



# Early predictors of female lifetime reproductive success in a solitary hibernator: evidence for “silver spoon” effect

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## Abstract

Fitness consequences of early-life conditions remain unclear and poorly studied in mammals. Based on long-term observations of yellow ground squirrels (*Spermophilus fulvus*), we identified early determinants of female fitness by analyzing the effects of early-life individual and environmental characteristics (weaning weight, weight gain rate, date of natal emergence, natal litter size, location of the natal burrow, local density of juveniles, population density and precipitation in the post-weaning period) on lifetime reproductive success (LRS). We found high variation and right-skewed distribution in all five LRS components (survival to adulthood, adult lifespan, and lifetime numbers of weaned litters, weanlings, and yearling offspring). Numbers of litters, weanlings, and adult offspring were correlated with each other and increased with lifespan, confirming that longevity is a better predictor of LRS than fecundity. Survival to adulthood was the most sensitive fitness component to early conditions and was higher in females (a) with greater weaning weight, (b) born further from human settlement and (c) born at lower population density. Population density at birth was the best early predictor of all LRS components and negatively influenced adult lifespan and numbers of weanlings and yearling offspring. Early growth rate positively affected the probability of reproducing after the first hibernation and the number of offspring weaned. Such syndrome of high-quality (heavy and fast-growing) young born in a favourable environment (“a silver spoon effect”) with downstream damping fitness consequences has been observed so far in only a few mammalian species.

**Keywords** Reproductive success · Lifespan · Reproductive skew · Growth rate · Ground squirrels

## Introduction

Lifetime reproductive success (LRS) quantified as the total number of descendants is a common approximation of Darwinian fitness (Clutton-Brock 1988). Studies of inter- and intraspecific variability of LRS aimed to detect the effects of life-history and phenotypic traits on fitness and to understand selective forces shaping the diversity of life history traits and strategies as well as the consequences of variation

in LRS for demography, population dynamics and genetic structure (Albon et al. 1987; Clutton-Brock 1988; King et al. 1991; Altmann and Alberts 2003; Armitage 2014). Although LRS studies have been performed on a great variety of animal taxa, from small invertebrates to large mammals and humans, data from wild mammal populations are scarce, because they require laborious longitudinal observations in the field to track individual life history trajectories. This lack of field data does not allow comprehensive comparative and meta-analyses, and, therefore, broadening the range of species involved in LRS studies is necessary (Altmann and Alberts 2003).

Intraspecific variability of LRS arises from complex interactions between environmental and demographic conditions, individual phenotypical traits, genotypes, and chance. In mammals, LRS has been shown to depend on climate, weather, environmental and demographic stochasticity (King et al. 1991; Lummaa 2003; Armitage 2014; Catton and Michener 2016), density-dependent and density-independent food and resource availability (McLoughlin et al. 2006;

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Armitage 2014), individual physical conditions, and timing of reproduction (King et al. 1991; English et al. 2013), social environment, group size, social status and personality (Réale et al. 2000; von Holst et al. 2002; Altmann and Alberts 2003; Boon et al. 2007; Armitage 2014). The majority of these studies focused on proximal immediate determinants of LRS during the reproductive lifespan, such as adult social rank (von Holst et al. 2002) or age of primiparity (Hayward et al. 2014), habitat quality during the period of maternal care (McLoughlin et al. 2007). However, the effects of distal early determinants of LRS (i.e., early-life conditions) on future life and success are much less known. Long-term fitness consequences of early individual characteristics and environment (“silver spoon effect”, Grafen 1988) have been broadly discussed from the theoretical perspective (Lindström 1999), but only a few field studies tracked long-lasting effects of early conditions on individual fitness in mammals (Marshall et al. 2017). For example, high population density at birth negatively influenced the reproduction and survival of offspring in some mammals (Clutton-Brock et al. 1987, 1992; Sinclair et al. 2003). Unfavorable ecological circumstances negatively affected maternal condition and, subsequently, offspring birthweight and survival (Albon et al. 1987; Clutton-Brock et al. 1992). Early-life weight, growth rate and development can, in turn, impose life-long downstream impacts on survival and reproduction in adulthood (Lummaa and Clutton-Brock 2002; Lummaa 2003; Ronget et al. 2018; Sundell et al. 2019, but see Keane et al. 2007). For instance, birthweight affected future fitness in red deer (*Cervus elaphus*, Albon et al. 1987; Kruuk et al. 1999); early growth rate was strong predictor of LRS in female meerkats (English et al. 2013) and male humans (Kuzawa et al. 2010). In red squirrels, increased early growth rate combined with earlier parturition date enhanced the survival of the young (McAdam and Boutin 2003). Birth date had long-term consequences for the length of reproductive lifespan and LRS in women (Lummaa 2003) and fitness in female roe deer (*Capreolus capreolus*, Plard et al. 2015).

Until recently, the majority of research on causes and consequences of the LRS variability has been focused on males, since males are expected to have higher reproductive skew due to higher mate competition (Bateman 1948). Contrary to traditional expectations, a growing body of data suggests a great variation in female reproductive success as well (Hare and Simmons 2018). However, studies of the LRS variability in females and its role in sexual selection and evolution of life-history strategies have been limited mainly to cooperative breeders or species with reversed sex roles. Causes of variation in female LRS in solitary species remain poorly studied and understood.

