Social Motivation and Residential Style in Prairie and Meadow Voles

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Abstract: The residential style of rodents varies across and within species from colonial to solitary and territorial [1]. A mechanism that supports this behavioral distinction might be differential levels of social motivation rather than explicit species-typical social behavior. Accordingly, socially motivated animals learn seeking behavior that leads to a colonial residential pattern and socially unmotivated animals do not learn this behavior and remain solitary. The present experiments test this hypothesis by measuring social motivation in a gregarious social species of vole, the prairie vole, and in a solitary species, the meadow vole. Although their explicit social behavior was similar, Prairie voles readily learned to perform an instrumental response for access to a target vole while meadow voles did not. Neither the estrus status nor the sex of the target affected instrumental responding in either species. In sum, differential social motivation may contribute to distinctive residential patterns in rodents.

Keywords: Prairie vole, meadow vole, operant conditioning, instrumental conditioning, social behavior, sexual behavior, estrogen, oxytocin, social motivation, sexual motivation.

INTRODUCTION

A growing body of evidence indicates that the hormones vasopressin and oxytocin mediate the emergence of a variety of social behaviors in rodents and other species [2]. In the female rodent in particular, the role of oxytocin (OT) has been experimentally studied by direct manipulation of OT levels through infusion [3], knock-out procedure [1], and OTR induction by viral vector [4]. The role of OT in social behavior has also been studied indirectly by observing the distribution of OTR receptors in specific brain areas differentially associated with distinctive patterns of social behavior [5]. Very useful comparisons have been provided by the case of voles, which occur in species that differ quite considerably in their social behavior.

The social behaviors that have received greatest attention are pair bonding[6] and partner preference [7], alloparenting [8], various measures of social preference (Bolles, Rapp [10]; Eliasson, 1975; [11-15], Pavlovian conditioning based on social exposure [16], cognitive functions such as social memory [17], and learned responses rewarded by social contact [1,11,18].

Of the above, only learned responses may be regarded as providing a measure of true social motivation. Pair-bonding, partner preference, and alloparenting behavior are essentially reflexive and though their occurrence may be conditional on hormone induced drive states, they do not reflect the operation of the "incentive" effect [19] of a rewarding stimulus. Rather, they are species-typical behavior forms that immediately follow presentation of an "instinctive" eliciting social stimulus, even on the first presentation of that stimulus.

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It is the incentive value of rewarding stimuli that allows them to cause learned or instrumental behavior to grow in strength when followed by a rewarding stimulus. This incentive property of the social stimulus allows animals to learn any response within its capabilities. In the instrumental conditioning paradigm, social motivation is expressed as the strength of the learned response and is a joint function of the level of drive (social deprivation) and incentive (social access) [20]. It is this paradigm for the study of social motivation that is the focus of the present work.

Studies that demonstrate instrumental behavior rewarded by social contact can be said to identify social motivation. Social motivation in this case is a state that is presumed to enable a social stimulus to effectively reinforce or reward an instrumental response that precedes it. Unlike reflexive behavior, the subject responds in the absence of the social stimulus as a result of past experience with the response-reinforcer succession. The present work seeks to expand our understanding of the neurobiological basis of social motivation.

Although this conception of social motivation is well established in the literature on learning and motivation, it is worth noting here that the term sexual reinforcement has also been used to refer to the Pavlovian effects of sexual stimuli [21]. In the Conditioned Place Preference procedure, subjects are exposed to a Pavlovian pairing of a particular place with a putative sexual stimulus and are then allowed to "choose" between the paired place and an unpaired place. Although stable preferences emerge from this procedure as indicated by greater amount of time spent in one place than the other, this does not assure that the behavior that produces this outcome is instrumental in character. It may as well be that the instrumental choosing is random but that once the subject

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arrives at a place that is associated with a sexual stimulus, it remains in the proximity of that conditioned place stimulus, just as it would the original eliciting stimulus with which it was paired. Thus, it cannot be assured that this procedure measures instrumental behavior, and by extension, sexual motivation.

