

A shortage of males causes female reproductive failure in yellow ground squirrels

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Sexual conflict theory suggests that female breeding success is strongly influenced by individual life history and environmental conditions and is much less affected by mate availability. Female mating failure due to a shortage of males remains poorly studied and understood. We present data on the effects of male availability on female breeding success in a wild colony of yellow ground squirrels (*Spermophilus fulvus*). A female's probability of breeding increased with the local density of males and was higher with higher male-biased operational sex ratio (OSR) but was independent of local female density, female age, and body condition, which are factors commonly assumed to influence female reproduction. The positive effect of male availability (as measured by OSR) on female breeding success was consistent across the years, and we conclude that male limitation contributes to female mating failure. This pattern, which is not commonly recorded in species with conventional sex roles, can be explained by a combination of sociodemographic and life history traits (sex differences in age of maturation, female-skewed adult sex ratio and seasonally varying OSR, solitary living at low population density, and low mobility of females combined with mate-searching tactics of males) that are not confined to *S. fulvus*. Our findings indicate that the role of female mating failure (due to a shortage of males) in shaping mammalian life history may be underestimated.

INTRODUCTION

Reproductive failure (that is, failure to produce progeny) due to mate limitation is not expected in females (1–4), except in a few role-reversed species in which males invest relatively more in parental care than do females and females compete for access to males (5, 6). In species with standard sex roles, females may compete for males (that is, “good males”), sperm, or additional matings, but typically not for mating opportunity per se (7–12). In some insects and spiders, male limitation was found to contribute to female reproductive failure, which is commonly attributed to environmental or physiological constraints (3, 13, 14). Female-female competition for access to males may increase when the operational sex ratio (OSR) (15) is more female-biased and males are limited as a result of sex differences in mortality, age at maturation, timing of emergence or arrival at breeding sites, estrous synchronization, and/or crowding of females (10, 16–18).

Ground squirrels are hibernating rodents with a single and very short period of female receptivity during the first days after vernal emergence (19–21). In many species, the sex ratio in the breeding population is strongly female-biased (22–24). In most species, females start to emerge later than males do, and the relative abundance of potential mates varies during the course of the breeding season. Yellow ground squirrel (or yellow souslik, *Spermophilus fulvus*) is a diurnal obligate hibernator whose mating season is restricted to a few weeks (25). Yellow sousliks live solitarily at a low population density and exhibit a scramble polygyny mating system, with males searching for sedentary females and with females typically mating with a single male (25, 26). Females start to reproduce as yearlings after the first hibernation, whereas males usually mature after the second hibernation (25). Yearly, about 30 to 40% of sexually mature females do not reproduce (26–28). Previously, we found that a female's probability of breeding did not

depend on her physical condition at emergence, age, and previous reproduction, which are factors commonly considered to influence female reproduction (28). Thus, the variation in breeding success among females remains unexplained, suggesting that other factors may be involved. Female-skewed OSR, combined with solitary living at low population density and low female mobility, can cause female mating failure in species where males use mate-searching tactics (3, 13, 14). We hypothesized that the probability of breeding in female yellow sousliks is influenced by mate availability.

RESULTS

Seasonal variation in sex ratio

Adult males emerged from hibernation, on average, 11 days earlier than did females (mean \pm SD, 24 March \pm 8 days and 4 April \pm 6 days, respectively; $t = -10.4$, $df = 264$, $P < 0.0001$), and 70% ($n = 54$) of adult males had emerged by the date of the appearance of the first female aboveground after the mating season started (Fig. 1). The adult sex ratio in the colony (that is, without taking into account the period of female receptivity) was male-biased only during the first days of the period of female emergence. But then, with more females emerging, the adult sex ratio became more and more female-biased; at the end of the mating season, the skew toward females had approached four females to one male.