Ground-dwelling squirrels represent a convenient model for LRS studies. Most ground squirrels are diurnal obligate hibernators with a highly time-ordered annual cycle (Dobson

1984; Waterman 2007). Generally, females are monoestrous and have a single breeding event per year; they are strongly philopatric making it easy to track them throughout the entire lifetime (Waterman 2007). Nevertheless, LRS data are available for only some ground squirrels (Hoogland and Foltz 1982; King et al. 1991; Armitage 2014; Neuhaus et al. 2004; Hackländer and Arnold 2012; Catton and Michener 2016), and almost nothing is known about LRS patterns in Eurasian species.

In this study, we used longitudinal individual-based observations of the solitary living yellow ground squirrel (*Spermophilus fulvus* Licht.) in a wild population to (1) describe the distributions of different metrics of female LRS as species life-history characteristics, and (2) identify early determinants of LRS by analyzing the effects of environmental conditions and individual characteristics of females during their first weeks after weaning on their survival and reproduction.

## Materials and methods

### Study species

The yellow ground squirrel inhabits arid zones of Central Asia, Iran, China, and Southern Russia. This large ground squirrel (pre-hibernation adult body mass up to 2 kg) with prolonged hibernation (8–9 months, Vasilieva et al. 2009) lives solitary at very low density (about 2–3 individuals per 1 ha); therefore, fitness is achieved through production of direct descendants as in other non-cooperatively breeding ground squirrels (Catton and Michener 2016). Males emerge from hibernation in mid-March–early April and females start to emerge about 1 week later. The mating system is scramble competition polygyny (Vasilieva et al. 2014; Vasilieva and Tchabovsky 2015) with males leaving females shortly after mating and not contributing to raising young or their survival. Females give birth to a single annual litter in separate burrows. Juveniles appear above ground around weaning at the age of 5 weeks in mid-May–early June, about 2 months after female vernal emergence. After juvenile emergence, a mother rarely interacts with them during daytime, keeps distance, and may move to a new burrow, leaving the nest burrow to the offspring. Consequently, the date of litter emergence coincides with the end of active maternal care. Pups begin to disperse 2 weeks after the emergence. Young females usually settle in or close to a natal area (Vasilieva and Tchabovsky 2015), while young males typically disperse over greater distances, but mostly stay within the colony (Vasilieva and Tchabovsky, unpublished data). Females mature after the first hibernation and breed as yearlings at a rate similar to older females (Vasilieva and Tchabovsky 2014). Some yearling males can also breed after their first

hibernation (Vasilieva et al. 2014). Thus, similar to other ground squirrel species (e.g., King et al. 1991; Catton and Michener 2016), the number of yearling offspring in this species represents the number of offspring recruited to the reproductive population.

### Study site and data collection

The study was carried out in the natural colony of yellow ground squirrels *S. fulvus orlovii* (Ogn. 1937) in Saratov region of Russia, in the vicinity of village Dyakovka (50°43'88" N, 46°46'04" E) in 2001–2011. The colony under observation was partially isolated from the other colonies by the village, the Yeruslan River and the Dyakovskii Forest. We started individual marking of squirrels in the core area (approximately 40 ha) of the colony (approximately 60 ha) in 2001. As a result, we knew the origin, longevities, and reproductive histories of almost all females in a 40-ha study area. We monitored females from their first emergence from the natal burrow and recorded the chronology of annual cycles and lifetime reproductive events.

Squirrels were captured using noncommercial custom-made snare loops (adults only) or wire cage traps without bait (both adults and juveniles). After capture, each squirrel was immediately removed from a trap, sexed, measured, weighed, and individually marked with microchips (Bayer AG, Leverkusen, Germany) and a unique black mark on the pelage with hair dye. We monitored the core area of the colony throughout the entire active season, from mid-March till mid-August and regularly surveyed the peripheral zone of the colony to complete the daily checklists of all marked individuals that were present within the colony. Detailed description of the methodology of trapping, handling, marking, colony scanning, and assessment of reproductive status, litter size and other individual variables can be found elsewhere (Vasilieva et al. 2014; Vasilieva and Tchabovsky 2014, 2015). All procedures conform to the ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research (Buchanan et al. 2012) and Teaching and to the laws of Russian Federation.

### Data analysis

Given that (a) females of *S. fulvus* are strongly philopatric and rarely emigrate, and (b) we actively searched for surviving females within the entire colony, we assumed that unobserved females had died. We included in the analyses females born in 2002–2007 and tracked until 2011. After 2010, the population had declined dramatically due to decreased livestock grazing, which stimulated the expansion of tall-grass vegetation, avoided by *S. fulvus* (Shilova et al. 2015). After this decline, squirrels became extremely shy and not all of them, including pups, could be trapped;

therefore, we could not reliably record reproductive events. Only one female of those born in 2007 or earlier survived to 2010; so all of them were tracked until their death.

### LRS predictors

When a female emerged from a natal burrow for the first time (i.e., around weaning), we measured the following predictors of her LRS.