Another method of studying sexual and social motivation is to test the preference shown by subjects when presented the opportunity to approach alternative target animals [22]. Although these data suggest that preference between targets can be modified by hormonal and genetic manipulations, it remains problematic that a preference, by itself, does not distinguish a motivation to approach a target animal from an aversion to the alternative target. Thus, a preference between targets does not unambiguously demonstrate social motivation.

Matthews *et al*. [1] have shown that female mice will respond for access to a conspecific at persistent rates regardless of the sex of the target mouse and regardless of whether the female mouse is in estrus or diestrus (as manipulated in ovariectomized females with estradiol and sham implants). Although females' instrumental response rates for access to a conspecific were unaffected by sexual motivation, response rates were shown to be sensitive to deprivation of social contact in their residential environments. Parallel manipulations were performed with male mice of the same strain and the results were in close alignment with the females [23]. Further, instrumental responding in females for social access is reduced by atosiban blockade of oxytocin receptors. The clear implication of this result is that social stimuli motivated new learning in mice but sexual stimuli did not. Sexual stimuli seemed to affect sexual behavior through elicitation of reflexive sexual behaviors but did not modulate social motivation.

A potential application of the notion of social motivation is the phenomenon of colonial verses solitary residential patterns [9, 17, 24]. One way to explain the fact that animals sometimes live in social groups and sometimes not, is that social animals are socially motivated. That is, social stimuli are rewarding for these animals and they therefore will perform a variety of learned behaviors that lead to increased social contact. Solitary animals may be much less socially motivated and so they do not learn and perform behaviors that result in social contact. The work presented here attempts to show that social motivation may be operative in animals living in colonies but not in animals adopting a more solitary style.

Some species of the genus Microtus have been studied in recent years because of the various ways in which species differ in social behavior. In addition to varying levels of pair bonding, partner preference, and alloparenting, prairie and meadow voles differ in residential style. Female prairie voles live socially in colonies, particularly in the fall [25], and meadow voles live in territorially defined isolation[26]. If, as reasoned above, social style derives from differential responsiveness to social reward, then it would follow that female prairie voles on a summer diurnal cycle would be responsive to social reward and meadow voles would not. The present studies provide this comparison.

1.1. Experiment 1

Matthews *et al*. [1] have reported a procedure for studying sexual and social motivation in mice that involves training the subject to make a traditional instrumental response, a bar press or touch, reinforced by a period of exposure to a target mouse. This method requires the subject to respond in the absence of the target mouse for a consequent access to the target. Accordingly, the initiation of responding can be said to be mediated by a motivational state rather than expressed as a reflexive response to a conditioned or unconditioned stimulus. Further, the rate of responding provides a measure of the effective level of motivation and can be used to study the effects of various parameters of sexual and social motivation. The parameters manipulated in the Matthews *et al*. [1] study were the level of blood estradiol in the female (corresponding to estrus and diestrus) and the sex of the target subject. Because both mice and prairie voles are gregarious and live in a colonial residential style, it is expected that like mice, voles, particularly female voles [27], will respond persistently for access to a target mouse but response rates will not vary as a function of either estradiol level or the sex of the target mouse. It is expected, however, that like mice, voles will exhibit appropriate sexual behavior in response to the level of estradiol and the sex of the target mouse**.**

1.2. Method

1.2.1. Participants

Twenty one prairie voles were used in this experiment; 19 females and 2 males. The voles were derived from a wild-caught colony and were laboratory reared. After weaning at 20-21 days, the animals were housed in individual cages (28 x 28 x 17 cm) with Bed-o'cobs bedding to a depth of 8 cm to allow tunneling. The animals were provided ad libitum water and rabbit LabDiet. The room was maintained on a reversed 12:12 hr day-night cycle. At approximately 3 months of age, the females were surgically ovariectomized under Isoflurane inhalation anesthetic. After nine days of behavioral testing and again after 7 additional days of testing, the 14 female subjects were subcutaneously implanted under light Isoflurane anesthesia with 1.3 x 0.2 mm pellets containing either 0.5 mg of estradiol benzoate or no drug (placebos). Both drug and placebo pellets were supplied by Innovative Research of America, Sarasota, Florida. The males were sexually experienced and 6 months of age or greater. All procedures were reviewed and approved by the New York University Institutional Animal Care and Use Committee.

