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Population sex-ratio affecting behavior and physiology of overwintering bank voles (*Myodes glareolus*)

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HIGHLIGHTS

- Female biased population sex-ratio induces social overwintering and winter breeding.
- Male biased sex-ratio can lead to solitary overwintering.
- Male biased sex-ratio induces elevated stress levels in overwintering females.

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ABSTRACT

Many boreal rodents are territorial during the breeding season but during winter become social and aggregate for more energy efficient thermoregulation. Communal winter nesting and social interactions are considered to play an important role for the winter survival of these species, yet the topic is relatively little explored. Females are suggested to be the initiators of winter aggregations and sometimes reported to survive better than males. This could be due to the higher social tolerance observed in overwintering females than males. Hormonal status could also affect winter behavior and survival. For instance, chronic stress can have a negative effect on survival, whereas high gonadal hormone levels, such as testosterone, often induce aggressive behavior. To test if the winter survival of females in a boreal rodent is better than that of males, and to assess the role of females in the winter aggregations, we generated bank vole (*Myodes glareolus*) populations of three different sex ratios (male-biased, female-biased and even density) under semi-natural conditions. We monitored survival, spatial behavior and hormonal status (stress and testosterone) during two winter months. We observed no significant differences in survival between the sexes or among populations with differing sex-ratios. The degree of movement area overlap was used as an indicator of social tolerance and potential communal nesting. Individuals in male biased populations showed a tendency to be solitary, whereas in female biased populations there was an indication of winter aggregation. Females living in male-biased populations had higher stress levels than the females from the other populations. The female-biased sex-ratio induced winter breeding and elevated testosterone levels in males. Thus, our results suggest that the sex-ratio of the overwintering population can lead to divergent overwintering strategies in bank voles.

1. Introduction

Overwintering strategies of different organisms in boreal and arctic regions can be divided roughly into three categories; migration, hibernation and resistance. Migration is most common among birds, whereas reptiles and amphibians, as well as some mammals rely on hibernation. However, surprisingly many animals remain active throughout the winter, despite the challenging environmental conditions. For instance, northern cervids, like moose, deer and caribou are very well equipped against cold with their large body size, thick winter pelage and fat reserves. But not all winter-active animals are large and armed with similar traits. In fact, many homeothermal winter-active animals are small mammals like rodents and shrews. Unlike large animals, their winter survival is directly and strongly dependent on snow cover. Under the snow pack these small animals exploit the subnivean space formed between the ground, withered vegetation and the snow for moving and foraging, but most importantly for protection against cold and predators. However, besides the importance of the physical protection provided by snow cover, also physiological and behavioral overwintering adaptations are required. Particularly, the hypothalamic-pituitary-adrenal axis (HPA axis) is essential in equipping mammals to endure the

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harsh conditions of northern winter [2,4]. It regulates several substantial body processes such as energy metabolism, reproduction, growth, immune system and stress reactions [4,8]. The function of the endocrine system during winter varies among species but in small winter-active rodents decreasing day length and temperature are known to induce changes e.g., in fur thickness and metabolism. Also, many small mammals reduce their body mass to lower energy needs, and often all reproductive functions cease in order to allocate energy for survival [1,11,14,15,21,22]. In addition to these physiological changes, the HPA axis is considered to be responsible for changes in winter time behavior as well [2]. Some species that are solitary and territorial during the breeding season are known to become more social during winter, and to construct communal nests [22,31,33,35,36]. This is often related to the seasonal decrease in gonadal steroid levels, e.g. testosterone in males [2,6].

The increased social tolerance and the social interactions in the overwintering population are considered to play an important role in the winter survival of many small rodents. The main benefit gained from aggregation seems to be social thermoregulation, as cold is one of the main stressors during winter. Huddling keeps the nest temperature higher, which is more energy efficient compared to individual nesting [26,29]. In Taiga voles (*Microtus xanthognathus*), foraging bouts are timed between individuals in a way that the nest is never left empty to prevent nest temperatures from dropping [34]. However, in case of scarce food resources the communal nesting creates an inevitable trade-off between energy gain and energy consumption [33]. Further, the degree of communal nesting seems to vary between species, years, habitats and winter characteristics [30,33] comprising incomplete understanding of the actual determinants of successful overwintering. Due to the nature of their overwintering environment, i.e. under the snow pack, the role of social interactions and behavior on winter survival in small winter-active ground-dwelling mammals is relatively little explored.

