

Reproductive Decisions in a “Fast-Living” Sciurid: A Case Study of the Yellow Ground Squirrel (*Spermophilus fulvus*)

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Abstract—The problem of the optimal distribution of time and energy between reproduction and the other vital functions and the choice of optimal reproductive tactics concerns all animals. The sequence of decisions largely determines overall individual reproductive success and fitness. The goal of the study was to summarize the factors determining the reproductive decision of the yellow ground squirrel (*Spermophilus fulvus*). Despite its relatively large size and extremely long hibernation, the yellow ground squirrel is characterized by rapid growth and maturation, in combination with a short life-span; the life cycle of the yellow ground squirrel proceeds according to the “fast” scenario. Analysis of the relationship between breeding indices of females and their individual characteristics has shown that the reproductive investment and success of females do not depend on the age, body condition, or previous reproductive history of the female. The only factor found to influence female reproduction is the date of emergence from hibernation: the later a female emerges, the lower the offspring mass is and the fewer offspring survive. At the same time, female annual investment in reproduction is very large and close to the mean lifetime reproductive investment estimated for female mammals. With a short life-span (approximately 2–3 years), females do not have the opportunity to distribute the reproductive effort across many breeding attempts, they seem to be able to recover quickly after reproduction. Nevertheless, a substantial portion of mature females (about 30%) annually do not produce litters for unknown reasons. The sex ratio among reproductively active individuals during the mating period is strongly biased toward females. This is due to the lower survival of males, the late maturation of young males in comparison with females, and the fact that, even in adult males, individuals in poor physical condition are not very active and hardly search for sexual partners, i.e., males demonstrate a trade-off in the distribution of costs for somatic processes and reproduction. When there is a surplus of females emerging from hibernation, there are more receptive females in the population than reproductively active males, and operational sex ratio (OSR, the ratio between females and males ready to mate) is skewed toward females. Since females live sparsely and are sedentary during the mating period, the probability of breeding for them depends on the availability of sexual partners: the females’ breeding chances increase with an increase in the local density of males and the proportion of males in the population at the time of the female’s estrus; the only explanation for the large proportion of non-breeding females is the shortage of sexual partners. Thus, the negative effect of the shortage of males on the probability of female reproduction is shown for the first time for a natural population of mammals; this opens a new perspective on the theory of sexual conflict. This phenomenon, which is not so typical of species in which the parental investment of the female far exceeds the male’s investment, is explained by the combination of sociodemographic conditions and the life-history patterns of the yellow ground squirrel.

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INTRODUCTION

According to the life-history theory (Stearns, 1992), an inherent component of the living processes of an individual is decision making regarding the distribution of efforts between different vital functions and/or tactics (Williams, 1966; Stearns, 1976, 1989; Morris, 1987). In this case, the expression “decision making” is related to the theory of decision making (decision theory, Lehmann, 1950) and does not imply (necessarily) conscious choice in a mandatory manner; this is only a convenient term that makes it possible to designate a realization of one or another living

strategy, tactics, or action by an individual in the presence of several alternatives. Decision making at a given point of the life cycle partly canalizes the further life course of an individual and, in turn, determines the conditions under which subsequent decisions will be made.

Reproductive decisions, simply speaking, are reduced to the choice of when, how much, how, and with whom to spend time and energy on reproduction. The totality and the sequence of the decisions determine the success of the current attempt at reproduction to a considerable degree, as well as the lifetime

reproductive success of an individual and its net fitness.

One category of reproductive decisions (“when” and “how much” to invest in reproduction) concerns the optimization of time and energy allocation during life under reproductive trade-off (Stearns, 1976; Roff, 1992) in accordance with the principle of optimal resource distribution (Levins, 1968). In other words, individuals can differently distribute energy and time over various competing living functions at each specific moment in time, which is often manifested in the form of inverse (negative) relationships between the costs for these processes.