1.2.2. Apparatus

Subjects were tested in their home cages in a darkened laboratory room with bedding reduced to a 1-cm layer on the cage floor. After the session, the removed bedding was returned to the cage. The test area was illuminated by a 75-w red incandescent light bulb suspended 1 m above the test chamber floor.

Release and sequestering of the target animal in the test chamber was accomplished by the use of a 25 X 12.5 X 12.5 cm black plastic container which was open at the top and bottom. At the beginning of the session, the target vole was placed inside target box through the open top of the box

which was tall enough to prevent the target animal from escaping. The target box was positioned in the left rear corner of the test chamber. To begin the access period, the experimenter lifted the target box releasing the target animal through the open bottom of the target box. During the access period, the target box was removed from the test chamber. At the end of the access period, the experimenter placed the target box over the target animal and slid the target box back to its starting position in the left rear corner of the test chamber.

The response detection device was a 6 x 1 x 0.5 cm metal bar affixed to the side of the target box 6 cm from the cage floor. A Faraday Switches (Littleton, CO) model FJ3W capacitance detector sensed the subject's contact with the bar. A computer controlled experimental events, generated auditory stimuli, and recorded instrumental responses and experimenter behavior coding.

1.2.3. Procedure

1.2.3.1. Trial Procedure

Behavior test sessions were 30 min in duration with the number of trials depending on the rate of responding by the subject. Test sessions were conducted daily. A typical trial was initiated by the experimenter pressing a handswitch to start a response timing program. The first subject instrumental response (training, testing) or the elapse of a programmed inter-reinforcer interval (pre-training) was signaled by a 3-s, 4000-hz, 65-db tone. At the onset of the tone, the experimenter initiated the 45-s access period by lifting the target box from the test chamber releasing the target animal into the test chamber. After 45 seconds, a 1-s, 50-hz, 50-db signal prompted the experimenter to cover the target animal with the target box and return the box to its position in the left rear quadrant of the test chamber.

1.2.3.2. Behavior Coding

During the 45-s access periods in the two testing phases, the experimenter used the computer keyboard to record observations of six behavior categories. On average, behavior was coded for about 10 minutes per session. The behavior categories were: Prosocial: subject nosing or sidling up to head or body of target; Mount: target approaches subject from rear, grasps subject around waist with forelegs; Lordosis: during mounting, subject arches back, averts tail, and bends forelegs lowering head [28]; Intromission; thrusting followed by sustained penetration; Threat/reject: rears on hind legs and faces target animal; Fight: subject and Target make abrupt physical contact while vocalizing.

The behavior classes during the access period were recorded by the experimenters during each test session. Experimenters were assigned uniformly to all subject, target, and treatment combinations. Using the Intra-class Correlation method [29], it was determined that the level of agreement among raters was extremely high, ICC = .961, $p < .001$.

1.2.3.3. Training

Training sessions began 4 days following the ovariectomy surgeries. For the first two days of training (Pre-training) the subjects were not required to respond nor were their responses effective. Instead, the 3-s reinforcer signal that began the access period was programmed on a random-interval schedule in which the probability of a signal was 1/30 in each second up to a maximum of 90 s. Thus the mean latency of the signal was 30 s. The purpose of this phase was to establish the signal as a conditioned reinforcer for the access period. For the following 7 days (Training), a subject instrumental response was required to initiate the reinforcer signal.

In Pre-training and Training, all subjects were exposed to all four target animals, two females and two males, in a counterbalanced order.

1.2.3.4. Testing

On the day following Training, subjects were divided into two groups matched for their response rates at the end of the training period. One group received estradiol pellet implants and the other received placebo implants.