In order to define the impact and importance of behavior and social dynamics on overwintering survival in a rodent species, we performed a field enclosure experiment at the onset of winter. As a model species we used the bank vole (*Myodes glareolus*), one of the most common winter-active boreal rodent in Eurasia. Bank voles are short lived, granivorous-omnivorous small rodents. During the breeding season, from April-May to September, they are territorial. Female bank voles, like all *Myodes* females, defend their exclusive breeding territories, whereas the home ranges of males are larger and overlap with each other and with several females' territories [7]. However, it appears that during winter their social tolerance increases, and similar to many *Microtus* species they exploit communal winter nests [35,36]. Interestingly, females are reported to survive better over winter than males [20,35]. Their smaller body size, and thus, lower absolute energetic need is assumed to be a major factor behind this. In addition, it has been suggested by Ylönen et al. [37] that females with their better "social skills" form the core of winter aggregations and that this could play an important role in the overwintering success of the whole overwintering population. Based on an experiment on odor preference, also Ferkin & Seamon [38] suggested that overwintering groups of meadow voles (*Microtus pennsyvanicus*) might be female biased. It was shown that non-breeding meadow vole females preferred the odor of female conspecifics, whereas males showed no preference and displayed more antagonistic acts against other males than females did against female conspecifics. Thus, male-male aggressive interactions may preclude males from joining the same winter aggregation with each other. A tendency for aggressive behavior could be reflected in higher hormonal levels related to competitive ability and aggression, like testosterone, as well as high stress levels if there are many competing males present. Being isolated from communal nests would also mean higher energetic costs in terms of thermoregulation and thus, possibly increased stress levels caused by the cold. This could decrease the survival possibility of solitary overwintering individuals. However, maintaining testosterone levels high enough for breeding during winter could be beneficial, because winter breeding occurs occasionally in many small boreal rodent species [14,16,19]. As the winter mortality of small rodents is relatively high, trading off survival for reproduction may increase fitness.

To test the hypothesis of better winter survival of females, assess their role as initiators of winter aggregations and investigate the impact of population structure and hormonal status on winter time behavior and survival, we generated three different population types in semi-natural outdoor enclosures in late October: Female-biased population type (F), male-biased population type (M) and even-sex ratio population type (E). Spatial and temporal variation in the sex-ratio is relatively common in natural animal populations and can be caused by several factors depending on the species [32]. For example, mammalian predators such as weasels tend to kill more female than male voles, whereas males are more susceptible to avian predation [24]. Thus, the relative abundance of different predator species could locally lead to biased population sex-ratios.

To estimate social dynamics, we monitored space use of the voles and the degree of movement area overlap as an indicator of social tolerance and decreased level of aggression between individuals which could imply communal nesting. We also observed how the hormonal status of individuals affects their behavior and survival, and further, whether the population type (F, M or E) affects hormonal status. To do this we monitored corticosterone (stress) and testosterone levels in the form of fecal steroid metabolites. Stress was monitored in both sexes, but testosterone only in males.

We hypothesized that voles in female biased populations would survive best and express the highest social tolerance and the lowest stress levels. Male biased populations were expected to survive worst and have the highest stress levels due to high encounter probability and low tolerance between males. Also, if females are the ones maintaining the communal winter nests it is likely that the total number of communal nests or aggregations would be lower in male biased populations due to the shortage of females. Bank voles are suggested to aggregate in groups of 2–5 individuals, of which the majority are females and perhaps 1 to 2 males [36]. This could mean that some of the males are left out of the aggregations. If these surplus males attempt to join these winter nests, it could disturb the nesting and increase stress level also in females. Further, males with high levels of testosterone were hypothesized to express low survival. Testosterone is known to be immunosuppressive, and maintaining high testosterone level is energy consuming [2,23]. High testosterone would likely maintain social intolerance and aggression and probably lead to isolation from communal nests. This would expose the individual to cold stress.

Briefly, the aims of this experiment were to verify the supposed better winter survival of females compared to males, and to test how the population sex-ratio affects winter survival, behavior and physiology in bank voles.

2. Material and methods

2.1. Experimental animals

All animals used in this study (72 males and 72 females) were born in the laboratory during April-July 2012 at Konnevesi research station. One month before the actual experiment commenced, all voles were transferred to a greenhouse for acclimatizing to outdoor temperatures and light rhythms. All test animals were adults at this point in time. The greenhouse was not heated and the temperature in the greenhouse was similar to outdoors. Voles were housed separately in standard mouse cages ($43 \times 26 \times 15$ cm) with wood shavings and hay as bedding. Standard mice pellets (Lab for R36, Lantmännen) and water were provided ad libitum.