In particular, a trade-off between the somatic investment in the broad sense and the investment in the current reproduction is shown for many animal (and even plant) species: for example, individuals in a poor physical state cancel reproduction, delaying it until better times; the reproduction of young individuals inhibits their growth; large reproductive investment suppresses immune activity and increases the risk of death (Williams, 1966; Stearns, 1976, 1992; Clutton-Brock, 1984; Charnov et al., 2007). The manifestations of a trade-off between investments in current and future reproductive events are also described for a wide range of species: for example, individuals who did not reproduce in the previous reproductive season reproduce more successfully in the future (Gittleman and Thompson, 1988; Charnov et al., 2007). This category of reproductive trade-offs determines the distribution of the overall potential reproductive investment for the entire period of life of an animal, which is, in theory, an optimal method in terms of inclusive fitness (Gittleman and Thompson, 1988; Dobson and Oli, 2007; Dunbar, 2014). Finally, the trade-off between the quality and quantity of the offspring within a single litter assumes reproductive decisions about the amount of parental investment into a particular offspring (Stearns, 1976; Dobson and Oli, 2007; Dunbar, 2014).

Another category of reproductive decisions is associated with the choice “with whom” and “how” to spend time and resources on the reproduction. The basic decisions in this category include, first of all, the choice of sexual partner (or partners) and, second, the choice of behavioral tactics for access to them, which is determined by age, physical state, social status, and the distribution of sexual partners in time and space (Emlen and Oring, 1977; Caro and Bateson, 1986; Clutton-Brock, 1989; Dunbar, 2014). The decisions associated with mate choice primarily concern females, and the choice of behavioral tactics of searching and getting access to a partner is the destiny of a male. According to the life-history theory and the theory of the sexual conflict, the fundamental differences in the reproductive strategies of males and females are based on the differences in the size of parental investment (Trivers, 1972).

In particular, a mammalian female usually invests many more resources into the production of offspring than a male and can produce a relatively small number of offsprings during its life, the number of which, as a rule, weakly depends on the number of the sexual partners (Bateman, 1948; Parker, 1984). The female spends much more time and energy on production, nursing the young, and recovery; accordingly, she is not engaged in mating process for a much longer period than the male.

On the contrary, males are ready to mate for a long period of time, and, for them, the number of offsprings is directly determined by the number of sexual partners. As a result, the ratio of potential sexual partners is biased towards males (this ratio, namely, the ratio of the number of receptive females to the number of reproductively active males, is called the operational sex ratio, Emlen and Oring, 1977). In this situation, it is reasonable to expect competition among males for receptive females, which are always “in scarce supply” and have the opportunity to choose a partner. Females compete with each other not for the partners as such, but for the key resources that ensure the nursing of high quality offspring (Trivers, 1972; Janetos, 1980; Andersson, 1994; Clutton-Brock et al., 2006; Kokko and Jennions, 2008). Despite a certain revision of these concepts in recent years (Clutton-Brock, 2007; Clutton-Brock and McAuliffe, 2009; Bro-Jørgensen, 2011), this pattern of the relationships between sexes is typical for mammals as a whole.

In recent decades, an enormous amount of data has been accumulated on the factors that can determine the reproductive decisions of individuals and the choice of reproductive tactics, both at current moment in time and for the entire life cycle. For many species, the reproductive decisions and reproductive success of an individual were shown to depend on specific features of the genotype, “personal” characteristics (personality), physical state, age, social status, age of the first reproduction, previous reproductive effort, distribution of sexual partners in time and space, sex ratio, and intensity of competition for mates, ecological conditions, and the social environment (Emlen and Oring, 1977; Clutton-Brock, 1984, 1989; Caro and Bateson, 1986; Wauters and Dhondt, 1989; Dobson and Michener, 1995; Kuester et al., 1995; Rieger, 1996; Festa-Bianchet et al., 1998; Huber et al., 1999; Wolf et al., 2007; Morrow and Nicol, 2009; Dunbar, 2014). In turn, the choice of reproductive tactics by individuals determines mating system and social structure at the population level. So far, however, studies in which the authors analyzed a wide range of factors influencing the reproductive decisions and reproductive success of individuals simultaneously have been published for only a few species. One of the reasons for this is the fact that such study must be based on long-term individual-based observations in which the fates of several generations of animals are

followed from birth to death (Clutton-Brock and Sheldon, 2010).