OSR (the daily ratio of receptive females to adult males in the colony) varied during the mating season in a different pattern. At the beginning of the mating season, when the first females emerged, the OSR was male-biased. In the middle of the mating season, the OSR skewed toward females. At the end of the mating season (that is, the end of the female emergence period, ca. 25 days), as more and more females became unreceptive and fewer females emerged, the OSR became male-biased again (fig. S1). The variation in OSR between early mating season (<5 days from the beginning), middle mating season (5 to 20 days), and late mating season (>20 days) was highly

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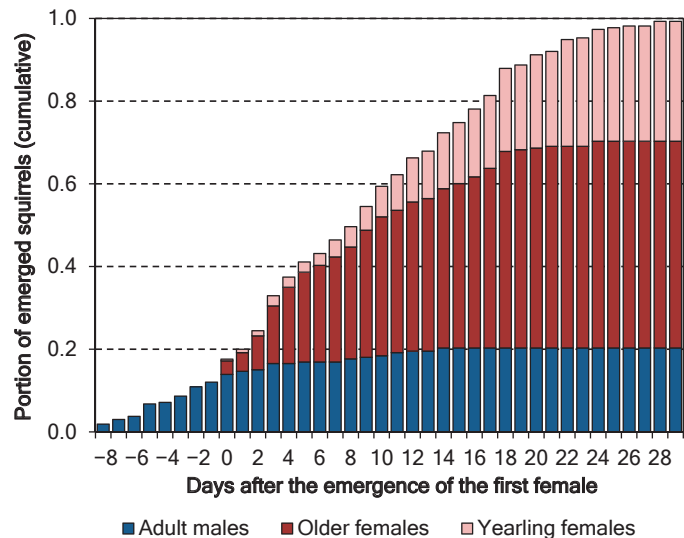


Fig. 1. Seasonal dynamics of emergence and adult sex ratio in a wild colony of yellow sousliks. Cumulative portions of emerged squirrels by sex-age categories are shown ($N = 244$, $n_{\text{males}} = 54$, $n_{\text{adult females}} = 120$, $n_{\text{yearling females}} = 70$; a pooled data sample for 2004–2007).

significant (analysis of variance: $F_{2,76} = 10.99$, $P < 0.0001$; Tukey honest significant difference test: early versus middle, $P = 0.0002$; late versus middle, $P = 0.037$; Fig. 2).

Male availability and female breeding success

Local male density [first principal component (PC1); table S1] and OSR at emergence received strong support in the model selection procedure for a female breeding status model [generalized linear mixed modeling (GLMM) with female identity as a random effect; Tables 1 and 2]. Male density was significantly higher, and OSR was significantly more male-biased for subsequent female breeders than for non-breeders. Yearling and older female breeders emerged, on average, at male-biased OSR, whereas nonbreeders emerged at equal or female-biased OSR (Tables 1 and 3). Females that emerged early and late in the season at a more male-biased OSR bred with higher probability than did females that emerged in the middle season at a more female-biased OSR ($\chi^2 = 8.36$, $df = 2$, $P = 0.015$; Fig. 2). The local density of receptive females [second principal component (PC2); table S1] and female age did not affect female breeding status (Tables 1 and 3). The best-fitted model for female breeding status with the lowest Akaike information criterion corrected for small sample size (AIC_c) score and the highest AIC_c weight included only two predictors: OSR and local male density (Table 2). We did not find any significant association of litter size with local male or female density, OSR at spring emergence, or female age (Table 1).

