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Environmental modulation of same-sex affiliative behavior in female meadow voles (*Microtus pennsylvanicus*)

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HIGHLIGHTS

- We examined how winter conditions affect affiliation between female meadow voles.
- Females held under long or short days, 21 °C or 10 °C, food ad lib or restricted.
- Low temperature disrupted retention of social bonds in long, but not short, days.
- Winter-like conditions enhanced affiliative behavior between females.
- Preexisting social bonds did not preclude integration into new social groups.

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ABSTRACT

The effects of temperature and food availability on social bonds and group formation are poorly understood. Because seasonal transitions in female social behavior facilitate the assembly of winter groups in meadow voles, we explored the role of same-sex female associations in winter sociality. To examine the effects of winter typical environmental conditions on same-sex female affiliative behavior, paired female meadow voles were housed in varying combinations of day length, temperature, and food availability for 7 weeks and then tested for social preference. In short days (SDs), lower ambient temperature increased huddling with unfamiliar females without interfering with existing social bonds, whereas lower temperature disrupted the retention of bonds in long days (LDs). Mild food restriction with no discernible effects on body mass enhanced affiliative behavior in SDs, but not LDs. A second experiment examined the effects of sex and day length on the propensity to aggregate with unfamiliar same-sex voles. Compared to LD females and SD males, SD females spent more time in group huddles with unfamiliar voles and displayed no social preference. These outcomes indicate that winter-like conditions enhance affiliative behavior between females and that pre-existing social bonds do not preclude integration into new winter social groups. The adaptive value of these behaviors is discussed.

1. Introduction

The effects of abiotic environmental factors, such as food availability and ambient temperature, on social bonding and group formation remain largely uninvestigated [1]. Social behavior has been examined extensively from evolutionary and physiological perspectives [2,3], but the physiological ecology of social affiliation—that is, how ecological factors influence physiological regulation of affiliation—requires attention if we are to understand the adaptive value of affiliative behavior and its underlying physiological mediators [4].

Winter social species are ideal, but underutilized, models for exploring integrated environmental and physiological regulation of social behavior. The identifying characteristic of winter sociality, the seasonal transition between solitary life during the breeding season and group living during the nonbreeding season [5,6], allows for intraspecific comparisons of different social phenotypes. Because these comparisons are unaffected by confounds introduced by differences in evolutionary history, they are useful for ascertaining the adaptive value of social behavior within particular environmental settings. Winter sociality occurs in a diversity of taxa, including reptilian, avian, and insect groups [7–9], and is particularly common in rodent species [5,10].

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It is widely held that the greatest physical benefit of winter sociality is heat conservation achieved by huddling [5,6,10]. The beneficial effects of huddling under low ambient temperatures are well documented [11–15]. Wild mice housed in pairs survive exposure to temperatures well below 0 °C twice as long as those housed singly [15]. Other studies suggest that huddling decreases metabolic demand and that the benefits of huddling increase as ambient temperature decreases [11–15]. Winter huddling purportedly improves survival during a period when mortality rates can be quite high [more than 90% in meadow voles; 16] and influences the composition of the breeding population at winter's end [5]. Thus, winter sociality represents a potentially critical means of dealing with the challenges of winter environmental conditions. However, very few investigations examine the effects of environmental conditions on the social dynamics of huddling [10,17], leaving a number of questions unanswered. How do social bonds influence the choice of huddling partners? Do different partners provide different benefits? Under what conditions do huddling groups form, and do individuals actively select for certain group sizes or compositions based on environmental conditions? Addressing these questions can clarify not only the adaptive value of winter sociality, but the general principles underlying social grouping.

Winter sociality in the free-living meadow vole (*Microtus pennsylvanicus*) has been thoroughly described [reviewed in 18]. Female meadow voles transition from a summer-aggressive to a winter-affiliative phenotype, a change that can be replicated under laboratory conditions using photoperiod manipulations [19]. Winter phenotype females permit immigration, share nest sites, and engage in group territorial defense. Group members sleep together in clusters of 2–5 individuals, synchronize their activity patterns, avoid other group territories, and exhibit little intra-group aggression [18,20–24]. Immediately after winter, some females remain in same-sex dyads that dissolve over the course of the breeding season [25]; barring this exception, females are highly territorial and do not cohabitate with other adults during the spring and summer breeding period. Unlike females, male meadow voles exposed to short day lengths do not increase interactions with unfamiliar voles [26] or decrease aggression towards same-sex conspecifics [27].