Ground squirrels are an ideal model group for investigating the reproductive decisions and their long-term consequences in terms of reproductive success and individual fitness. This rodent group is characterized by a wide variety of social and mating systems and, on the other hand, by comparatively small morphological, physiological, and ecological differences among the species and a similar annual cycle, which includes prolonged hibernation in most species (Dobson, 1984; Armitage, 1986; Waterman, 2007). Reproduction in these species occurs only once a year within the strictly defined periods; they are diurnal animals that live in the open habitats and use the same burrows from year to year (Phillips, 1984; Shilova, 2000, 2004; Waterman, 2007); all of these facts facilitate observations and allow to observe an individual during the entire lifespan.

The yellow ground squirrel (*Spermophilus fulvus*) is one of the largest representatives of ground squirrels, excluding marmots (body mass before the hibernation of up to 2 kg, Gromov and Erbaeva, 1995; Vasilieva et al., 2009) with a prolonged hibernation up to 8–9 months (Shilova, 2000).

The aim of this paper is to summarize the results of the long-term field study of the factors that determine the reproductive decisions of males and females in the yellow ground squirrel and to compare these data to the traditional concepts of the life-history theory in ground squirrels.

This work is based on observations of individually marked yellow ground squirrels (*Spermophilus fulvus*) in nature. Population studies in Saratov oblast have been conducted from 2001 to the present day, which makes it possible to trace the fates of several generations from birth to death. The methods of collection and data analysis are described in detail in other publications (Vasilieva et al., 2014; Vasilieva and Tchabovsky, 2014, 2015).

We studied (a) the influence of age, physical state (body mass and fatness), previous reproduction, dates of emergence from the hibernation, as well as the spatiotemporal distribution of males on the parameters that describe female reproductive effort and reproductive success in the present year; and (b) the variation of behavioral mate-searching tactics in males in relation to their age, physical state, and social status.

RESULTS

“Fast” and “Slow” Scenarios of the Life Cycle in Ground Squirrels

The parameters of the animal life cycle are tightly interrelated. In particular, the body mass of an adult individual is one of the key parameters that determines the course of other life-cycle processes: the young of large species require more time in order to reach the

size and mass of an adult individual. Consequently, in small-sized species, the young disperse early and enter reproduction after the first hibernation, while, in large-sized ground squirrels, young individuals do not disperse for long and produce offspring no earlier than the second or third wintering (Armitage, 1981, 1999; Vasilieva et al., 2009).

Another key parameter of the life cycle for winter hibernating species of ground squirrels is the ratio of the duration of the season of aboveground activity and the duration of the winter hibernation. Obligatory prolonged hibernation does not allow young individuals to grow and develop as rapidly as the young of species with short or facultative hibernation; therefore, other conditions being equal, a slow growth rate and late start of reproduction is typical of species with long hibernation (Armitage, 1981, 1999; Neuhaus et al., 2004).

Thus, similar to mammals as a whole, the life cycle can go according to different scenarios with two polar versions in different species of ground squirrels: a “slow” version typical of large species and a “fast” version typical of small species (fast–slow continuum, Stearns, 1983; Promislow and Harvey, 1990; Dobson and Oli, 2007). The relationship between the body size and the position of species on the fast–slow continuum is indirect, through the longevity and the mortality level, which determine the opportunities for partition of the reproductive efforts (Promislow and Harvey 1990; Bielby et al., 2007). The slow scenario assumes a slow growth rate, late maturation and dispersal of young individuals, and great longevity. This scenario favors the formation of stable social relationships and the formation of a complex social structure with a wide variety of socio-demographic roles. The fast scenario of species with a short lifespan, on the contrary, implies a fast growth rate, early maturation and dispersal, high fecundity, and intensive reproduction with the minimum intervals. A fast dispersal and maturation does not create prerequisites for the formation of stable social communications between the individuals.

Special Features of the Life Cycle of Yellow Ground Squirrel

The sequence of events and stages of the annual cycle of the yellow ground squirrel corresponds to the scheme described for the majority of other hibernating species of ground squirrels. The males emerge first (in March), and the females emerge 10–15 days later, becoming receptive immediately after emerging from hibernation. According to observations in different populations, the mating period lasts from 10 (Kydyrbayev, 1960) to 40 days (Afanas'ev et al., 1953). Mating in the yellow ground squirrel occurs in the burrow. After mating, the males proceed with fattening and enter hibernation already at the beginning of June. Pregnancy lasts approximately 30 days, the lactation

lasts 30–40 days (Mironov, 2000). Young animals leave the burrows in the second half of May at the age of 23–25 days (Ismagilov, 1969). Adult females enter the hibernation only 1–1.5 months after the emergence of young individuals, at the end of June to the beginning of July. The young animals enter hibernation the latest (the second half of July to the beginning of August), after 2–2.5 months aboveground.