Local male and female densities around receptive females and the mean OSR varied across 4 years. When we added the year of the study as an additional predictor to the set of candidate models in GLMM (together with OSR, male density, and female density), the effect of OSR on female breeding success remained highly significant: subsequent breeders emerged at a more male-biased sex ratio than did non-breeders on all years (model-averaged estimate = 1.15, $SE = 0.38$, $\chi^2 = 11.2$, $P = 0.0008$; Fig. 3). The effect of local male density became insignificant, and the best model contained two variables that predicted

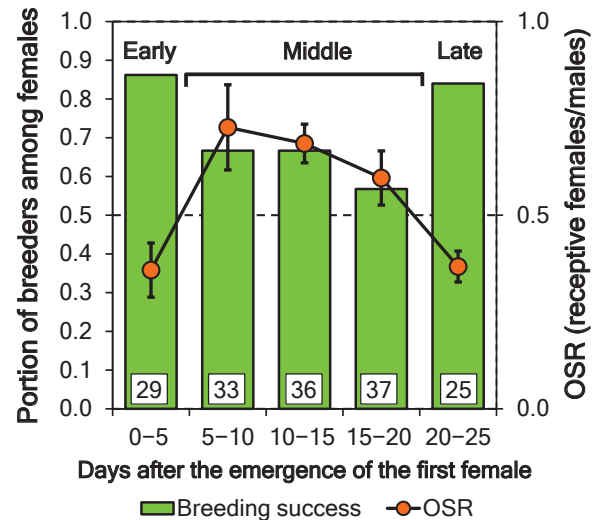


Fig. 2. Seasonal dynamics of OSR and female breeding success. Breeding success is measured as a portion of subsequent breeders from all females emerged at 5-day intervals. Numbers in boxes are sample sizes of females with determined breeding status. OSR is presented as mean \pm SE at 5-day intervals (a pooled data sample for 2004–2007). The mating season is subdivided into early season (<5 days after the beginning), middle season (5 to 20 days), and late season (>20 days).

female breeding status: OSR at female emergence and the year of the study (table S2). The effects of OSR and local male and female densities on female fecundity were insignificant ($P > 0.05$).

To confirm the independent effect of male availability on female breeding success, we ran the analysis with female body condition and date of female emergence from our previous study again [for details on data collection and treatment, see Vasilieva *et al.* (28)] as additional predictors of female breeding status in a generalized linear model, along with all other factors. We used a generalized linear model because the sample did not contain repeated measurements for the same female. The positive effect of male availability on a female's probability of breeding was significant: the best-fitted model among a full set of candidate models included OSR (estimate = -0.9 , $SE = 0.4$, Wald $\chi^2 = 5.5$, $P = 0.02$) and local male density (estimate = 1.0 , $SE = 0.4$, Wald $\chi^2 = 4.8$, $P = 0.03$; table S3), whereas other factors were not associated with female breeding status.

DISCUSSION

Our findings support the hypothesis that male availability affects breeding success in female yellow sousliks and that male limitation can result in female reproductive failure (that is, failure to mate and wean young). Besides male limitation, reproductive failure in females could also be explained by their failure to mate because of poor physical condition or improper physiological condition. However, physical condition and previous reproductive effort did not explain the variation in female breeding status among yellow sousliks (28), and the positive effect of male availability (in terms of OSR and local male density) on female breeding success was independent of female age; yearling and older females that emerged when and where males were more available had more chances to breed. Moreover, OSR and local male density were

Table 1. Effects of local male density, local female density, and standardized OSR at spring emergence on female reproduction in GLMM. Female identity was fitted as a random effect in all models. *B* and SE correspond to model-averaged parameter estimates and SEs in GLMM, whereas χ^2 corresponds to likelihood ratio test. All interactions between predictors were insignificant ($P > 0.1$).

Predictors	Parameters of female reproduction	
	Breeding success (breeder/nonbreeder), <i>n</i> = 98	Litter size, <i>n</i> = 65
Local male density (PC1)	<i>B</i> = 0.81, SE = 0.28, χ^2 = 8.6, <i>P</i> = 0.003	<i>B</i> = 0.20, SE = 0.23, χ^2 = 0.8, <i>P</i> = 0.4
Local female density (PC2)	<i>B</i> = -0.01, SE = 0.33, χ^2 = 0.0, <i>P</i> = 1.0	<i>B</i> = -0.20, SE = 0.26, χ^2 = 0.6, <i>P</i> = 0.4
OSR (female/male)	<i>B</i> = -0.82, SE = 0.28, χ^2 = 10.1, <i>P</i> = 0.0015	<i>B</i> = -0.24, SE = 0.23, χ^2 = 1.1, <i>P</i> = 0.3
Female age	<i>B</i> = -0.65, SE = 0.55, χ^2 = 1.4, <i>P</i> = 0.2	<i>B</i> = 0.39, SE = 0.47, χ^2 = 0.7, <i>P</i> = 0.4