- (a) *Weaning weight* was measured within 5 days after the first emergence (Mean  $\pm$  SD = 1.6  $\pm$  1.6 days,  $N = 212$ ) as an indicator of starting body condition. We expected a positive effect of weaning weight on female LRS.
- (b) *Weight gain rate* as a measure of early growth rate was calculated as the difference between consecutive weighings divided by the number of days between them ( $N_{\text{days}} \geq 15$ , on average, 38  $\pm$  12 days; the first weighing was the weaning weight). The weighing interval did not correlate with weight gain rate ( $r = -0.11$ ,  $p = 0.4$ ,  $N = 55$ ). In our earlier study, we found that juvenile *S. fulvus* grew very fast and exhibited linear weight gain during their first active season (Vasilieva et al. 2009). We expected that a rapid growth rate would produce a positive effect on LRS.
- (c) *Date of natal emergence*. Since the active season is short in hibernating sciurids, juveniles that emerge earlier in the season may have an advantage in terms of better survival and development over those from late litters. Therefore, we predicted a negative relationship between the date of the first emergence of a female and her LRS.
- (d) *Natal litter size at weaning*. We used the size of the litter at weaning in which a subject female was born as a possible correlate of within-litter competition and expected its negative effect on LRS.
- (e) *Local density of juveniles*. We used an average distance (m) from the natal burrow of a subject female to burrows of 20 nearest juveniles, including her littermates (between-juvenile distance), as an inverse measure of the local density of juveniles that the female experienced at natal emergence; the higher the distance, the lower the density. Unlike natal litter size, this measure describes spatial aggregation of juveniles, both littermates and non-littermates. Although the two measures were correlated (but not strongly:  $r = 0.33$ ), local density of juveniles could affect focal females in a different way than natal litter size. Aggregation of juveniles could, on the one hand, increase competition and attract predators, and on the other hand, indicate high quality of the habitat; so, we had no clear prediction about the relationship between the juvenile local density at female natal emergence and her LRS.

- (f) *Population density.* We estimated population density within the colony in the year of a female birth as the number of adults per ha, and expected its negative effect on female LRS.
- (g) *Location of the natal burrow.* We used the shortest distance (m) from the natal burrow of a female 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. We predicted that female LRS would increase with the distance from her natal burrow to the village.
- (h) *Amount of rain in May–June.* We included the total precipitation during May and June (the period when the young are small, vulnerable to environmental influences and depend on fresh green vegetation) to assess the effect of weather during the post-weaning period on LRS (with no clear prediction about the direction of a trend). Since the mean daily temperature in May and June strongly correlated negatively with the amount of rain, we did not include temperature in the models.

We did not include the possible effects of mother's age and body condition on their daughters' LRS in the analysis, since previous studies revealed no relationships between female age or body condition and annual reproductive success (Vasilieva and Tchabovsky 2014, 2015).

### LRS components

We partitioned the variation in female fitness into components corresponding to survival to adulthood, reproductive lifespan, fecundity, and offspring survival. Although proximal (e.g., litter size) and distal (e.g., number of yearling offspring) metrics of LRS were found to be strongly correlated in other ground squirrels (Catton and Michener 2016), we used both categories and analyzed them separately, because different sets of predictors could determine the LRS variability at different stages of the female life cycle.

- (a) *Female survival to adulthood.* We assumed that a female survived to adulthood if it was recorded in, at the earliest, mid-May after its first hibernation (expected time of litter emergence, 2 months after female vernal emergence), i.e., could potentially wean at least one litter. This was the shortest lifespan for which non-zero LRS values could potentially exist given that we aimed to obtain data for a complete life-cycle with the same reference points (Barrowclough and Rockwell 1993). We used expected weaning time as such reference point, and estimated reproductive success based on the number of weaned litters and the number of weaned offspring (McLoughlin et al. 2006).

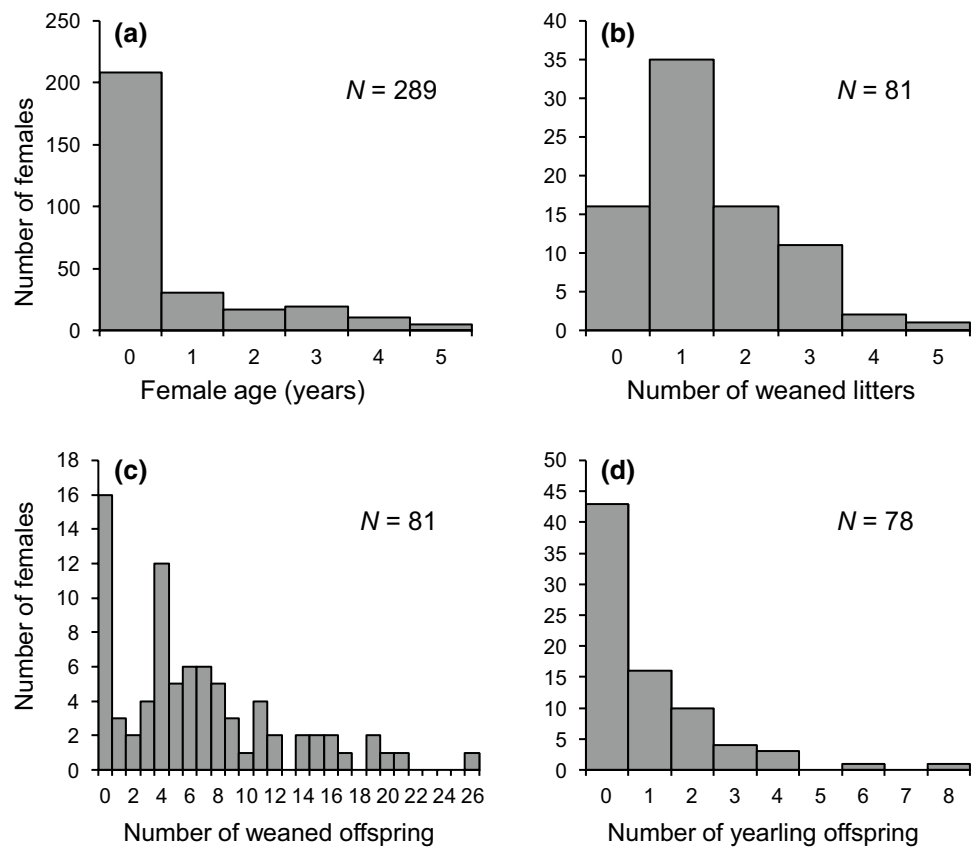
Correspondingly, we considered females that disappeared before expected time of litter emergence in mid-May, including those that emerged from hibernation, not to survive to adulthood. Survival to adulthood was, thus, a binary variable (survived/not survived); so, we applied generalized linear mixed models (GLMM) for binomial distribution with logit link function and natal litter identity as a random effect using package *lme4* (Bates et al. 2015) implemented in R.