The yellow ground squirrel is the largest of the ground squirrels with prolonged hibernation (Shilova, 2000). Therefore, this species was expected to have a slow growth rate and late maturation of young animals. Despite these assumptions, females of yellow ground squirrel reach the size and mass of an adult individual after the first hibernation (males reach the mass of an adult only after the second hibernation) (Vasilieva et al., 2009). Moreover, females and, possibly, some males can reproduce already after the first wintering (Shubin and Kydyrbaev, 1975; Popov et al., 2006; Vasilieva et al., 2009). The young of yellow ground squirrel play with each other in the first weeks after emerging from the natal burrow, but the frequency of social contacts between young ground squirrels decreases practically to zero on the fourth week of the aboveground life (Vasilieva and Tchabovsky, 2009). The yellow ground squirrel is a solitary species that is not prone to forming complex social organizations; after the first wintering, individuals live sparsely and rarely contact each other outside of the mating period (*Materialy...*, 1929; Ismagilov, 1969; Mironov, 2000). The lifespan in this large species is relatively short: for the females that survived the first winter (i.e., excluding the mortality of the young in the first weeks of life), it varies from 1 to 6 years and is 3 years on average. This is less than in some smaller species, for example, of Columbian ground squirrels (*Urocitellus columbianus*, Armitage, 1981; Neuhaus et al., 2004), which live for 10–11 years, entering the reproduction on the third to fourth and even the fifth year of life.

In other words, despite the large size and prolonged hibernation, the life cycle of the yellow ground squirrel follows the fast scenario. This forces one to assume that male and female yellow ground squirrels do not have possibility to distribute the potential reproductive investment between many subsequent reproductive seasons.

Reproductive Compromises in Female Yellow Ground Squirrels

Female yellow ground squirrels produce only one litter per year. Annually, approximately 30% of females on average do not breed, and the litter size in those that reproduced varies within a wide range: from one to 14 pups in a litter (Ismagilov, 1969; Shubin and Kydyrbaev, 1975; Mironov, 2000; Vasilieva et al., 2014). Thus, high individual variability in the size of reproductive investment and reproductive success is

typical for female yellow ground squirrels. Under the conditions of prolonged hibernation and need to grow fast and accumulate fat during the short active season, one may expect the trade-offs in the form of the negative feedback between the somatic and reproductive functions, which would explain the high variability of the parameters of the female reproduction. At the same time, both reproducing females (which become pregnant, carry and produce offspring, recover after reproduction and be prepared for the following hibernation within 3–4 months of aboveground activity) and the young, which emerge from the burrows in the end of May to the beginning of June and must rapidly gain body mass necessary for the wintering after 1.5–2 months, must be put in conditions of time and energy deficiency (Vasilieva and Tchabovsky, 2009).

Above all, one may expect differences between the average annual reproductive investments in females of different ages. At the moment of emergence from hibernation, the body mass of yearling females is almost half of that in adults; they also have smaller sizes and are in a somewhat worse physical state (Vasilieva et al., 2009; Vasilieva and Tchabovsky, 2014). In other words, females after the first wintering still continue to grow and must invest a lot of energy, into both their own growth and an increase in body mass in order to prepare for the following hibernation.

It is reasonable to assume that, with such a substantial investment into the somatic processes, the possibilities for reproductive investment in yearling females will be limited in comparison with those in older ones, which must be manifested in a larger portion of non-breeding females among the yearlings, by a smaller litter size and/or the smaller mass of the young in comparison with the adult females.

The same reasoning is valid for individuals in a worse physical state, which, in order to survive the following winter, must gain more mass and accumulate more fat.

Finally, a smaller reproductive investment and the lower reproductive success can be expected for females that emerged from the hibernation later than others, since their time for conception, rearing, subsequent recovery, and fattening before the following hibernation is rigidly limited in comparison with the individuals that arise from hibernation early. Since the variation in dates of female emergence from hibernation within the colony is relatively great and reaches 3–4 weeks, it is possible to expect reverse correlation between the date of female emergence from hibernation and its annual reproductive investment/success.