Table 2. AIC_c values for candidate models describing the effects of local male density (Males), local female density (Females), OSR, and female age (Age) on female breeding status in yellow ground squirrels. Female identity was fitted as a random effect in all models (*n* = 98). *k* is the number of parameters estimated by the model, ΔAIC_c is the difference between the AIC_c score of the given model and AIC_c score of the best model (the lowest AIC_c score was 108.0), and AIC_c weight reflects relative support for each model. Models with $\Delta AIC_c > 2.0$ are in boldface.

Model	<i>k</i>	ΔAIC_c	AIC _c weight
OSR + Males	4	0	0.44
OSR + Males + Age	5	0.86	0.28
OSR + Males + Females	5	2.2	0.14
OSR + Males + Females + Age	6	3.1	0.09
OSR + Age	4	7.3	0.01
Males	3	8.0	0.01
OSR	3	8.4	0.01
Males + Age	4	9.3	0.00
Males + Females	4	9.4	0.00
OSR + Females + Age	5	9.4	0.00
OSR + Females	4	10.6	0.00
Males + Females + Age	5	10.9	0.00
Age	3	15.1	0.00
Intercept	2	15.2	0.00
Females	3	16.8	0.00
Females + Age	4	17.0	0.00

the only predictors in the best-fitted model of female breeding status among other sets of factors usually considered to influence female breeding success. The positive effect of OSR (as a measure of relative male abundance at the time of female receptivity) on female breeding success was consistent across the years. A lack of “male density effect” in the cross-year model suggests that the relative abundance of males in the colony at the time of female receptivity is a more important and reliable predictor of female breeding success or failure.

Furthermore, sperm limitation and male prudence in sperm allocation may be responsible for reproductive failure in females that copulated but were not fertilized (12). However, in *S. fulvus*, males typically interact with only one to four females during the mating season (25); thus, they exhibit prudent sperm allocation and are unlikely to become sperm-limited.

None of the considered factors, except male availability, can explain the variation in female breeding success in *S. fulvus*. One may argue that male availability and breeding success in females are indirectly correlated through some other unspecified factors (for example, seasonal, yearly, or spatial variation in environmental conditions or female and male quality). However, if this were the case, male abundance would have correlated not only with a female’s probability of breeding but also with fecundity, which is highly variable in *S. fulvus* (28). In other words, females emerging under some unfavorable conditions would not only have had fewer chances to be fertilized but also would have produced smaller litters if fertilized. We found no variation in fecundity (related to OSR or local density of males and females) among females, whereas the positive effect of male availability on female breeding success was highly significant. The spatial distribution of males and females in the spring is preset in the previous summer (when squirrels immerse in hibernation), and the distribution of males around receptive females is predetermined before the mating season starts. Finally, the major factor that was found to affect female breeding success was daily OSR, whose effect was consistent across the years. OSR is independent of habitat heterogeneity or of the spatial distribution of individuals in the colony but varies seasonally. Environmental conditions are much more severe in early spring; nevertheless, females that emerged early had more chances to breed at a more male-biased OSR compared with females that emerged in the middle season, when conditions were more favorable but males were less available.