- (b) *Female adult lifespan* was estimated for females that survived to adulthood as the number of full years between natal emergence and disappearance from the colony and analyzed using generalized linear models (GLZ) for Poisson error structure implemented in package *lme4*.
- (c) *Lifetime number of weaned litters* was estimated as the number of litters emerged from the natal burrows. We did not perform separate model for this variable due to its high correlation with other variables.
- (d) *Lifetime number of weaned offspring (weanlings).* The frequency distribution of the number of weanlings was bimodal with many zero values (Fig. 1) and fitted the Tweedie distribution with an estimated index parameter = 1.21 (Bonat et al. 2018). We modeled number of weanlings, calculated estimates, and assessed the significance of predictors with Tweedie compound Poisson linear models using function *cpglm* in the R package *cplm* (Zhang 2013).
- (e) *Lifetime number of yearling offspring* (i.e., the total number of offspring survived the first hibernation) fitted Poisson distribution, so we conducted GLZ with Poisson error structure. Since young males are less philopatric than females and their disappearance due to dispersal beyond the study area could be more likely, we controlled for the effect of offspring sex ratio (calculated as the proportion of females in the weaned offspring) on the lifetime number of yearlings produced.

Adult lifespan, numbers of litters, weanlings and yearlings produced were calculated only for females that survived to adulthood (to the next mid-May) and, thus, could wean at least one litter. Since the majority of females did not survive to adulthood (see "Results"), LRS measurements of females from the same litter during the adulthood were replicated a few times only (10 pairs of sisters from 47 females with full set of predictors measured). Therefore, no random effects were included in the models for these LRS components.

For all LRS components, we evaluated the sets of candidate models with all combinations of predictors and used a model selection procedure based on Akaike's information criterion ( $AIC_c$ ) in the library *MuMIn* (Barton 2019). The  $AIC_c$  weights were calculated, and estimates with their errors were averaged for models with  $\Delta AIC_c < 7$  (Burnham

**Fig. 1** Frequency distributions of four fitness metrics in female yellow ground squirrels (*Spermophilus fulvus*): **a** longevity (for all females), **b** the number of weaned litters, **c** the number of weaned offspring, **d** the number of yearling offspring; **b–d** for females survived to adulthood). All distributions are highly right-skewed



et al. 2011) since the set of models with  $\Delta AIC_c < 2$  did not include all fixed effects. We used likelihood ratio tests (LRT) to assess the significance of fixed effects for survival to adulthood, adult lifespan, number of weaned litters and number of yearling offspring.

We did not have data on post-weaning weight gain for about 25% of adult females. Consequently, to avoid a decrease in the statistical power for other predictors, we did not include the weight gain rate in the initial set of LRS predictors and performed a separate analysis to test its effects on LRS components with the number of days between weighings as a possible confounding factor.

All predictors were standardized and the significance level was set at  $p < 0.05$ . Statistical analyses were performed using R 3.6.1 (R Core Team 2019). Data are presented as mean  $\pm$  SD. Sample sizes may vary between different tests because of missing values.

## Results

### Components of the lifetime reproductive success

A high percentage of females (208 of 289 or 72.0%, Fig. 1) died before they reached adulthood and the first opportunity to wean a litter. Among those survived to adulthood

( $N = 81$ ), lifespan varied from 1 to 5 years, with majority (66 of 81 or 81%) living for  $\leq 3$  years. The probability to survive to the next mid-May was 63% for 1-year-old, 67% for 2-year-old, 44% for 3-year-old, and 33% for 4-year-old females.

Forty-seven females that survived to adulthood for which a full set of LRS component was measured weaned on average  $1.4 \pm 1.0$  litters and  $6.5 \pm 5.8$  juveniles, and produced  $0.8 \pm 1.4$  yearlings (both males and females) per lifetime. Lifetime numbers of weaned litters, weanlings and yearling offspring were highly inter-correlated (Table 1). Sixteen of 81 adult females (20%) weaned no offspring in their lifetime; whereas, 10 females that produced more than 10 weanlings each accounted for 53% ( $N = 279$ ) of the total number of 527 weanlings (Fig. 1). About a half of adult females (43 of 78 or 55%), including those that lived for 3–5 years, produced no yearlings. Numbers of weaned litters, weaned