Contrary to expectations, multivariate analysis revealed that the female's age, body weight, and fatness at the time of emergence from hibernation did not affect any of the following reproductive parameters: probability of producing a litter, litter size, pup mass, and number of pups in a litter surviving to dispersal or to the next spring (Vasilieva and Tchabovsky, 2014,

2015). At the same time, the dates of female emergence from hibernation significantly influence reproduction of females in the corresponding year: the later the female emerges, the lower is the average mass of the young in her litter, and, accordingly, the higher their mortality will be (Vasilieva and Tchabovsky, 2014; it should be noted that there was no significant correlation within the age groups between the date of female emergence and its body mass/fatness, $p > 0.05$).

Thus, in female yellow ground squirrels, no obvious trade-offs between the reproductive investment and the somatic needs were revealed, except for the negative influence of late emergence from hibernation on the quality of the offspring (but not on their quantity). Moreover, no negative consequences of the reproductive investment of a female were discovered for its subsequent survival and subsequent reproduction according to any of the evaluated reproduction parameters (Vasilieva and Tchabovsky, 2014). Thus, we did not reveal any explicit mechanisms that optimize the size of the reproductive investment of a female with respect to its physical state. The data of Shubin and Kydyrbaev (1975), who did not reveal any connection between a female's number of embryos and its body mass, correspond to this result.

In other words, female yellow ground squirrels make the maximum reproductive investment independently of their individual characteristics, and only females that emerge from hibernation late reduce their investment in the offspring, apparently, via shortening of the duration of lactation in favor of fattening and preparation for the following hibernation. It is possible to say that this uncompromising "approach" to making the reproductive decisions is more typical for species with the fast life cycle that do not have an opportunity to distribute the reproductive investment during their lifespan across a large number of sequential reproductive events with an accounting for the favorableness of conditions. Actually, according to theoretical calculations, a mammalian female for its entire life on average nurses the young by overall mass no more than 1.4 of the mass of its own body (Charnov et al., 2007). The mass of one litter of yellow ground squirrels at the end of lactation is approximately 850 g on average, whereas the average mass of a year-old female at the moment of waking from hibernation is approximately 350 g and the adult's mass is 550 g. Thus, already for one reproductive season, the female yellow ground squirrel makes a reproductive investment comparable with the average reproductive investment of mammals for its entire lifespan.

With this reproductive strategy, the "unconditional" (almost uncompromising) making of a decision about reproduction and the maximal one-time reproductive investment and the reasons for the high proportion of non-breeding females in the population remain unexplained: reproductive trade-offs in case of

the yellow ground squirrel are manifested only through a decrease of the investment in offspring in females that emerge late, and none of the other individual characteristics explain a complete failure of reproduction.

Reproductive Decisions and Behavioral Tactics of Males

Due to asynchronism of female emergence from winter hibernation at the beginning of an annual cycle (and the reproductive season), the sex ratio in the population of yellow ground squirrel is strongly skewed towards males: the majority of males have already emerged by the time when the first females begin to arise. In this situation, one may expect an acute competition between males for females and the choice of different tactics for access to receptive females by males in accordance with their individual traits. For females, especially for those that emerged earlier than others, the possibilities for the choice of the best sexual partner are greater.

Actually, analysis of the use of space by males in the mating period, as well as their social contacts between themselves and with the females, showed the presence of two clusters of males in the mating period: "active" and "passive" (Vasilieva et al., 2014). Active males emerge earlier, engage in social interactions more frequently, move over greater distances, and contact with a large number of females. Active males are represented exclusively by adult individuals (overwintered at least twice) in a good physical state and with high competitive ability, as indicated by more victories in the conflicts. Both yearling males and adults, but in a poor physical state and with a low competitive ability, proved to be among the passive males that emerge late, move less, and sit next to their burrows, waiting for a chance to meet a female. It is obvious that the more effective active tactics of the search for females incur high energy costs, which young males, as well as adult males in a poor physical state, cannot afford, thus demonstrating a trade-off in the distribution of costs for somatic processes and reproduction.