Thus, even if there are other factors responsible for the variation in breeding status among female *S. fulvus*, the fact that female breeding success depends on male availability but is independent of female density, age, and physical condition indicates that mate limitation appears to be the most likely reason for reproductive failure. To our knowledge, this is the first case study report on female reproductive failure due to male limitation in wild mammals. Female mating failure due to a lack of mating opportunity was observed in yellow-bellied marmots (29), wherein some females did not reproduce in snowfall during the mating season, when male mobility was low. Moreover, a shortage of males as a result of selective poaching determined mating failure in the critically endangered ungulate *Saiga tatarica* (30).

Table 3. OSR and parameters of male and female distribution at female vernal emergence for subsequent breeders and nonbreeders. Data are presented as mean ± SD [range] (n) (see statistics in Table 1).

Parameters	Breeders		Nonbreeders	
	Yearlings	Females aged ≥2 years	Yearlings	Females aged ≥2 years
Mean distance to the five nearest male burrows, m	95 ± 54 [26–236] (18)	106 ± 57 [42–251] (38)	152 ± 60 [29–230] (12)	105 ± 34 [59–251] (16)
Number of male* burrows within 100 m of the female's burrow	3.2 ± 2.3 [0–6] (18)	3.1 ± 1.7 [0–6] (38)	1.7 ± 1.6 [0–6] (12)	2.4 ± 1.4 [1–5] (16)
Mean distance to the five nearest female burrows, m	50 ± 29 [26–128] (18)	66 ± 61 [18–352] (38)	50 ± 26 [23–95] (12)	59 ± 30 [18–109] (16)
Number of female† burrows within 70 m of the female's burrow	3.4 ± 3.1 [0–9] (18)	3.7 ± 3.1 [0–12] (38)	2.5 ± 2.2 [0–8] (12)	2.9 ± 2.3 [0–9] (16)
OSR (female/male)	0.6 ± 0.3 [0.2–1.1] (27)	0.7 ± 0.4 [0.08–1.3] (47)	0.9 ± 0.3 [0.6–1.2] (12)	1.0 ± 0.3 [0.2–1.3] (19)

*Only ≥2-year-old males that emerged no later than the fifth day after the date of emergence of the focal female. †Only females that emerged within ±5 days from the date of emergence of the focal female.

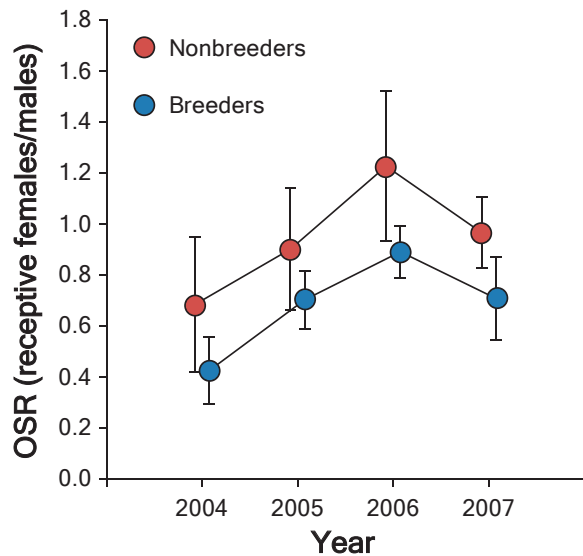


Fig. 3. Effects of OSR at emergence on female breeding success across the years. The effects were highly significant in GLMM ($P = 0.0008$). The sample sizes are 25, 33, 37, and 31 females for 2004–2007, respectively. Error bars represent mean ± 95% confidence interval.