Both groups of subjects were tested daily for 7 days (Test I) with each subject exposed to each target in a counterbalanced order. Pilot work indicated that the effectiveness of the estradiol implants in eliciting sexual receptiveness dissipated in about 7 days.

On the day following the last day of Test I, subjects were reimplanted with estradiol and placebos, but with the assignments reversed so that the subjects that originally had estradiol implants received placebo implants and vice-versa.

One day following reimplantation, Test II began and continued for another seven days. Again, all subjects were exposed to all target animals in a counterbalanced order.

1.3. Results

1.3.1. Training

All but three of the subjects reached a criterion of 10 responses per session within the seven training days following pre-training. One had a response rate slightly below 10 responses per session but was allowed to continue in the experiment. This subject's response rate remained low but steady.

1.3.2. Test Conditions

The effects of the two major variables in this study, estradiol replacement level or the sex of the target animal are shown in Fig. (**1**). A two-way ANOVA for repeated measures clearly confirmed that neither the estradiol manipulation ($F(1,13) = 1.08$, n.s.) nor the Target Sex ($F(1,13) = 0.89$, n.s.) nor an interaction effect ($F(1,13) = 0.14$, n.s.) were significant.

Although there was no effect of the estradiol manipulation on instrumental response rate, estradiol did have the predicted effect on elicited sexual behavior. As shown in Fig. (**2**), sexual behavior including mounting, lordosis, and intromission occurred only with male targets but, more to the point, these behaviors together occurred significantly more often when the subjects had estradiol replacement than when they did not ($t(13) = 2.66$, $p < .02$, matched sample test).

The effect of estradiol replacement was also not selective to social behavior. Looking at prosocial behavior as shown in Fig. (**3**), it can be seen that with both male and female

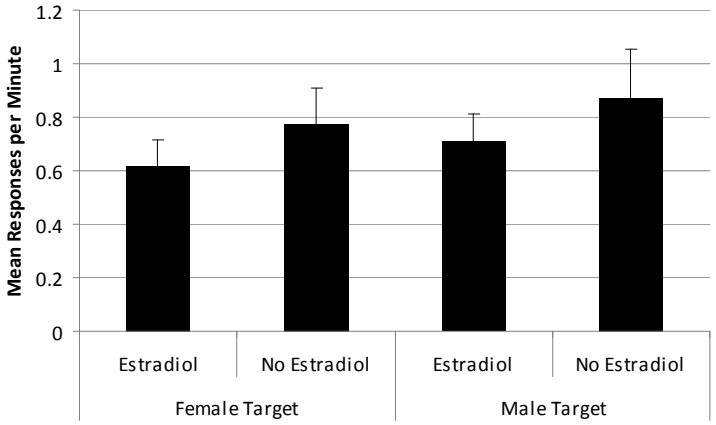

Fig. (1). Mean operant responses per minute over all subjects and test sessions are shown for each treatment combination with error bars representing the standard error of the mean.

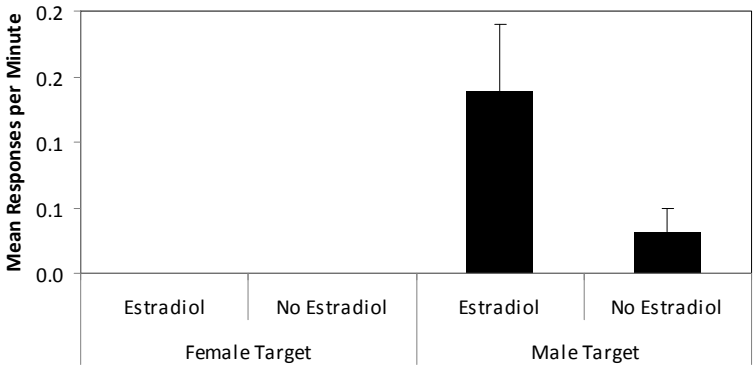

Fig. (2). The mean rate of the sum of the Mount, Lordosis, and Intromission behavior classes per minute are shown for each treatment combination. Error bars indicate the standard error of the mean.