Nevertheless, the level of androgens can be relatively high and correspond to that of an adult in some yearling males, and they can move widely in search for the females on a par with the adults (Vasilieva et al., 2014). Thus, probably, some of them mate with the females, and we have actually registered several such cases.

Reproductive Decisions of Females during the Mating Season

At the first emergence of the young from the burrow, the sex ratio in the yellow ground squirrel is close to 1 : 1. However, as in many others ground squirrels, the females of this species are inclined to phylopatriy to a larger degree than males (Armitage, 1986; Popov et al., 2003, Vasilieva, 2011). Consequently, the mortal-

ity of dispersing males in the first year of life exceeds the mortality of females, and, already after the first wintering, the sex ratio shifts in favor of the females: the ratio of females and males surviving the first winter is 1.9 : 1.

Our data (Vasilieva et al., 2014), as well as data of other researchers (Shubin and Kydyrbaev, 1975), indicate that yearling males are not involved in reproduction on a par with adults and usually mature only after the second wintering. Only few yearling males participated in the free search for the females and tried to mate with them, but their contribution to the reproductive male cohort in the population is apparently very small, whereas females maturing after the first wintering participate in reproduction on a par with the older ones (Vasilieva and Tchabovsky, 2014), significantly increase the proportion of reproductively active females in the population. If there are individuals participating in reproduction among the yearling males, their portion is apparently small and they should not be considered in the estimation of the sex ratio between mature (reproductively active) animals. At the beginning of mating season, the sex ratio among sexually mature individuals shifts towards males. However, as more and more females emerge to the surface, it begins to shift in favour of females, and, by the time the majority of females emerge, the ratio reaches 4 : 1 (Vasilieva and Tchabovsky, 2015). The situation is further aggravated by the fact that, even among adult males, individuals in poor physical condition (passive) do not participate in reproduction equally with active ones. The proportion of active males in the population is small (not above 30%), which creates an even stronger bias in the sex ratio in favor of females among reproductively active individuals.

The operational sex ratio during the mating period varies in other way than the adult sex ratio. Estrus in females is very short (several hours) and starts immediately after emergence from hibernation, in the first 2–3 days (Vasilieva and Tchabovsky, 2015). Therefore, at the beginning of the mating period, when the first females begin to emerge and the majority of males have long been on the surface, as well as at the end of the mating period, when the last of the females emerge and estrus has already ended in the rest of them, the operational sex ratio is skewed towards males. However, in the middle of the mating season in the period of the mass emergence of females, the situation changes, and the sex ratio is shifted more and more towards females. In other words, despite the short period of female receptivity in the days when they arise from hibernation en masse, there are significantly more females ready to mate than reproductively active males.

We found that females emerging from hibernation under a lower density of males near their wintering burrows and under a lower proportion of males in the

population at the time of female emergence from hibernation (i.e., during the brief period of its receptivity) are more likely to remain unmated than females that emerged from burrows surrounded by numerous males and when the operational sex ratio was skewed towards males (Vasilieva and Tchabovsky, 2015). The abundance of males during the period of the female receptivity was the only factor in the multivariate analysis that predicted the probability of its reproduction. In other words, females trapped in conditions of a low abundance of males suffered from a lack of mates and missed reproduction, despite the strategy of unconditional “yes” decision-making on reproduction performed independently on their physical condition and other individual life-history traits.

DISCUSSION AND CONCLUSION

Patterns of the reproductive decision-making in yellow ground squirrels, coupled with data on their annual and life cycle and social organization, are not quite typical for mammals.

First, despite its large body mass and prolonged hibernation, the yellow ground squirrel has a life scenario that can be described more closely as a fast than a slow one. It grows rapidly, matures early, and has a short life expectancy; most females have no more than 2–3 potential breeding attempts in their lives. Yearling females participate in the reproduction practically on the same level as the adults, and even some yearling males are apparently ready to reproduce. It can be assumed that this rapid development and maturation is associated with the ecology of this species: the yellow ground squirrel inhabits deserts and semideserts, primarily in Kazakhstan and Central Asia (Ismagilov, 1969; Gromov and Erbaeva, 1995). Fast growth and weight gain could have evolved under the influence of extreme habitat conditions, in which extremely hot and dry summers are combined with cold, harsh winters, when the supply of food resources is limited by a short season and is poorly predictable, which requires the maximal effective resource use “here and now.” Another reason for a fast scenario can be the high mortality and low life expectancy in yellow ground squirrel, which overbalance the “slow-down” effect of large body size (Promislow and Harvey 1990; Bielby et al., 2007).