This pattern of female reproduction, which is not commonly recorded in species with conventional sex roles, can be explained by a combination of sociodemographic, breeding, and life history patterns: (i) highly female-skewed adult sex ratio and seasonally varying OSR; (ii) scramble competition polygyny, when only males in good condition actively search for sedentary females and females typically mate with only one male; (iii) solitary living at low population density and low contact frequency; (iv) low mobility of females; and (v) short period of female receptivity. All of these can make it difficult for males to find all females at the right time and can decrease females' chances to encounter a partner and to mate. Most mature yellow souslik females have three or fewer chances to breed in their lifetime (28), and the cost of missed mating is very high. This suggests that *S. fulvus* females should use any mating opportunity and explains why their breeding

success does not depend on age, body condition, or previous reproductive effort. These patterns of life history, social organization, and mating system that may cause female mating failure are not confined to *S. fulvus*. In other species characterized by a short breeding season, a highly female-skewed sex ratio, sex differences in age at maturation, increased male mortality, solitary living at low population density, and mate-searching tactics among males, females may also face a lack of mating opportunities.

Classic sexual selection theory suggests that female reproductive success is not determined by the spatiotemporal distribution of mates (15). Our findings indicate that the role of male limitation in female mating failure may be underestimated and that mate availability can have profound effects on female reproductive success and on males.

MATERIALS AND METHODS

Experimental design

In a wild colony of yellow sousliks, we studied variations in female breeding success (breeder/nonbreeder) and fecundity (litter size) in relation to male availability during the period of female receptivity. To estimate the availability of males, we used OSR as a measure of the relative abundance of males in the colony at the time of female receptivity and assessed the spatiotemporal distribution of males and females around focal receptive females.

Study area and sampling

The yellow or long-teeth souslik *S. fulvus* lives in the arid zones of Central Asia, Iran, China, and Southern Russia. It is a large (up to 2 kg) (31) species that goes into prolonged hibernation. Like other ground squirrels, females emerge from hibernation later than do males (mid-March to mid-April) and become estrous in the first several days after emergence (26, 27).

We monitored a natural colony of individually marked yellow ground squirrels *S. fulvus orlovii* (Ogn. 1937) in Saratovskaya oblast, Russia, in the vicinity of the village Dyakovka (50°43'88"N, 46°46'04"E) from mid-March to mid-August 2004–2007. We had begun permanent individual marking in the colony in 2001; therefore, we knew the origin

and exact age of nearly all individuals (number of females = 112). Trapping, marking, and observation procedures are described in detail elsewhere [Vasilieva *et al.* (25), Vasilieva *et al.* (28)]. Our work conforms to the “Guidelines for the treatment of animals in behavioural research and teaching” (32) and to Russian Federation laws.

Data analysis

We used the presence or absence of a weaned litter as a qualitative measure of female breeding success. We avoided trapping and handling adult females during the first days after emergence to minimize interference in the mating process, and we did not perform a direct examination of females to determine their mating status (mated/unmated). Nevertheless, in *S. fulvus*, the absence of an emerged litter almost unequivocally indicates that a female has not mated or has lost the progeny prenatally (28). The rate of embryo resorption in *S. fulvus* is not very high (3 to 5%), and resorption of a whole litter has never been recorded (26, 27); therefore, the absence of a weaned litter is a reliable indicator of mating failure. Herein, we define “female reproductive failure” as failure to wean a litter in the current breeding season, which is most likely due to failure to mate. We called females with a weaned litter “breeders” and females without a weaned litter “nonbreeders.” Quantitatively, for breeders, we used litter size at the first emergence as an estimator of female fecundity.

For every female, we calculated OSR on the day of vernal emergence. Following Emlen and Oring (15), we estimated OSR as the daily ratio of fertilizable (receptive) females to sexually active males in the entire colony. Females (≥ 1 hibernation) were assumed to be receptive in the first 5 days after emergence. In other ground squirrel species, females usually mate within 5 days of spring emergence [for example, (19, 33)]. In *S. fulvus*, all male-female sexual contacts and burrow visits together with a male (indicative of mating) (25) occurred within the first 5 days after the female’s emergence, with most contacts occurring in the first 2 days ($n = 37$; minimum to maximum, 1 to 5; median, 2). Adult males (≥ 2 hibernations) were assumed to be sexually active during the entire mating season.

