



Stress impairs new but not established relationships in seasonally social voles



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ABSTRACT

Affiliative social relationships are impacted by stressors and can shape responses to stress. However, the effects of stress on social relationships in different contexts are not well understood. Meadow voles provide an opportunity to study these effects on peer relationships outside of a reproductive context. In winter months, female meadow voles cohabit with peers of both sexes, and social huddling is facilitated by exposure to short, winter-like day lengths in the lab. We investigated the role of stress and corticosterone (cort) levels in social behavior in short day-housed female meadow voles. A brief forced swim elevated cort levels, and we assessed the effects of this stressor on new and established relationships between females. In pairs formed following exposure to swim stress, the stressor significantly reduced the fraction of huddling time subjects spent with a familiar partner. Swim stress did not affect partner preferences in pairs established prior to the stressor. Finally, we examined fecal glucocorticoid metabolite levels via immunoassay in voles housed under short day (10 h light) versus long day (14 h light) conditions and detected higher glucocorticoid levels in long day-housed voles. These findings support a role for stress regulation in the formation of social relationships in female meadow voles, and are consistent with a potential role for seasonal variation in cort in the behavioral transition from solitary to social. Together they highlight the importance of stress and possibly glucocorticoid signaling for social behavior.

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Introduction

Social relationships are important for many aspects of life, from reproduction to the provision of emotional support and more direct physical survival benefits. The need for – and targets of – social behaviors also change across the lifespan (Anacker and Beery, 2013). In the wild, animals alter many behaviors with changing seasons (Prendergast et al., 2002). Female meadow voles (*Microtus pennsylvanicus*) transition from solitary and aggressive during the summer reproductive season to communally nesting and affiliative towards other specific individuals in winter. These changes coincide with changes in the regulation of corticosterone (cort) – a glucocorticoid hormone important in the stress response – providing an opportunity to examine the role of stress and corticosterone exposure in social relationships.

Stress and social behaviors affect each other in a variety of ways, which are dependent on the type of stressor, context, and sex of the individual, among other factors (reviewed in Beery and Kaufer, 2015;

Hostetler and Ryabinin, 2013). In rats, social defeat stress decreased subsequent social affiliation (Meerlo et al., 1996), while a non-social stressor increased huddling in groups, perhaps as a defense mechanism (Bowen et al., 2012). Affiliation can also moderate the response to stress. Female prairie voles (*Microtus ochrogaster*) exposed to restraint stress showed elevated levels of cort and anxiety-like behavior when isolated following stress, but showed no rise in signs of stress when recovering with a male partner. Active social behavior from the partner, such as allogrooming, is presumed to be an important aspect of these social buffering effects of social partner presence following stress, and is mediated through hypothalamic oxytocin release (Smith and Wang, 2014).

Studies of the development of male–female bonds in socially monogamous prairie voles have revealed declines in cort concentration in both females and males upon pairing with an unfamiliar individual of the opposite sex (DeVries et al., 1995; DeVries et al., 1997). However, the consequences of stress and cort exposure for pair-bonding are sexually dimorphic: development of male partner preferences can be enhanced by exposure to a stressor (forced swim) or an injection of cort, and is inhibited by prevention of the physiological stress response via adrenalectomy (DeVries et al., 1996). In females, in striking contrast, development of a partner preference for a mate is reduced following the rise in cort due to stress or cort injection, while adrenalectomy enhances

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the preference (DeVries et al., 1995; DeVries et al., 1996). The timing of the changes in cort levels may be crucial to the development of the pair bond, as the decrease in cort early in cohabitation appears to be important for females to develop a bond, while the relative increase and return to baseline levels of cort later in cohabitation may be key for males to develop a bond (DeVries et al., 2007). Both meadow and prairie voles have unusually high cort levels — about 3–6 times higher than lab mice, rats, and montane voles (Boonstra and Boag, 1992; Seabloom, 1985; Taymans et al., 1997). The higher basal levels of cort are likely due to target tissue glucocorticoid resistance as demonstrated in prairie voles (Taymans et al., 1997), but changes in cort levels are nonetheless capable of affecting behavior in these voles, as described above.

While the role of stress in the development of mate-pair bonds has been well studied in socially monogamous prairie voles, the potential roles of stress and glucocorticoids in same-sex social affiliation remain largely uninvestigated. Same-sex relationships in female meadow voles allow for the study of neurobiological factors supporting the winter transition to social tolerance and affiliation. At an evolutionary level, communal nesting is likely driven by the physical benefits of energy conservation in group huddles; meadow voles do not hibernate, and social huddling enhances survival through the winter (Madison, 1984; West and Dublin, 1984). Nonetheless, day length in the absence of temperature change is a sufficient cue to promote the transition to social huddling in the laboratory, although temperature, food availability, and cohabitation timing and duration also shape social behavior of meadow voles (Beery et al., 2008; Beery et al., 2009; Ondrasek et al., 2015; Parker and Lee, 2003). After a period of cohabitation, females express a preference for huddling more with the partner they have cohabited with than a stranger female, regardless of whether they are siblings or unrelated (Beery et al., 2009). Additional factors that change seasonally and may contribute to this transition include levels of steroid hormones such as estradiol, and oxytocin receptor and corticotropin releasing factor receptor densities and distributions (Beery et al., 2008; Beery et al., 2014; Beery and Zucker, 2010; Ferkin and Gorman, 1992; Ferkin and Zucker, 1991).