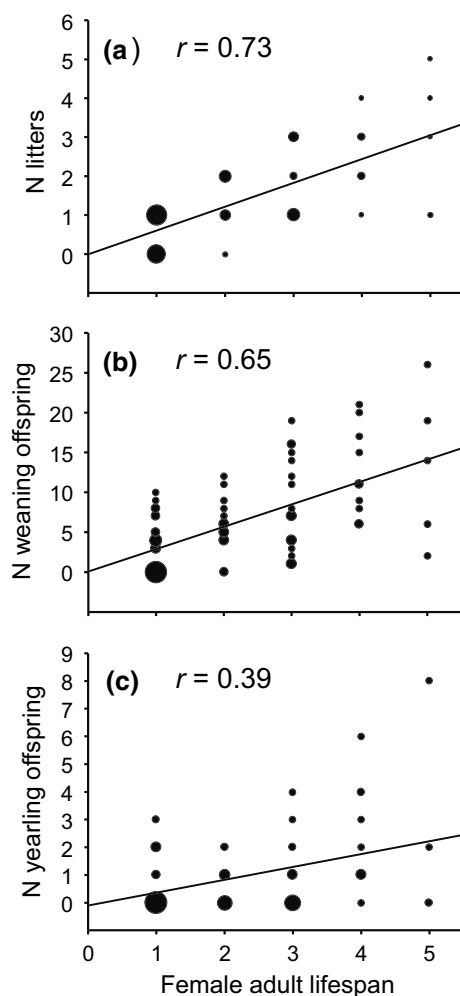
**Table 1** Pearson correlations coefficients ( $r$ ) between the components of lifetime reproductive success for female yellow ground squirrels that survived their first year ( $N = 78$ ,  $p < 0.0001$  in all cases)

Variables	Adult lifespan	$N$ litters	$N$ weaned offspring
$N$ litters	0.73		
$N$ weaned offspring	0.65	0.93	
$N$ yearling offspring	0.39	0.61	0.59

juveniles, and yearling offspring increased significantly with an increase in female adult lifespan, and the effect size of lifespan extension was the highest for the lifetime number of litters (more proximal LRS component) and the lowest for the number of yearling offspring (the most distal LRS component) (Table 1, Fig. 2). Since the correlation between the numbers of weaned offspring and litters was very high, we excluded the number of litters from the further analysis to avoid overanalyzing.

### Early determinants of lifetime reproductive success

**Female survival to adulthood.** The most parsimonious model included three significant predictors: female weaning weight, minimal distance from the natal burrow to the village, and population density in the year of birth (GLMM, Table 2; Online Resource 1). Females with greater weaning weight



**Fig. 2** The relationships between adult lifespan of a female yellow ground squirrel (*Spermophilus fulvus*) and lifetime numbers of **a** litters, **b** weaned offspring, and **c** yearling offspring ( $N=78$ ,  $p<0.0001$  in all cases)

had higher probability to survive to adulthood. Females born in burrows closer to the village and at higher population density had lower chances to survive to adulthood (Tables 2 and 3). The date of natal emergence, natal litter size, between-juvenile distance, or total rain in May and June had no effect on the probability of a young female surviving to the next mid-May.

**Female adult lifespan.** In females survived to adulthood, the only significant predictor of lifespan was population density in the year of birth (GLZ, Online Resource 1) with adult lifespan decreasing with an increase in population density (Table 2).

**Lifetime number of weaned offspring.** The lifetime number of weanlings was affected only by population density in the year of birth with the lower number of weanlings in females born at higher population densities. No significant associations between other early characteristics and lifetime number of offspring weaned were found (Tweedie compound Poisson linear models, Table 2; Online Resource 1).

**Lifetime number of yearling offspring.** The best model for lifetime number of yearling offspring included three significant predictors: between-juvenile distance at female weaning, and amount of rain in May–June and population density in the year of female birth (Online Resource 1) with greater number of yearlings produced by females born at lower population density and rainfall and higher between-juvenile distance (GLZ, Table 2).

Since sex ratio of the offspring could be measured only for females that weaned at least one juvenile ( $N=42$ ), we tested its effect on lifetime number of yearling offspring using additional model. This model included also the full set of aforementioned predictors. Offspring sex ratio had no effect on the number of yearlings produced (GLZ,  $B=0.77\pm 0.78$ ,  $\chi^2=0.5$ ,  $p=0.5$ ) and was not included in the best-fitted model. Effects of other predictors were similar to their effects in the previous analysis (Online Resource 2).

### Early weight gain rate

Death of 74 of 216 (34%) females during the first 5 days after their emergence from natal burrows did not allow us to estimate the effect of weight gain rate on the probability of surviving to adulthood. Therefore, we analyzed the possible effects of early growth rate on LRS components only for females that survived to adulthood. Average weight gain in young females was  $9.2\pm 1.9$  g/day ( $N=35$ ,  $N$  days between weighings =  $41.1\pm 9.5$ ). We did not find any significant effect of the early weight gain rate on female adult lifespan (GLZ;  $B=0.10$ ,  $SE=0.19$ ,  $p=0.6$ ) or the number of yearling offspring ( $B=-0.25$ ,  $SE=0.49$ ,  $p=0.6$ ). However, weight gain rate positively affected the lifetime number of weaned offspring (Table 4; Online Resource 3). In addition, early growth rate was higher in females that weaned litters as

**Table 2** Effects of early-life characteristics on the components of lifetime reproductive success (LRS) for female yellow ground squirrels

