. Alternatively, a short active season may speed up life processes and, in particular, juvenile development to achieve a sufficient body condition and independence by the time of immergence into hibernation.

In small mammals, including ground squirrels, individual survival is often analyzed as a binary variable, for example, as a probability of surviving to a specific stage or age, such as recruitment or maturation (Wauters et al. 1993), or, more typically, to 1 year of age (Rieger 1996; Gaillard and Yoccoz 2003; Ozgul et al. 2006; Kerr et al. 2007). One-year survival probability is a product of summer and winter survival, where first summer and first hibernation mortality are driven by different sets of factors. Thus, modeling 1 of the 2 components should give more clear relationships with lesser noise than the analysis of their combination. Compared to the traditional probability analysis, the analysis of individual survival curves is a more powerful analytical tool. It can predict time to events (such as death or recruitment) and reveal inflection points and critical periods in individual life trajectories (Efron 1988; Liu 2012), thus providing valuable information for ecological studies.

Here we used longitudinal individual-based observations in a wild population of yellow ground squirrels *Spermophilus fulvus*, a solitary species with an extremely prolonged hibernation, to analyze the effects of early-life conditions on survival curves of young during their first active season, from emergence from the nest to hibernation. In particular, we investigated the effects of (1) individual characteristics, (2) external conditions at weaning, and (3) parameters of maternal investment. We hypothesized 2 alternative life-history scenarios: The first one suggests that females would adjust maternal investment to regulate offspring quality, and thus, longer care would provide better juvenile condition and higher survival. Alternatively, under severe time constraints, females would not be able to prolong maternal care and thereby influence juvenile quality and survival by mitigating the adverse effects of other factors. Instead, they would terminate maternal care early to save energy and time to prepare for hibernation. Therefore, under the second scenario, juvenile mortality would be high, and early survival would depend mainly on individual juvenile characteristics and external conditions.

Materials and Methods

Study species
The yellow ground squirrels are large hibernating folivorous diurnal rodents with male adult pre-hibernation body mass up to 2 kg and a very short active season of 3–4 months (Vasilieva et al. 2009). They live solitarily at low population densities in open landscapes of the arid and semiarid zones of Central Asia, Iran, China, and Southern Russia. In southern Russia, they inhabit dry steppes where they live in patchily distributed more or less isolated colonies on sandy soils (Shilova et al. 2015). Summer heat and drought force them to enter estivation, followed by hibernation until spring. Females can only have 1 litter per year and nurse pups in separate burrows (Vasilieva and Tchabovsky 2014). Juveniles emerge aboveground around weaning (about 3–4 weeks of age) in mid-May to early June and stay near the natal burrow for the first days after emergence. Like in other solitary ground squirrel species, where males leave females after mating and do not take care of their offspring, the weaning indicates the end of intensive parental care (Michener 1989; Rieger 1996; Nunes et al. 1997; Skibiel et al. 2009). Two weeks after emergence, pups (mostly males) begin to disperse (Vasilieva and Tchabovsky 2020). Newly emerged juveniles suffer high predation from domestic cats *Felis catus* and dogs *Canis familiaris*, steppe polecats *Mustela eversmanii*, black kites *Milvus migrans*, and booted eagles *Hieraaetus pennatus*. Large-sized adult yellow ground squirrels very seldom suffer predation. Females are philopatric and form spatial kin clusters (Batova et al. 2021); however, they use separate burrows and only have partially overlapping home ranges. Young males typically leave the natal site and disperse within the colony. From mid-July to early August, young squirrels immerge into hibernation and emerge in March or early April of the following year (Vasilieva and Tchabovsky 2015).

Study area and sampling
We studied yellow ground squirrels *S. fulvus orlovii* (Ogn. 1937) in a natural colony in the Saratov region of Russia, in the vicinity of village Dyakovka (50°43′88″ N, 46°46′04″ E) from 2001 to 2020. The colony (approximately 60 ha) was partially isolated from the other colonies by the village, the Yeruslan River, and the Dyakovskii Forest. This is a typical colony of yellow ground squirrels in southern Russia (Shilova et al. 2015). The high proportion of closely related males and females within the colony suggested that the dispersal beyond

the colony was rare (Batova et al. 2021). We have permanently marked squirrels in the colony since 2001; therefore, we knew the origin and the fates of almost all litters in the study area.

We captured adult ground squirrels with noncommercial custom-made snare loops or wire cage traps without bait; juveniles were trapped by cage traps only. We immediately removed squirrels from the traps, weighted them, and individually marked them with passive integrated transponders (BayerAG, Leverkusen, Germany) and with black hair dye for visual identification. We monitored the colony during the vernal emergence and mating season (late March to April) and then from litter emergence (mid-May) to immergence into hibernation (mid-July to mid-August). We scanned the colony as well as its peripheral zone several times a day to locate all active individuals. A detailed description of the methods can be found elsewhere (Vasilieva and Tchabovsky 2014, 2015; Vasilieva et al. 2014). All procedures conform to the ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research and Teaching (Buchanan et al. 2012) and the laws of the Russian Federation. The research protocol for this study was approved by the Ethical Committee of A.N. Severtsov Institute of Ecology and Evolution (research protocols: 2018-18 and 2019-31).