Glucocorticoids are known to change seasonally in many species including meadow voles (Galea and McEwen, 1999; Pyter et al., 2005; Seabloom, 1985), and may contribute to seasonal changes in social behavior. Evidence for the magnitude and direction of seasonal changes in corticosterone is mixed, in part because changes are likely related to the sex and reproductive status of the individual; pregnant and lactating female meadow voles have the highest corticosterone levels (Boonstra and Boag, 1992). We hypothesized that higher cort levels, such as those seen during reproduction, are not conducive to affiliative behavior, and that lower cort levels in the winter are permissive of more affiliative behavior. We examined the effects of stress on affiliation in female meadow voles housed under short day lengths, as well as effects of stress on cort. We hypothesized that female meadow voles would show reduced formation of same-sex partner preferences following a stressor that raised cort levels, as with opposite-sex partner preferences in female prairie voles. We also examined whether transient stress would affect the expression of partner preferences in pre-existing pairs. We further predicted that voles housed under long day lengths comparable to the breeding season would display increased cort levels compared to those housed under short day lengths, consistent with seasonal variation in behavior. These studies provide insight into the biological mechanisms and environmental factors that impact changes in social behavior.

Methods

Meadow voles were bred locally, with periodic outbreeding to wild-caught individuals trapped within 10 miles of Smith College in Hampshire County, MA. Breeding pairs were housed under a 14:10 light:dark cycle (long day; LD) with lights off at 5 pm EST. Offspring were weaned at postnatal day 19 ± 1 . Females used for these experiments were

housed either under LD conditions or a 10:14 light:dark cycle (short day; SD) from weaning. All procedures were approved by the Smith College Institutional Animal Care and Use Committee and conformed to national guidelines.

Experiment 1: effect of acute stress on corticosterone levels

To test whether acute swim stress affects corticosterone levels, subjects were exposed to a forced swim test (described below) and rapidly decapitated for collection of plasma at one of six times after the stressor. Adult female meadow voles 103 ± 18 days old that had previously been used as stimulus animals in behavioral tests were used in this study, at least three days following any prior testing. Blood was collected from subjects at: 30 min ($n = 9$ swim, 8 control), 1 h ($n = 7$ swim, 6 control), 3 h ($n = 6$ swim, 5 control), 6 h ($n = 6$ swim, 6 control), 12 h ($n = 5$ swim, 5 control), or 24 h ($n = 5$ swim, 5 control) following the end of the swim. Subjects experienced the 3-minute swim stress three hours after the start of the light phase of the day, within a 15-minute range. Subjects were returned to their home cages following the swim and continued to be housed alone until the time of blood collection. “No swim” control subjects were not handled in this time period.

Experiment 2: effect of acute stress on partner preference formation

To test the effects of acute stress on partner preference formation, adult female voles ($n = 16$ per group, 72 ± 9 days old, housed under SD conditions) were exposed to the forced swim test (swim stress), or received no stress (no swim control). All subjects were then moved into a new cage for pairing with a novel female partner. Partners in the swim group were exposed to swim stress immediately prior to pairing. Focal voles were distinguished from partners by a small patch of shaved fur. All pairs cohabitated for 24 h following swim or control treatment, after which they were tested in the partner preference (PP) test (PPT).

Experiment 3: effect of acute stress on partner preference in established relationships

Female subjects were paired with same-sex littermates from weaning until the time of the experiment ($n = 10$ per group, 75 ± 5 days old, housed under SD conditions), when they were given the forced swim stress and returned to their home cage. The PPT was conducted following 2 h of cohabitation.

Experiment 4: effect of day length on corticosterone levels

To test the effect of day length on corticosterone, glucocorticoid metabolite levels were analyzed in feces of LD and SD females (83 ± 55 days old). Approximately 20 fecal boli were collected from the home cage 24 h following a cage change, 6–8 h following the start of the light cycle, while the voles were kept in a separate holding cage. The boli were frozen in foil on dry ice and stored at -80°C . Hormone levels were analyzed by an enzyme-linked immunosorbent assay (ELISA, see below for details).

Forced swim stressor

The swim stress was induced using a Porsolt Forced Swim Test Apparatus (#60160, Stoelting Co., Wood Dale, IL, USA), a clear cylinder with a diameter of 20 cm and height of 45 cm, with room temperature tap water filled to a height of 18 cm. Each vole was moved from its home cage directly into the water where it remained for 3 min, until it was removed from the water using a mesh strainer, and dried briefly with a towel prior to being returned to the home cage (experiments 1 and 3) or placed in a clean cage (experiment 2). Voles exhibited active swimming, pawing at the sides of the apparatus, as well as floating

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