Predictors	LRS components			
	Survival to adulthood (yes/no), <i>N</i> = 212	Adult lifespan <sup>a</sup> ( <i>N</i> = 47)	<i>N</i> weaned offspring <sup>a</sup> ( <i>N</i> = 47)	<i>N</i> yearling offspring <sup>a</sup> ( <i>N</i> = 47)
Weaning weight	<b><i>B</i> = 0.79 ± 0.24, <math>\chi^2</math> = 8.8, <i>p</i> = 0.003</b>	<i>B</i> = - 0.05 ± 0.11, $\chi^2$ = 0.04, <i>p</i> = 0.8	<i>B</i> = 0.03 ± 0.16, <i>t</i> = 0.16, <i>p</i> = 0.9	<i>B</i> = - 0.02 ± 0.24, $\chi^2$ = 0.8, <i>p</i> = 0.4
Date of natal emergence	<i>B</i> = - 0.008 ± 0.21, $\chi^2$ = 0.04, <i>p</i> = 0.8	<i>B</i> = - 0.003 ± 0.08, $\chi^2$ = 0.005, <i>p</i> = 0.9	<i>B</i> = 0.14 ± 0.17, <i>t</i> = 0.8, <i>p</i> = 0.4	<i>B</i> = 0.27 ± 0.22, $\chi^2$ = 3.4, <i>p</i> = 0.07
Natal litter size	<i>B</i> = - 0.28 ± 0.24, $\chi^2$ = 1.5, <i>p</i> = 0.2	<i>B</i> = 0.07 ± 0.12, $\chi^2$ = 0.3, <i>p</i> = 0.6	<i>B</i> = 0.16 ± 0.14, <i>t</i> = 1.2, <i>p</i> = 0.2	<i>B</i> = 0.25 ± 0.19, $\chi^2$ = 2.2, <i>p</i> = 0.1
Distance to the village	<b><i>B</i> = 0.50 ± 0.22, <math>\chi^2</math> = 5.2, <i>p</i> = 0.02</b>	<i>B</i> = 0.09 ± 0.10, $\chi^2$ = 0.9, <i>p</i> = 0.3	<i>B</i> = - 0.22 ± 0.14, <i>t</i> = - 1.6, <i>p</i> = 0.1	<i>B</i> = - 0.12 ± 0.20, $\chi^2$ = 0.06, <i>p</i> = 0.8
Distance to 20 nearest juveniles	<i>B</i> = - 0.04 ± 0.20, $\chi^2$ = 0.26, <i>p</i> = 0.6	<i>B</i> = - 0.02 ± 0.10, $\chi^2$ = 0.07, <i>p</i> = 0.8	<i>B</i> = 0.12 ± 0.13, <i>t</i> = 0.9, <i>p</i> = 0.4	<b><i>B</i> = 0.40 ± 0.17, <math>\chi^2</math> = 7.1, <i>p</i> = 0.008</b>
Adult population density	<b><i>B</i> = - 0.78 ± 0.24, <math>\chi^2</math> = 11.7, <i>p</i> = 0.0006</b>	<b><i>B</i> = - 0.22 ± 0.10, <math>\chi^2</math> = 5.0, <i>p</i> = 0.03</b>	<b><i>B</i> = - 0.29 ± 0.14, <i>t</i> = - 2.1, <i>p</i> = 0.04</b>	<b><i>B</i> = - 0.53 ± 0.23, <math>\chi^2</math> = 3.8, <i>p</i> = 0.05</b>
Amount of rain	<i>B</i> = 0.005 ± 0.24, $\chi^2$ = 0.03, <i>p</i> = 0.9	<i>B</i> = - 0.007 ± 0.11, $\chi^2$ = 0.05, <i>p</i> = 0.8	<i>B</i> = - 0.07 ± 0.17, <i>t</i> = - 0.4, <i>p</i> = 0.7	<b><i>B</i> = - 0.42 ± 0.22, <math>\chi^2</math> = 5.4, <i>p</i> = 0.02</b>
Litter ID	$\chi^2$ = 0.16, <i>p</i> = 0.7	–	–	–

*B* and SE correspond to model-averaged parameter estimates and standard errors in GLMM (for survival to adulthood) and in GLZ (for lifespan and *N* yearling offspring);  $\chi^2$  corresponds to likelihood ratio test. Female natal litter identity (Litter ID) was introduced as a random effect in all GLMMs. For *N* weaned offspring *B* ± SE and *t* correspond to parameter estimates, standard errors and *t* values in Tweedie compound Poisson linear models. Significant effects (*p* < 0.05) are marked with bold

<sup>a</sup>Only females that survived the first year

**Table 3** Early-life characteristics for subsequent first-year survivors and non-survivors in yellow ground squirrel females (mean ± SD; range in parentheses; see statistics in Table 2)

Characteristics	Survival to adulthood	
	Survived ( <i>N</i> = 47)	Disappeared ( <i>N</i> = 165)
Weaning weight (g)	<b>196 ± 48 (115–319)</b>	<b>164 ± 44 (71–304)</b>
Date of natal emergence	30 May ± 8.8 (15 May–14 June)	1 June ± 6.3 (15 May–18 June)
Natal litter size	5.1 ± 1.7 (2–9)	5.8 ± 2.0 (2–10)
Distance to the village (m)	<b>198 ± 115 (20–381)</b>	<b>162 ± 117 (15–405)</b>
Mean distance to burrows of 20 nearest juveniles (m)	49 ± 28 (18–132)	43 ± 28 (11–138)
Adult population density (ind/ha)	<b>2.6 ± 1.1 (0.6–4.4)</b>	<b>3.2 ± 1.1 (0.6–4.4)</b>
Amount of rain in May–June (mm)	65 ± 31 (27–107)	73 ± 33 (27–107)

Significant effects (*p* < 0.05) are marked with bold

1-year olds than in those that did not (9.8 ± 1.9 g/day, *N* = 20 vs 8.4 ± 1.6 g/day, *N* = 15, respectively; *t* test, *t* = 2.3, *df* = 33, *p* = 0.03). Those female yearling breeders that grew faster when they were young had higher weaning weight (*r* = 0.49, *p* = 0.03, *N* = 20) and higher body mass at their first litter emergence (*r* = 0.55, *p* = 0.02, *N* = 18).