Data analysis

We included in the analyses juveniles that were born in 2002–2009 and in 2017–2019 because in 2010–2016, the population of squirrels was very low (Figure S1). During the decline, many pups had disappeared or had been predated before they were trapped; thus, we could not obtain valid information for survival analysis. We included in the sample 525 juveniles with the full set of variables.

Time to the disappearance

We used the time to disappearance (i.e., the time interval between the first emergence of a juvenile from the natal burrow and its last sighting in the season) as the minimum estimation of a juvenile's first active season duration to construct survival curves and examine their dynamic patterns.

Juvenile dispersal starts at the earliest 2 weeks after natal emergence; therefore, all pups that had disappeared before that time (the minimum age of dispersal) were presumed dead. For those who were seen for the last time after the 14th day after emergence, we could not distinguish between death and immergence into hibernation or emigration to another colony. Although some of the disappeared juveniles could potentially disperse beyond the observed area, we considered the probability of successful migrations between colonies to be low, because only a few unmarked juveniles with undetermined origin appeared within the colony every year (on average, 8.0% ± 5.0% from the total number of trapped juveniles per year). For accuracy, we used the time to disappearance as a conservative estimate of a minimum early life expectancy. To validate the time to disappearance as a measure of survival success, we analyzed its relationship with the probability of surviving the first hibernation (see Results). We assumed that a young ground squirrel survived its first hibernation if it was recaptured in the next spring or later.

Since in some years, we stopped observations when some juveniles were still active, we considered them censored cases. The remaining cases in the sample (93%, see Results) were treated as uncensored.

Individual characteristics
Weaning body mass

Juveniles began to eat fresh green vegetation as soon as they emerged from the natal burrow, and the mother often moved to a separate burrow after the litter emergence. Thus, the day of natal emergence approximately corresponds to weaning. We weighted juveniles within 5 days after their natal emergence (Mean ± SD = 1.8 ± 1.6 days, N = 525) and used this measurement as a correlate for both juvenile size and body condition. We expected that heavier juveniles would disappear later than lighter ones.

Sex

We suggested that the sex of juveniles would modulate the survival curves because males are dispersing sex while females are philopatric (Batova et al. 2021). Thus, we expected the survival curves of males and females to diverge from the 14th day after the emergence and later due to higher mortality in males.

Litter size at weaning

We included the litter size in the models because it varied strongly, and juveniles from small and large litters likely faced different levels of competition for food; after weaning, pups stay close to the natal burrow and feed on fresh green vegetation available nearby. We expected the negative effect of litter size on juvenile survival.

Date of natal emergence

The date of litter emergence varied strongly, from mid-May to mid-June, and, therefore, late and early juveniles faced different environmental (weather and vegetation characteristics) and social conditions (i.e., juvenile density). We suggested that the environmental and social conditions could be crucial for juvenile survival within the first days around weaning, yet we had no specific predictions about these effects.

Environmental characteristics
Interjuvenile distance

We used an average distance (m) from the natal burrow of each juvenile to the burrows of 20 nearest juveniles, including littermates, as an inverse measure of the local density of juveniles—the higher the distance, the lower the density (details can be found elsewhere—Vasilieva and Tchabovsky 2020). Aggregation of young may incur costs of increased resource competition and predator attraction while, on the other hand, reducing predation risk through the group-size effect. Thus, the relationship between the local density and survival of juveniles could go in either direction depending on the balance between the costs and benefits of aggregation.

Population density

We included population density within the colony in the model because a previous study revealed its negative effect on the survival to adulthood in juvenile females (Vasilieva and Tchabovsky 2020). The density was estimated yearly as the number of all adult ground squirrels per hectare.

Distance to the village

For each juvenile, we measured the shortest distance (m) from the natal burrow to the nearest garden fence in the village adjacent to the colony as a correlate of the potential

negative human impact and disturbance, including predation from domestic cats and dogs. Previously, we observed massive predation in the areas closest to the human settlement (cats purposefully looked for and hunted small newly emerged juveniles) and found a weak negative effect of proximity to the village on female recruitment (Vasilieva and Tchabovsky 2020).

Habitat type

Based on vegetation patterns, grazing impact, and natural borders (country roads, rows of trees, and shrubbery), we subdivided the colony area into four patches: "ruderal," "pasture," "steppe," and "village." Detailed descriptions of these types of habitats can be found in Supplementary Material. Four patches were taken by ground squirrels as natural fragments so that they moved within patches more frequently than between them. We used habitat type to control the effect of landscape heterogeneity on juvenile survival. *S. fulvus* lives in open landscapes, and short-grass grazed habitats should be more favorable for early survival than tall-grass ungrazed patches.