To assess variation in the local density of males and females, we used the distribution of hibernaculum burrows in the colony area. After emergence and during the mating period, males and females use the hibernaculum burrow as the main (usually the only) nest burrow, which can be considered as a center of activity. It means that the spatial distribution of males and females during the mating season is preset in the previous summer, when squirrels immerse in hibernation. Moreover, males immerse and emerge much earlier than females do (26); therefore, the distribution of males around receptive females is predetermined before the mating season starts. For every female, we described the spatiotemporal distribution of males and females around her main burrow using four variables: the mean distance from a female’s burrow to the nearest (i) five males and (ii) five female burrows, (iii) the number of females that emerged synchronously (within ± 5 days from the date of focal female emergence) within 70 m of the female’s burrow, and (iv) the number of males that emerged before the end of the period of female receptivity (that is, not later than 5 days after the date of emergence of the focal female) within 100 m of her burrow. We used the number of five nearest neighbors because it maximized the variance of the parameters compared to smaller or larger numbers. Moreover, the use of larger numbers would have included in the sample individuals at distances that are not reasonable, being larger than a typical ranging distance (ca. 100 m). The radius to estimate the local density of males was greater than that of females because the burrows

of males were sparse compared with those of females and because males ranged more widely.

Statistical analysis

To reduce the dimensionality in the data set and to simplify the analysis, we applied principal components analysis (PCA) on all four parameters describing male and female spatiotemporal distribution. All variables were standardized, and two principal components were extracted after Varimax raw rotation (table S1). The two components explained 86% of the variance in the spatiotemporal distribution of males and females. PC1 reflected an increase in the number of adult males within 100 m of the focal female’s hibernaculum within 5 days after the female’s emergence and a decrease in the mean distance from the female’s burrow to the nearest five male burrows (that is, PC1 described the variation in local male density during the period of female receptivity). PC2 reflected an increase in the number of females within 70 m of the female’s burrow within ± 5 days from the date of her emergence and a decrease in the mean distance to the nearest five female burrows (that is, PC2 described the variation in the local density of females with synchronized periods of receptivity).

To analyze the effects of local male and female densities and OSR at emergence on female breeding success (breeder/nonbreeder), we used GLMM [glmer in R package lme4 (34)] for binomial distribution with logit link function. Litter size for breeders fitted a normal distribution and was analyzed using GLMM for normal distribution with identity link function. Female identity was fitted in the models as a random factor because some females appeared more than once in the data sets in the subsequent years. We evaluated the sets of candidate models for breeding status and litter size based on all combinations of possible predictors: the two principal components, standardized OSR, and female age. Female age category (yearling/older females) was added as a factor in GLMM because yearling females emerged later than did older ones (24); thus, the mean time of receptivity varied between age categories. We initially fitted full models with all main effects and interactions. All interactions were insignificant ($P > 0.1$); thus, we did not include them in the set of candidate models. We compared the candidate models for breeding success and litter size and selected the best models using AIC_c (35), AIC_c weight, and model-averaged estimates, with their errors computed in the AICcmodavg package of R (36). The models were considered to have substantial support if ΔAIC_c (that is, the difference between the AIC_c score of the given model and the AIC_c score of the best model) was less than 2.0. In addition, we tested the significance of the predictors by comparing models using likelihood ratio test. Not all females had the full set of data; thus, sample sizes varied among statistical tests.

Statistical analyses were performed using the software packages R 3.2.1 (R Development Core Team, 2015) and STATISTICA version 8.0 (StatSoft). All tests were two-tailed, with a significance level of 0.05.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/1/9/e1500401/DC1>

Fig. S1. Seasonal dynamics of OSR (daily ratio of receptive females to adult males).

Table S1. PCA of four variables describing the spatiotemporal distribution of females and males around receptive females.

Table S2. AIC_c values for GLMM explaining female breeding status in yellow ground squirrels, with study year as additional predictor.

Table S3. AIC_c values for generalized linear models explaining female breeding status in yellow ground squirrels.

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