One of the consequences of the fast growth and development of the yellow ground squirrel is the relatively early disruption of social bonds between siblings and mother and early dispersal. This prevents the formation of strong social bonds between individuals; indeed, the yellow ground squirrels have practically no contact with each other outside the mating period and live sparsely (3–10 individuals/ha, Ismagilov, 1969; Bockstein et al., 1989; Shilova et al., 2015). The degree of social complexity for the yellow ground squirrel that characterizes stability and complexity of social relationships in the population and the diversity of socio-

demographic roles is close to minimal for ground squirrels (Michener, 1983; Blumstein and Armitage, 1998). The mating system in the population of yellow ground squirrel does not assume stable social bonds between a male and a female. Among the ground squirrels, it corresponds to the scramble competition polygyny typical for small fast-living species in which males use the tactic of competitive mate searching, widely moving in search of more and more new partners (Schwagmeyer and Brown, 1983; Schwagmeyer and Woontner, 1986; Millesi et al., 1998).

Another feature of a short life cycle is the inability to distribute reproductive investments over a lifetime over many reproductive seasons, in contrast to the slow-cycle scenario of long-lived species (Ruf et al., 2012). With high mortality rates and low life expectancy, missed reproduction event or even reduced reproductive investment are inadaptable because subsequent breeding attempts may not occur, which forces animals to live according to the fast scenario (Bielby et al., 2007). Indeed, female yellow ground squirrels generally makes a large investment in single reproductive event comparable with the average lifetime reproductive investment of a mammalian female, almost regardless of their age and physical condition. At the same time, for many ground squirrel species, it is known that young females under conditions of a trade-off between growth and reproduction, as well as the females in the worst physical condition, wean litters less likely and/or smaller in size in comparison with older individuals, and the survival of their pups is decreased (Murie and Dobson, 1987; Dobson and Michener, 1995; Hoogland, 1995; Rieger, 1996; Dobson et al., 1999; Huber et al., 1999; Hackländer and Arnold, 1999; Millesi et al., 2000; Neuhaus, 2000; Broussard, et al., 2003; Babitsky et al., 2006; Skibieli et al., 2009). It should be noted that a positive relationship between the physical condition of female and parameters of its reproduction has been found in all species previously studied. Thus, reproductive trade-offs, as well as reproductive decisions and the distribution of reproductive efforts in accordance with physical state, are typical for the females of ground squirrels.

The hypothesis of “the high cost of missed reproduction.” Decisions can be irrational or suboptimal in the short term, but optimal (maximizing fitness) in the long-term (Houston et al., 2012). The strategy of unconditional reproduction and maximal “one-time” reproductive investment in female yellow ground squirrels may be the result of a fast life, which seems paradoxical and inadaptable for large species and seems nonadaptive at first glance. However, the cost of refusal of reproduction for females with 2–3 chances to reproduce for the rest of their life may be too high to regulate the distribution of reproductive efforts depending on somatic needs. Indeed, on the average, a female that survived the first winter produces only 1.65 ± 1.1 litters for the entire life ($N = 64$). At the same time, in the case of reproductive failure or a

reduction of reproductive effort, the solitary living does not allow an increase of fitness in another way: cooperation with relatives. On the other hand, a short lifespan may not be the cause but the consequence of unconditional (uncompromising) maximization of each reproductive effort. In this sense, the uncompromising reproductive strategy of the females of yellow ground squirrel may be called “optimistic” (Houston et al., 2012), in which an individual underestimates the possible costs for reproduction and overestimates reproductive expectations (expected success of current reproduction).

The hypothesis of low reproductive costs. An additional explanation of such breeding “at any cost” for female yellow ground squirrels may be the ability to compensate easily and quickly large expenditures on reproduction, such that even young females and females in poor condition can recover after reproduction and successfully prepare for hibernation. The evidence in favor of this assumption is a lack of negative influence of reproduction, either on the subsequent survival of a female or her subsequent reproduction (Vasilieva and Tchabovsky, 2014).