Weather conditions

Cold and wet weather as well as very high ambient temperature suppress the aboveground activity of ground squirrels (e.g., Williams et al. 2014). Thus, the temperature and rainfalls could affect juvenile survival positively as well as negatively. To assess the effect of weather on juvenile early survival, we used (1) the total precipitation during May and June (amount of rain) and (2) the mean daily temperature in June.

Maternal expenditure: total duration of gestation and lactation period

Yellow ground squirrel females are receptive once a year; their estrous is very short and starts within the first days after vernal emergence (Vasilieva and Tchabovsky, 2014, 2015). Since juveniles emerge from their natal burrows approximately at weaning, an interval between female vernal emergence and the emergence of her young aboveground can be considered as an estimation of the total duration of female GL. In other ground squirrel species (i.e., Millesi et al. 1999), females are able to adjust their reproductive effort by prolongation or early termination of lactation. We considered the length of the GL period as a correlate of maternal expenditure and expected a positive effect of the GL length on juvenile survival times. To control for possible effects of maternal traits on maternal expenditures, we tested if the female age (yearling/adult), date of vernal emergence, and the size of her litter at weaning affected the GL length.

In our previous studies, we did not find significant effects of female age, body mass, or body condition on juvenile survival probabilities (Vasilieva and Tchabovsky 2014, 2015); therefore, we did not include these female characteristics in the analysis of juvenile survival curves.

Statistical modeling
Main model

To analyze the effects of juvenile individual characteristics at weaning and environmental conditions on time to the disappearance, we performed Cox mixed-effects models (coxme function in R package *coxme*, Therneau 2019). The main model included juvenile weaning mass, sex, litter size, date of

natal emergence, interjuvenile distance, the density of adult animals, the distance to the village, habitat type, amount of rain in May–June, and mean daily temperature in June as fixed effects, litter identity and year as random effects, and the time to disappearance as a response. The full model is presented in Table S1. Although numerical data were statistically analyzed as continuous variables, we divided them into tertiles for illustrative purposes in the figures. The negative coefficient β and the hazard ratio <1 indicate that the predictor is protective and has a positive effect on survival (Kleinbaum and Klein 2012; Emmert-Streib and Dehmer 2019).

Total duration of gestation and lactation

Since we had valid data for the length of GL period not for all, but about one-third of litters, we performed a separate Cox mixed-effects model to test whether the total duration of GL affected juvenile survival. We included in the model all predictors from the main model with significance level $P < 0.1$ as possible confounding factors. The litter identity and year were fitted as random terms in the model.

Predictors of gestation and lactation duration

To examine factors that could influence the GL duration, we ran additional models with the mother age (yearling/adult), date of the mother's vernal emergence, and litter size as fixed effects, and year as a random effect. We suggested that the date of female emergence and the litter size could affect the size of maternal expenditure, because the active season is very short in *S. fulvus*, and females need sufficient time for fattening before the next hibernation. GL length conformed to the normal distribution (Shapiro–Wilk's test, $P > 0.05$), so we performed linear mixed-effect models in R package *lme4*.

For Cox and linear mixed-effects models, we assessed relative model fit using Akaike's information criteria corrected for small sample sizes (AIC_c) in the library *MuMIn* (Barton 2018). The estimates with their errors were averaged for models with $\Delta AIC_c < 2$ (Burnham et al. 2011). We used the Pearson correlation coefficient as a measure of linear correlation between pairs of variables. To access the biological significance of the 2-group comparison, we used Cohen's *d* effect size measure (Cohen, 1988).

All continuous predictors were standardized and checked for collinearity. Statistical analyses were performed using R 4.1.0 (R Core Team 2021).

Results

General characteristics of juvenile survival ($N_{juveniles}$ = 525, including $N_{censored}$ =36)

To validate the time to disappearance as a measure of early survival time, we compared time to the disappearance for juveniles who survived their first winter and were recaptured the next year (and, thus, their time to disappearance was close to the time of immergence), and juveniles that disappeared and were not seen afterward (only uncensored cases for juveniles with known 1-year survival success, $N = 426$). The median time to disappearance for juveniles that survived their first winter was 57 days (Quartile range, QR = 52–63 days, $N = 46$) compared to 8 days for juveniles that did not survive (QR = 3–21 days, $N = 380$). The logistic regression analysis indicated that the probability of surviving to the first spring increased with increasing time to disappearance with an inflection point at about 52 days after emergence

(B = 0.11 ± 0.01, P < 0.0001, Figure S2). Therefore, the time of disappearance of those juveniles who survived to the next year corresponded to the time of immergence, and we assumed that after 50 days aboveground (the nominal time of immergence), juveniles more likely disappeared due to immergence into hibernation and less likely due to death.