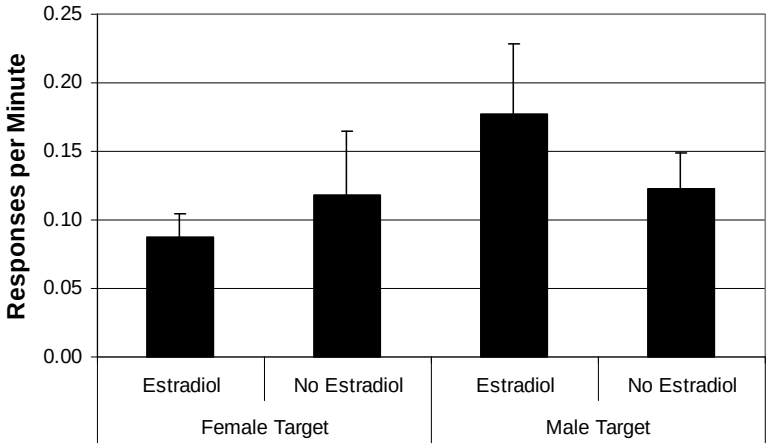

Fig. (3). Mean instances of prosocial behavior per minute over all subjects and test sessions for each treatment combination. Bars represent responses for subject Estradiol and No Estradiol conditions responding for male and female targets. Error bars represent the standard error of the mean.

targets, there was no difference between the subjects with and without estradiol replacement ($F(1,13) = 1.64$, n.s.). Although there was some indication that the sex of the target animal might have mattered, it too was not significant ($F(1,13) = 3.77$, $p < .07$). The interaction was also not significant ($F(1,13) = 1.45$; n.s.).

Agonistic behavior too, was not influenced by estradiol replacement. Combining fight and threat behavior, neither estradiol replacement ($F(1,13) = 0.13$; n.s.) nor target sex ($F(1,13) = 0.73$; n.s.) produced significant effects. Interestingly, however when fighting was treated alone, a strongly significant effect of target sex emerged ($F(1,13) = 8.58$. $p < .01$), with fighting between females much higher than fighting between the female subjects and the male targets (Fig. **4**). Again, the estradiol effect ($F(1,13) = 0.13$), and the interaction ($F(1,13) = 0.41$) were not significant.

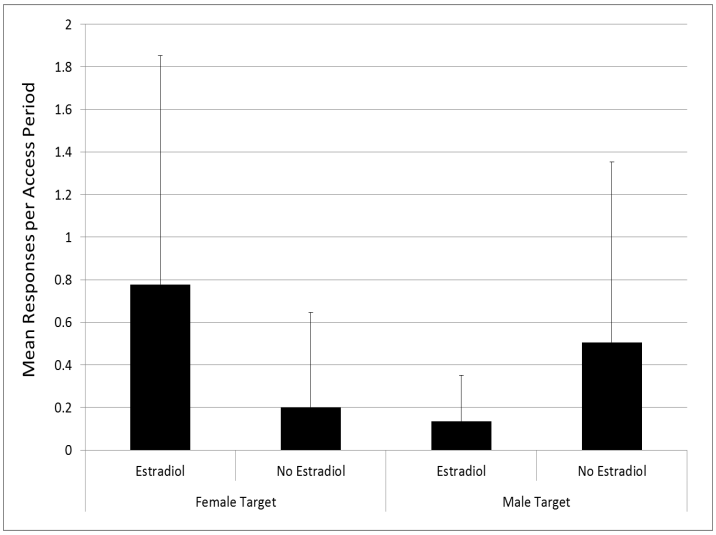

Fig. (4). Mean instances of fighting behavior per minute over all subjects and test sessions for each treatment combination. Bars represent responses for subject Estradiol and No Estradiol conditions responding for male and female targets. Error bars represent the standard error of the mean.