## Discussion

### Fitness components in yellow ground squirrel females

*Total lifespan.*—Lifespan varied from 0 to 5 years, and, generally, only one of the five females survived to the first

chance to wean offspring. The major cause of low survival to adulthood is early juvenile mortality—about half of young animals die after weaning and prior to dispersal (on average, only 2–2.5 pups from 4 to 5 in a litter survive to dispersal, Vasilieva and Tchabovsky 2014). After weaning the young, females do not provide much maternal care, and pups are very vulnerable to predation by raptors, domestic cats and dogs. Sometimes, juveniles died from starvation after natal emergence, probably failing to switch from milk to solid food or due to too early weaning (Vasilieva and Tchabovsky 2014). Survival to adulthood is very low in most mammals and is a primary and major component of fitness for any organism (Silk et al. 2003; Ronget et al. 2018) and the greatest source of variation in female LRS in many mammals (Clutton-Brock 1988; McAdam et al. 2007), including

**Table 4** Effects of early-life characteristics on lifetime number of weaned offspring in yellow ground squirrel females in Tweedie compound Poisson linear models

Predictors	Statistics
Weight gain rate	<b><math>B = 0.65 \pm 0.24, t = 2.7, p = 0.01</math></b>
<i>N</i> days between weighings	$B = 0.19 \pm 0.19, t = 1.0, p = 0.3$
Weaning weight	$B = 0.08 \pm 0.22, t = 0.37, p = 0.7$
Date of natal emergence	$B = 0.37 \pm 0.26, t = 1.4, p = 0.2$
Natal litter size	<b><math>B = 0.44 \pm 0.20, t = 2.3, p = 0.03</math></b>
Distance to the village	$B = 0.17 \pm 0.23, t = 0.7, p = 0.5$
Distance to 20 nearest juveniles	$B = 0.05 \pm 0.19, t = 0.3, p = 0.8$
Adult population density	$B = -0.31 \pm 0.19, t = -1.6, p = 0.1$
Amount of rain in May–June	$B = -0.32 \pm 0.20, t = -1.6, p = 0.13$

$B \pm SE$  and  $t$  correspond to parameter estimates, standard errors and  $t$  values; estimated index parameter = 1.18;  $N$  females = 34. Significant effects ( $p < 0.05$ ) are marked with bold

ground squirrels (King et al. 1991; Catton and Michener 2016).

**Adult lifespan.**—Variation in lifespan of females that managed to survive to adulthood was also very high; however, most of them survived for only one or two additional years and, thus, had only from one to three chances to reproduce in their entire lifetime, which is very short for such a large hibernating rodent (Turbill et al. 2011). Adult lifespan clearly, linearly and positively predicted female LRS supporting the theory and previous findings that longevity and annual survivorship are the best and more reliable predictors of female fitness than fecundity (Crone 2001; McAdam et al. 2007). This also evidences that female *S. fulvus* usually die before demographical senescence (in terms of decreased fertility and fecundity, Soulsbury and Halsey 2018). Even the oldest females were able to wean litters successfully—two 6-year-old and one 10-year-old females, not included in the analysis due to the lack of a full set of data, weaned their last litters at the age of 6 and 9 years, respectively.

Earlier, we showed that age did not affect annual reproductive success in female *S. fulvus* (Vasilieva and Tchabovsky 2014). Dying before senescence is common in small mammals and is usually explained by high vulnerability to predation (Austad and Fischer 1991, but see Soulsbury and Halsey 2018). However, large-sized adult yellow ground squirrels do not suffer high risk of predation. Instead, adult females usually disappear during the hibernation. It is, thus, unclear why the selection towards longer lifespan was ineffective in relatively large-sized female *S. fulvus*. One possible explanation is the fast pace of life strategy of *S. fulvus* (Vasilieva and Tchabovsky 2018) and very large annual reproductive investment made by females into their offspring (Vasilieva and Tchabovsky 2014). Although we have not found negative short-term effects of large reproductive effort on survival and future reproduction in females

(Vasilieva and Tchabovsky 2014), it can have long-term consequences for body performance and health, resulting in early functional (as indicated by sharply declining probability of survival for females  $> 2$  years old), but not demographical, senescence (Soulsbury and Halsey 2018) and, therefore, short lifespan. In addition, yellow ground squirrel is characterized by extremely long hibernation period which can negatively affect adult longevity through various physiological drawbacks such as immune suppression (i.e., Bouma et al. 2010), sleep deprivation (Daan et al. 1991), cellular stress (Carey et al. 2003).

**Lifetime offspring production.**—A small number of breeding attempts per lifetime with very long (1 year) intervals between them is a common feature of monoestrous hibernating ground squirrels. Combined with high variability of lifespan, this increases the contribution of random chance and stochastic events to variation in LRS (Catton and Michener 2016; Snyder and Ellner 2018) and predetermines its high inter-individual variability and right-skewed distribution when few females produce many offspring, while many females have no or low LRS. This is exactly what was observed in female *S. fulvus* as well as in other ground-dwelling squirrels (King et al. 1991; Armitage 2014; Catton and Michener 2016).