Although most laboratory investigations focus on day length as the primary regulator of seasonality [28,29], seasonal variations in meadow vole social behavior likely are influenced by the combined effects of several abiotic factors that signal impending or immediate thermoregulatory challenge [30]. Winter grouping in free-living meadow voles is facultative and varies with several environmental factors, including ambient temperature and snowfall [5,6,31]. Density, quality, and distribution of food resources are also potential environmental regulators of social behavior, since food intake and the energetic demands of thermogenesis are strongly linked [6,10,22].

Because seasonal transitions in female affiliative behavior are a significant precursor to the formation of winter groups in meadow voles [22] and same-sex interactions have been described for both wild and captive female meadow voles [19,25,27], we designed two experiments to explore the role of female affiliations in winter sociality. Our aim was to address the question: do environmental factors that promote huddling as a means of energy conservation also affect social preferences and bonding? In Experiment 1, we examined the interactive effects of ambient temperature, food availability, and day length on same-sex affiliative behavior between female meadow voles. Because SD females spend more time than LD females huddling with unfamiliar voles [19], we hypothesized that female meadow voles in short versus long day lengths would use different forms of social thermoregulation to compensate for energy loss imposed by low temperatures and food restriction. Specifically, we predicted that SD females would increase social interaction with novel individuals, whereas LD females would only increase time spent huddling with familiar voles. We alternatively hypothesized that voles in both day lengths would primarily rely upon non-social means of coping with low temperatures and reduced food availability. We predicted that females would increase food intake or body mass [32] and that SD voles would develop a day length-induced reduction in energy requirements—a physiological adaptation that has been demonstrated in meadow voles [33]—without concurrent effects of temperature and food availability on affiliative preferences.

Some researchers have cautioned against assuming that all forms of social behavior are identically regulated. Equating the physiological mechanisms underlying social bonding with those that regulate social grouping is particularly common, although experimental assessments of this conjecture are limited in number [1,34]. Social bonding and group formation do not always occur concurrently, suggesting that distinctions in the regulation of grouping and bonding may exist [34]. Meadow voles have been extensively studied to investigate factors that influence social bonding, but not grouping behavior [2,34]. Thus, in Experiment 2, we assessed seasonal and sex differences in same-sex grouping behavior in meadow voles. Because free-living female meadow voles are winter social [5] and winter females display less aggression than winter males towards same-sex conspecifics [27], we hypothesized that SD females would display a greater tendency towards forming social groups than LD females and SD males. We predicted that LD females and SD males would retain their partner preference and spend little time with a group of novel same-sex conspecifics, whereas SD females would spend a greater proportion of their time with the group.

2. Methods

2.1. General colony maintenance

All voles were descendants of original stock generously provided by Michael Ferkin of the University of Memphis. Breeding pairs were co-housed under 21 ± 1 °C in LDs (14:10 light:dark cycle) in opaque plastic cages (48 × 25 × 15 cm), each containing pine bedding, cotton squares (Nestlets) for nest building, one breeder box, a paper nest tent, and one opaque refuge tube. Voles were provided tap water and food ad libitum (mouse chow no. 5015, Purina Mills, St. Louis, MO) and housed with onset of darkness at 17:00 PDT. Breeders were supplemented biweekly with lettuce and alfalfa.

2.2. Experiment 1: effects of winter-typical conditions on same-sex affiliation in females

2.2.1. Voles

Female pups were weaned at 18–20 days of age into same-sex pairs and housed as described above, but with two cotton squares per pair and no breeder box or nest tent. When females from two or more litters were weaned concurrently, non-sibling pairs were assembled; otherwise, pairs consisted of siblings. Animal care and experimental procedures were approved by the Animal Care and Use Committee of the University of California, Berkeley and conformed to USDA guidelines for the care and use of laboratory animals.

2.2.2. Experimental design and timeline

A full factorial design was employed that included 8 treatment groups with varying combinations of day length (SDs or LDs), ambient temperature (10 °C or 21 °C), and food availability (ad libitum or food restricted). The groups were: 1) LDs, food ad libitum, 10 °C (LDadlib10); 2) LDs, food restricted, 10 °C (LDfr10); 3) LDs, food ad libitum, 21 °C (LDadlib21); 4) LDs, food restricted, 21 °C (LDfr21); 5) SDadlib10; 6) SDfr10; 7) SDadlib21; and 8) SDfr21 ($n = 12$ female pairs/group). This design allowed for examination of the independent and interactive effects of day length, temperature, and food availability on huddling behavior and social preference.

Beginning at 30–45 days of age, females were assessed for food intake (by pair; $n = 12$ pairs/group) and body mass (by individual; $n = 24$ females/group) at weekly intervals for 8 wks. After the first