The median time to disappearance for the entire sample of juveniles (N = 525) was 13 days (QR = 4–31). The disappearance rate was the highest during the first days aboveground, and most pups (52%) disappeared before the 14th day after emergence, the minimum time of dispersal, and so were assumed dead. Afterward, the slope of the survival curve became much shallower and leveled off (Figure 1). On the whole, only 17% of pups survived to hibernation (to the 50th day aboveground).

All numerical juvenile characteristics varied strongly among individuals: Weaning body mass ranged from 71 to 338 g, litter size from 1 to 11 juveniles, and the date of natal emergence from 15 May to 18 June. Therefore, juveniles at weaning faced very unequal conditions. Juvenile body mass decreased with an increasing date of emergence (r = –0.24, P < 0.0001). Sex differences in juvenile weaning mass were not significant (Student's t-test, df = 524; t = 1.9, P = 0.05) and the effect size was small (Cohen's d = 0.17). There were no differences between males and females in the date of emergence (t = –1.4, P = 0.2, small effect size, d = 0.12) or litter size (t = –1.4, P = 0.2, small effect size, d = 0.12).

The effects of individual and environmental characteristics

The most parsimonious model for juvenile time to disappearance with the lowest AIC_c score included 6 predictors: weaning mass, sex, date of natal emergence, interjuvenile distance, proximity to the village, and habitat type (Table 1). Litter size, adult population density, and weather (temperature and precipitation) did not receive support in the model selection procedure and had no significant effect on juvenile survival (see the characteristics of the full model in Table S1 and the results of the model selection procedure in Table S2).

The strongest predictor of the time to the disappearance was the weaning body mass (Table 1)—heavier pups disappeared later and survived to dispersal and hibernation better than did lighter pups (Figure 1A). The daily difference in survival rates increased during the first 3 weeks and was particularly strong at 7–14 days after emergence from the nest. The effect of sex was significant, yet weak (Table 1, Figure 1B): Females disappeared somewhat later than males, and the effect was most pronounced at the beginning of dispersal. The effect of the date of emergence was only marginally significant (Table 1, Figure 1C). Nevertheless, the time to the disappearance was twice as long for the earliest emerged juveniles as for later emerged pups, and the higher proportions of early pups survived to dispersal and hibernation compared to later ones. The most profound differences in survival rates between early- and late-emerged pups were observed during the first 2 weeks.

Among environmental characteristics, the distance to the nearest 20 juveniles had the strongest effect on juvenile survival—the shorter the distance, the longer the time to the disappearance. Nevertheless, pups weaned at medium interjuvenile distances enjoyed higher survival rates after the onset of dispersal and before immergence into hibernation than pups that emerged at short or long distances to the nearest

juveniles (Table 1, Figure 1D). We found a slight effect of the habitat type on juvenile survival (Table 1): in the pasture patch, juveniles disappeared slower, and around 15–25 days after emergence the mortality rate there was the lowest, as compared with the steppe and especially the village patch (Figure 1E). The proximity to the village did not influence the time to disappearance significantly. The effects of litter identity and year (random terms in the model) were highly significant (likelihood ratio test performed with anova.coxme function in R, χ^2 = 112, P < 0.0001, χ^2 = 12.1, P = 0.0005), indicating nonindependence of littermates' disappearance.

The effect of the length of the GL period (N = 173, including $N_{censored}$ = 10)

Variation in the total duration of GL period was not high (mean = 55.5 ± 3.0 days min–max = 52–62 days, CV = 5.35%). Neither the dam's date of vernal emergence (B = –0.05 ± 0.5, P = 0.9), nor dam's age (adult/yearling; B = –0.15 ± 0.9, P = 0.9), nor litter size (B = –0.43 ± 0.4, P = 0.3) influenced the duration of GL period (linear mixed-effect models, $N_{litters}$ = 57, the effect of the year was fitted in the model as a random term). The most parsimonious model with the lowest AIC_c (286.8) did not include any fixed terms.

GL length correlated with juvenile date of emergence—the longer GL period, the later in the season the litter emerged (r = 0.45, P = 0.0005, $N_{litters}$ = 57). Juvenile weaning mass and GL period were not correlated (r = 0.08, P = 0.6, $N_{litters}$ = 45).

Unexpectedly, juveniles from litters with a shorter GL period disappeared proportionally later and survived to dispersal better than juveniles from litters with a more prolonged GL period (Table 2, Figure 1F). This difference increased with time and was the greatest between 15 and 25 days after natal emergence. Similar to the main model, the weaning mass had a significant positive effect on juvenile survival; other fixed effects were insignificant (P > 0.1), apparently due to the reduced sample size and, therefore, power.