Among all of the studied parameters of individual life cycle of yellow ground squirrels, only the time deficiency for females that emerged later from hibernation leads to a certain decrease in the reproductive investment, which is typical for other mammalian species that hibernate, ground squirrels in particular (Holmes and Landau, 1986; Dobson et al., 1999; Ahmad, 2008). However, in yellow ground squirrels, regulation of the size of reproductive investment accordingly to the time supply is realized not through the refusal of reproduction, not even through a decrease in the number of offsprings but only at the expense of their quality. A possible mechanism for the reduction in investment in this case is early weaning, as in the European ground squirrel *Spermophilus citellus* (Millesi et al., 2000), which leads to a reduction in the quality of late pups and a worse survival rate. However, in some species of ground squirrels, later pups emerge with a larger body mass (due to the smaller size of litters) than earlier ones. The authors attributed this to the fact that early pups have more time for fattening, and so the female can afford to limit her investment in each of them. Indeed, the masses of early and late pups are leveled at the time of hibernation (Reiger, 1996).

Female yellow ground squirrels live sparsely, do not form stable bonds with males, and enter hibernation later than males. As a result, the spatial distribution of receptive females during the mating season is unpredictable for males. On the other hand, the difference in the time of maturation of males and females, the initial greater mortality of young males, and the tendency of males in poor physical condition to abandon the active search for females create a skewed sex ratio among reproductively active individuals in favor of females (Vasilieva et al., 2014; Vasilieva and Tch-

abovskiy, 2015). Combined with the low mobility of females and very short estrus, this increases a risk for a female not to meet a male at the right time in the right place.

Indeed, the only variable among all of those analyzed that would be correlated with the probability of females to stay solitary turned out to be the abundance of males. At the same time, the relative abundance of males in the population (the operational sex ratio) was more crucial for female reproduction than the local abundance of males around wintering burrow, which is probably explained by the high mobility of adult males. In other words, females with an estrus period that coincides with a low relative abundance of males could remain unmated due to a lack of mating partners.

Hence, a decrease in the yellow ground squirrel population lower than a certain level can have catastrophic consequences for the population as a result of the Allee effect under low numbers: a population growth with descending density (Courchamp et al., 1999). The Allee effect assumes that a decrease in the population to a critical level can lead to a significant reduction in the probability to meet mate, which will, in turn, lead to a further decrease of the population. Indeed, as shown by Neronov and Shilova (2011), the drought of 2009 resulted in a significant (two-week) reduction in the period of ground activity of populations of yellow ground squirrel; the population then, and especially in the next year, decreased sharply and has not recovered since (Shilova et al., 2015).

The theory of sexual conflict implies that breeding females (as opposed to males) do not depend on the abundance of sexual partners (Emlen and Oring, 1977). However, we demonstrated that, for the yellow ground squirrel, the most probable reason of female reproductive failure is the shortage of mates. This is the first study that demonstrated a negative impact of the scarcity of males on breeding in females in natural, intact populations of wild mammals. The negative effect of low abundance of males on reproduction was shown for saiga antelope (*Saiga tatarica*, Milner-Gulland et al., 2003), which led to population collapse, but in this case, the effect was caused by a strong anthropogenic impact: the selective harvesting of males as the result of poaching.

Such a phenomenon, which is quite untypical for species in which the parental investment of females far exceeds the investment of males, is explained by a combination of socio-demographic conditions and life-history traits of the yellow ground squirrel: (a) the adult sex ratio biased toward females and high fluctuations in operational sex ratio during the mating period; (b) the use of the strategy of competitive mate search by males, when only males in good physical condition are capable of actively moving in search for females; (c) the low population density, the solitary living without social bonds between individuals;

(d) female low mobility in the period of receptivity; (e) extremely short estrus in females.

All of these factors, in combination with low life expectancy, explain the female strategy to use any opportunity to produce offspring and make the maximal investment in reproduction regardless of age, physical condition, and previous reproductive history. We can conclude that the negative effect of low availability of males on female reproduction may be underestimated in modern theory and the practice of studies of the sexual conflict, and it can be found in other species with similar life-history traits.

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