Highly variable and right-skewed female LRS is common for many mammals, including solitary species, in which fitness is achieved through production of direct descendants (Wauters and Dhondt 1995; von Holst et al. 2002; Catton and Michener 2016; Bercovitch and Berry 2017). However, unlike males, reproductive skew in females is rarely discussed in terms of its role in sexual conflict and potential for sexual selection (Hare and Simmons 2018). Meanwhile, high variability of female LRS not only raises questions about the underlying causes and evolutionary significance for shaping female adaptive strategies (Catton and Michener 2016), but also can be viewed as a variance component of male LRS. Thus, we believe that the role of female reproductive skew as a selective force in shaping life-history and reproductive strategies should not be underestimated.

### Early determinants of female fitness

**Determinants of lifespan.**—Survival to adulthood was the most sensitive to early conditions component of female fitness and was determined by a combination of individual and environmental early-life characteristics. Low weaning weight and/or proximity of the natal place to the village could increase the risk of predation by raptors and domestic cats and dogs. In addition, low early weight likely indicates poor physical conditions and low viability of young females resulted from negative impact of large litter size or adverse early environmental circumstances. However, we found no



effect of rainfall in the post-weaning period or natal litter size on female survival during the first year of life.

Although we do not have direct evidence for negative influence of poor pre-hibernation body conditions on survival, our results indirectly support this effect. We found that heavier pups grew faster and survived their first hibernation better than their lighter counterparts (see also Vasilieva and Tchabovsky 2009). This suggests that pups with greater weaning weight achieved higher pre-hibernation body weight, which should determine their better survival during hibernation.

In addition to low weaning weight and proximity to the village, high population density negatively influenced survival to the adulthood. Negative density effects on weaning weight and survival are reported for many mammals including sciurids and explained by increased competition for food and other resources in saturated habitats (McLoughlin et al. 2006; Armitage 2014; Albon et al. 1987; Clutton-Brock et al. 1992, Wauters and Lens 1995). In *S. fulvus*, competition for food unlikely plays any substantial role, as indicated by the lack of the effects of natal litter size and juvenile density at natal emergence on female survival during the first year of life. Instead, habitat saturation at high density may stimulate dispersal and competition for suitable hibernating and breeding sites. In saturated habitats, dispersal and/or hibernation costs could increase mortality during the first year and produce long-lasting negative effects on LRS.

Negative effect of high population density on animal performance (survival and reproduction) through increased intraspecific competition is widely recognized as one of the most important mechanisms of population regulation (Krebs and Myers 1974, Sinclair and Pech 1996; Turchin 2003). However, long-lasting downstream effects of the population density at birth on fitness have been studied so far in only some mammals (Lummaa and Clutton-Brock 2002; Sinclair et al. 2003; Sundell et al. 2019). In *S. fulvus*, high population density at birth negatively influenced both proximate and distal fitness components—survival to adulthood, adult lifespan, the lifetime number of weaned offspring and adult offspring, i.e., affected each step in cumulative LRS. This suggests that habitat saturation in the year of birth could have long-term negative consequences for lifetime physical parameters through increased costs of competition for space, hibernating and breeding sites, and, probably, settling in suboptimal sites.

**Determinants of lifetime offspring production.** —In a nutshell, more distal components of female LRS were not predicted by early conditions as successfully as survival to adulthood, the most proximal one, and were influenced by different factors. The discrepancy between the effects of early conditions on proximal and distal components of LRS is not surprising. First, survival to adulthood, unlike more distal LRS metrics, is under the direct effect of early-life

conditions and, thus, should be the most responsive LRS component. Second, different LRS components are obviously controlled by different factors. For example, the number of weaned young depends on female fecundity; whereas, the number of survived yearlings depends also on their quality. Finally and more important, despite proximal and distal LRS metrics being usually correlated, proximal metrics can poorly predict distal LRS components due to an increase of stochastic effects with each extra LRS step (Catton and Michener 2016). In support of this view, our data show that the effect of lifetime extension is lower for more distal LRS components and is not strong for the lifetime number of reproductive offspring, the most essential component of fitness.

Positive effect of early growth rate on female LRS measured as the number of weaned offspring was expected for female *S. fulvus* based on theoretical reasons; however, so far, it has been observed in only a few mammalian species, including humans (Albon et al. 1987; Kruuk et al. 1999; Lummaa and Clutton-Brock 2002; Lummaa 2003; English et al. 2013). We found that early growth rate depended on upstream conditions and, in turn, produced downstream effects—on the one hand, fast growth of females was determined by higher weaning weight, and, on the other hand, they were more likely to wean a litter in their first breeding season and were in better conditions after weaning their first young. This suggests that the costs of breeding as yearlings are lower for females with higher early growth rate and explains their higher LRS. Moreover, earlier we have shown that pups with higher weaning weight not only grow faster, but also play more frequently and for a longer period than pups in poorer condition (Vasilieva and Tchabovsky 2009). The positive relationship between high weaning weight, fast early growth, social development and LRS can be explained by inter-individual phenotypic variation and/or spatio-temporal environmental heterogeneity (e.g., habitat quality). Females born in better conditions may combine all benefits at no or low cost (“increasing returns”, Dobson et al. 1999) and bequeath them to philopatric matriline offspring (“grandmother effect”). Such syndrome of high-quality young born in a favourable environment (“silver spoon effect” Grafen 1988; Monaghan et al. 2008) can have downstream rippling fitness consequences damping with age and each step on the way of LRS.

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**Data accessibility** The dataset supporting this article is available on the Figshare Digital Repository <https://doi.org/10.6084/m9.figshare.8247812>.

## Compliance with ethical standards

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

**Ethical approval** All applicable institutional and/or national guidelines for the care and use of animals were followed.

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