Discussion

To our knowledge, this is the first detailed study of prehibernation life expectancy in ground squirrels that used survival analysis. We found significant effects of weaning mass, juvenile density, sex, habitat type, and GL duration on juvenile early survival. The effect of the date of natal emergence was marginally significant; the other factors (litter size, adult population density, proximity to human settlement, and weather) did not influence juvenile survival times (Tables 1, 2, and S1). Our results show that early-life characteristics varied in the magnitude of their effects and influenced juvenile survival at different periods of early life.

The strongest factor that positively affected juvenile pre-hibernation survival time was body mass at emergence (Table 1, Figure 1A). The protective effect of high body mass at weaning has been widely described: Body mass is a correlate of fat and protein reserves, structural size, and body condition (Gerhart et al. 1996; Festa-Bianchet 1998), vital fitness components, especially important in early life of mammals and ground squirrels, in particular (Rieger 1996; Hall et al. 2001; Huber et al. 2001; Maness and Anderson 2013). In ground squirrels, juvenile body mass correlates with motor skills development (Nunes et al. 2004), and large juveniles can use their body size per se to optimize their interactions with their environment, as was reported for other animals (Garnett 1981; Lewin et
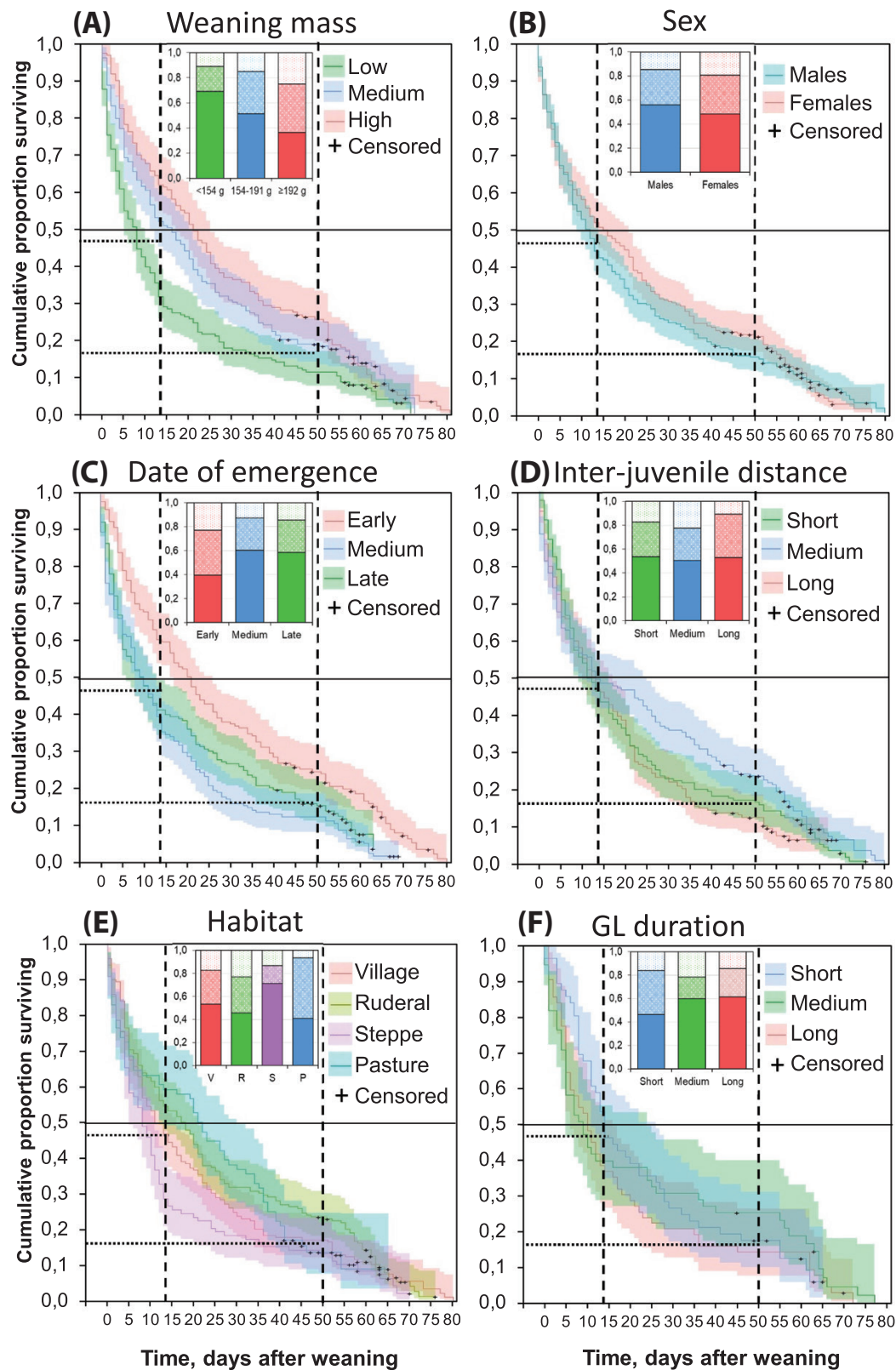
Figure 1 Kaplan–Meier survival curves (with 95% confidence intervals) during the first active season for juvenile yellow ground squirrels in relation to (A) weaning weight, (B) sex, (C) date of natal emergence, (D) distance to the nearest 20 juveniles, (E) habitat type, (F) the length of gestation/ lactation period. Numerical data (A, C, D, and F) were statistically analyzed as continuous variables and partitioned into tertiles to categorize juveniles for illustrative purposes only. Vertical dashed lines indicate the minimum time of dispersal (14 days) and the nominal time of immergence into hibernation (50 days). Horizontal dotted lines show the proportions of young survived to dispersal and hibernation for the whole sample. Horizontal solid lines show a 50% of survived juveniles. The bar plots show the raw percentages of juveniles who disappeared before the 14th day (solid), between 15 and 49 days, (dashed), and later than 50 days (open) after emergence for each category of juveniles. Colors in the bar plots correspond to the colors in survival plots. Heavier pups, females (as compared to males), pups that emerged earlier, at a shorter interjuvenile distance, in pasture (as compared to other habitat types), and nursed for a shorter period survived at higher rates than their counterparts (Table 1).

Table 1 Effects of juvenile characteristics and early environment on the time to disappearance in yellow ground squirrels (N = 525, $N_{censored}$ = 36)

Predictor variable	β	Hazard ratio	Z	P
Sex (male)	**0.23**	**1.25**	**2.10**	**0.036**
Weaning weight	**−0.48**	**0.62**	**−4.9**	**< 0.0001**
Date of natal emergence	0.25	1.29	1.96	0.05
Distance to 20 nearest juveniles	**0.44**	**1.55**	**3.05**	**0.002**
Distance to the village	0.32	1.37	1.31	0.19
Habitat type (ruderal)	−0.74	0.48	−1.33	0.18
Habitat type (pasture)	**−1.11**	**0.33**	**−2.13**	**0.03**
Habitat type (steppe)	−0.05	0.95	−0.14	0.89

Only effects included in the best model are presented (mixed-effects Cox models were selected using AICc; see the full model in Table S1, litter identity and year were fitted in the model as random terms (likelihood ratio test, χ^2 = 105, P < 0.0001, χ^2 = 18.1, P < 0.0001). Parameter estimates β are presented for the best model (for model-averaged coefficient, see Table S1). Significant effects (P < 0.05) are marked with bold.

Table 2 Effect of the total duration of gestation and lactation on the time to the disappearance of juveniles in yellow ground squirrels (N = 173, $N_{censored}$ = 10)

Predictor variable	β	Hazard ratio	Z	P
Gestation/lactation duration	**0.51**	**1.66**	**2.41**	**0.015**
Sex (male)	0.28	1.32	1.55	0.12
Weaning weight	**−0.61**	**0.55**	**−4.09**	**< 0.0001**
Date of natal emergence	0.32	1.38	1.35	0.18
Distance to 20 nearest juveniles	0.23	1.26	0.91	0.36
Habitat type (ruderal)	−0.35	0.70	−1.05	0.29
Habitat type (pasture)	0.08	1.08	0.13	0.89
Habitat type (steppe)	−0.52	0.59	−0.98	0.32

Effects with P < 0.1 from Table 1 were included in the reduced model as possible confounding factors. Mixed-effects Cox model; litter identity and year effect were fitted in the model as random terms (likelihood ratio test, χ^2 = 12.0, P = 0.0005; χ^2 = 2.4, P = 0.12). Significant effects (P < 0.05) are marked in bold.

al. 2017). Thus, there could be some threshold body size that made young yellow ground squirrels invulnerable to small predator species. The analysis of the survival curves in *S. fulvus* showed that juvenile survivorship depended on weaning mass mostly within the first 14 days of aboveground activity, when there were almost 70% survivors among the heaviest pups versus more than 70% of disappeared pups among the lightest juveniles (Figure 1A). This indicates that body mass is especially important for survival soon after weaning and before dispersal.

After the onset of dispersal, the mortality rate decreased and was minimal at the 28–48 days after emergence (Figures 1 and S3). This pattern does not correspond to data from other ground squirrel species: For example, in Arctic ground squirrels *U. parryii*, dramatic loss of the juveniles was observed after the 20th day after emergence (Byrom and Krebs 1999); in 13-lined ground squirrels, a weekly loss of juveniles peaked about 3–4 weeks after emergence (*Ictidomys tridecemlineatus*; Freeman and Bachman 2016); in European ground squirrel *Spermophilus citellus*, most juveniles died during 4–7 decades after emergence (Hoffmann et al. 2004). In these and some other ground squirrel species, young females survived better than males (Michener, 1989), which is often attributed to male-biased dispersal and male risky behavior. Dispersal is male biased in yellow ground squirrels (Batova et al. 2021). In addition, although they are of similar body

mass at weaning, males grow faster than females (Vasilieva et al. 2009; Vasilieva and Tchabovsky 2018). Therefore, we expected that dispersal hazards and nutritional stress would result in higher early mortality in males. Indeed, the survival curves of males and females diverged at the onset of dispersal during 15–25 days after emergence, resulting in a higher proportion of female survivors by the onset of hibernation (20% vs. 15% in males, Figure 1B). Nonetheless, the survival curves were close to each other, and we found only minor differences in survival times between young males and females in *fulvus* (Table 1, Figure 1B). The lack of between-sex variation can be attributed to the overwhelming effect of body mass at weaning which masked the overall sex differences in dispersal.

Litter size per se, despite being negatively correlated with offspring weaning mass (Vasilieva et al. 2009; Vasilieva and Tchabovsky 2018), did not influence the survival times of juveniles (Table S1). This contradicts our expectations and corresponds to data from some other mammals (callitrichids, Jaquish et al. 1991; muskrats, Boutin et al. 1998; ground squirrels, Risch et al. 2007). Probably, in *S. fulvus*, the competition among littermates was weak or mitigated by other, more strong factors.

The very earliest juveniles enjoyed longer survival times, and albeit the effect of the date of natal emergence was only marginally significant, it remained consistent throughout the entire active season (Figure 1C). The negative effect of late

emergence on juvenile survival is common among ground squirrels (e.g., *U. armatus*, Rieger 1996; *S. citellus*, Millesi et al. 2000; *Marmota flaviventris*, Monclús et al. 2014). Probably, late litters suffered higher predation because predators needed time to discover the first-emerging pups at the onset of emergence period. In addition, there are more green and juicy vegetation early in the season, which is a valuable food resource for postweaned pups of folivorous *S. fulvus*. Overall, our data support that the timing of birth and weaning is an important factor of early survival in seasonal environment, especially in hibernators who live under severe time constraints.

The effect of the juvenile local density was positive and nonlinear (Figure 1D): Juveniles weaned at the medium interjuvenile distance (i.e., at medium density) enjoyed the longest survival. Low survival at high density (i.e., at a short interjuvenile distance) can be explained by predator attraction to aggregations of small juveniles ("grouping of prey", Madison et al. 1984; Rogovin et al. 2004) or competition for food (Plaisir et al. 2022). In addition, high juvenile concentration may stimulate dispersal (as was shown for other ground squirrels: *U. beldingi*, Nunes et al. 1997; *U. parryii*, Byrom and Krebs 1999) and intensify competition for suitable sites, increasing the mortality risk. On the other hand, low survival at the lowest juvenile densities can be attributed to the lack of protective group-size effects (i.e., higher predation risk and increased vigilance at the cost of foraging—Quenette 1990; Beauchamp et al. 2021). The overall positive effect of juvenile density on their survival suggests that ultimately the benefits of grouping offset its costs.

We observed slight differences in juvenile survival times between habitats (Table 1, Figure 1E): The steppe ungrazed patch seemed to be the least favorable for juveniles, while the pasture being the most suitable, especially during a relatively short period of 10 days after the onset of dispersal. The vegetation differed between patches, and habitat quality varied in terms of food availability and visibility, which may affect foraging and predator avoidance behavior as well as growth in young ground squirrels (Wheeler and Hik 2014). In these terms, short-grass pasture habitat is more suitable for open-dwelling ground squirrels such as *S. fulvus* than tall-grass steppe. The lack of influence of weather or proximity to human settlement on the juvenile survival times suggests that the effects of environmental conditions could be diluted by stronger effects of individual characteristics or juvenile density.

In this study, we found that female age, time of vernal emergence, or litter size did not affect the length of GL, and previously, we found no effects of maternal condition on offspring number, quality, or survival in yellow ground squirrels (Vasilieva and Tchabovsky 2014, 2015; 2020). In contrast, in many other ground squirrel species, maternal expenditures depend on the female age and body condition and are driven by the trade-off between maternal investment and maintenance: Females in better condition can invest more in reproduction as compared with mothers in worse condition (e.g., Rieger 1996; Dobson et al. 1999; Hoogland 2001; Risch et al. 2007). Timing of reproduction is also important in ground squirrels: Late-breeding females produce smaller litters with heavier pups than early-breeding females, thereby mitigating strong time constraints on the growth and development of their offspring (Rieger 1996; Huber et al. 2001). In the present study, juvenile body mass at emergence decreased with an increasing date of emergence; therefore, late-breeding females did not wean heavier offspring, even though the GL period was longer in late-emerging pups. Moreover, the GL length affected negatively offspring weaning mass and survival in *S. fulvus*: Young nursed for a longer time survived shorter than young nursed for a shorter time (Table 2, Figure 1F). In contrast, in other ground squirrels, juvenile quality and survival are positively influenced by the size of maternal allocation reflected by the lactation duration (Huber et al. 2001; Ahmad 2008; Monclús et al. 2014). All these findings support the hypothesis that females of *S. fulvus* are limited in their ability to adjust their reproductive investment and cannot efficiently regulate maternal expenditures to mitigate the negative effects of individual and environmental characteristics on their offspring.

In this study, the GL period varied within 52–62 days, and given that the pregnancy lasts for about 30 days (Sludskiy 1969), the lactation duration ranged from 22 to 32 days (26 days, on average), which is an exceptionally short period for such a large-sized ground squirrel. Even in smaller species, the lactation typically lasts for 30–40 and more days (Michener 1985; Waterman 1996; Hoogland 1997; Thorington et al. 2012) (Table S3). The drastic increase in juvenile mortality around weaning in *S. fulvus* (Figures 1 and S3) is probably due to an abrupt and early termination of maternal care as compared with other ground squirrel species.

The dramatic decline in juvenile numbers between the natal emergence and immergence into hibernation (Figure 1) is similar to other solitary ground squirrel species with long hibernation: Only 17% of young survived their first summer, which is less but comparable to *S. citellus*: 32% (Hoffmann et al. 2004), *I. tridecemlineatus*: 32%, (Freeman and Bachman 2016), in contrast to more social species such as *Urocitellus parryii* (about 40–75%—Byrom and Krebs 1999; about 80%—Wilbur et al. 2022), *U. columbianus* (not less than 45–70%—Bennett 1999; Neuhaus et al. 2004), prairie dogs or marmots, where young survival is high as well (Van Vuren and Armitage 1994; Farand et al. 2002; Farid et al. 2022). Thus, sociality appears to be beneficial for early juvenile survival in ground squirrels, which conforms to the previous findings on its positive effect on the annual survival of the young (Bhumstein and Armitage 1998).

All our findings support previous observations that the duration of lactation varies negatively with the duration of hibernation among ground squirrel species (Table S3; Armitage 1981; Waterman, 1996). We suggest that extremely long hibernation in yellow ground squirrels constrains the time available for preparing for the next hibernation, forcing females to limit maternal investment, which minimizes the costs of reproduction at the cost of juvenile quality and survival. Based on the interspecific comparison (Table S3), we propose 2 alternative strategies for ground squirrels with prolonged hibernation to deal with seasonal time constraints on reproduction based on maternal–offspring conflict and corresponding to the fast–slow continuum of life history and sociality (Armitage 1981; Promislow and Harvey 1990; Bhumstein and Armitage 1998). One ("slow-social") suggests long lifespan and slow development, delayed dispersal and maturation of young, and prolonged maternal care which favors retention in the natal group and protects small young from early mortality, like in social Columbian ground squirrels (*U. columbianus*; e.g., Ritchie and Belovsky 1990) or social species of marmots

(Armitage 1999; Table S3). This strategy can be viewed as a way to reduce juvenile mortality by slowing the life cycle. An alternative way ("fast-solitary") is an early termination of maternal care at the cost of juvenile quality leading to high juvenile mortality, early juvenile dispersal and maturation, fast growth, and short lifespan, like in many small solitary ground squirrels with long hibernation. Given its large size, the largest among ground squirrels excluding marmots, and fast pace of life (Table S3; Vasilieva and Tchabovsky 2018), *S. fulvus* represents an extreme example of the second strategy. This conforms to the conclusion by Oli (2004) that the fast–slow continuum in mammalian life history is independent of body size.

In conclusion, we suggest that folivory combined with living in harsh environment of hot arid zones determines a prolonged estivation–hibernation period and a very short active season in *S. fulvus*. Large size and low-quality diet require a lot of time for foraging to gain sufficient body mass before hibernation, which sets even stronger constraints on all other activities, including maternal care and social interactions. Indeed, after emergence, littermates very rarely interact with each other and their mother—on average, about only 2 times per 100 min (Vasilieva and Tchabovsky 2009). This specific combination of life-history traits determines low maternal investment and high early mortality, which characterize the "fast-solitary" life strategy of *S. fulvus* among hibernating ground squirrels.

Conflict of Interest

The authors declare no conflict of interest.

Author Contributions

N.A.V. designed the study and analyzed the data; L.E.S, N.A.V., and A.V.T. conducted fieldwork and discussed the general concept; and N.A.V. and A.V.T. wrote the manuscript.

Data Availability

The datasets supporting this article is available on the Figshare Digital Repository (https://doi.org/10.6084/m9.figshare.21625595.v1).

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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