1.4. Discussion

The principal results of this experiment confirm two central results seen in comparable procedures with Swiss Webster mice [1]. First, in neither mice nor prairie voles did estradiol replacement or the sex of the target animal significantly affect instrumental response rate for access to a target conspecific. Second, in both mice and prairie voles, the estradiol replacement clearly induced sexual behavior with male targets. Thus, in both studies it has been shown that while estradiol replacement is sufficient to induce species typical sexual responses, it does not appear that this heightened sexual responsiveness has any influence on the reward value of social contact. This result is entirely consistent with the interpretation that the motivation for social contact is not sexual in nature, but rather is probably more essentially social in character.

Although estrogen is known to be responsible for triggering the production of the social hormone oxytocin [24], it does not appear that estrogen level has any effect on prosocial behavior. It should be acknowledged, however, that the estrogen levels were not deficient long enough after the ovariectomy to reduce oxytocin levels so that an indirect suppression effect of estradiol replacement on prosocial behavior would be seen.

The elevated levels of fighting seen between the female subjects and targets, regardless of estradiol replacement level confirms observations of aggressive behavior between female prairie voles regardless of hormonal status [30]. Although they did not report comparable measures between males or between males and females, the indifference to estradiol levels suggests that this aggression may be more related to territoriality than reproductive or parental motivations.

2.1. Experiment 2

The primary reason for repeating the Matthews *et al*. [1] procedure with prairie voles was to provide a test of the hypothesis that the dominance of social motivation is related to the social residential pattern of these species. In the following experiment, this notion will be tested by comparing the prairie voles to the meadow voles which, during summer months (long light period) are relatively territorial and do not gather in a colonial residential pattern.

2.2. Methods

2.2.1. Participants

Ten meadow voles derived from wild-caught stock were used in this experiment; eight females and two males. The voles were laboratory reared and treated in every way identically to those in the previous experiment with two exceptions. On the basis of pilot work, it was determined that a higher concentration of estradiol in the implanted pellets was necessary to accomplish a comparable degree of receptiveness in female subjects. Second, in order to assure that the solitary tendency in the meadow voles was comparable in the strength to the affiliative tendency in the prairie voles, the day-night cycle was 15:9 hrs to approximate a summer period during which solitary territoriality peaks in the meadow vole [17, 31].

2.2.2. Apparatus

The apparatus for this experiment was identical to that described for the Experiment 1.

2.2.3 Procedure

The procedure for this experiment was identical to Experiment 1.

2.3. Results

Because meadow voles are described as solitary during the long daylight hours phase of the calendar [26], it was expected that social contact during the access period would not function as a reinforcer for instrumental responding. During initial training of the 18 prairie vole subjects in Experiment 1, three did not reach a criterion of 10 instrumental responses per session during any of the 7 training sessions. Of the 6 meadow voles exposed to the same training procedure, none met the same criterion.

Fig. (**5**) shows the mean response rates for the prairie and meadow voles over the last four days of acquisition. meadow voles rates were significantly lower, $t(10) = 7.14$; $p < .001$.

Despite this difference in rate of instrumental responding, there were no differences in the coded social behaviors between prairie and meadow voles. Fig. (**6**) shows the mean rates of the coded social behaviors for the prairie and meadow voles during the two test periods. Although the meadow voles rates of prosocial behavior were somewhat higher than for the prairie voles, the difference was not statistically significant. None of the other comparisons approached significance. Sexual behavior in the meadow voles was negligible and did not warrant a statistical comparison.

Neither the estradiol ($F(1,5) = 3.55$, n.s.) nor the target sex ($F(1,5) = 0.23$, n.s.) manipulations significantly affected instrumental behavior. The same was true for prosocial behavior ($F(1,5) = 0.09$, n.s.), Target Sex ($F(1,5) = 3.20$, n.s.), and agonistic behavior ($F(1,5) = .02$, n.s.). Finally, with the exception of one session in which some mounting was shown by one male target, no sexual behavior was observed in the 72 test sessions.

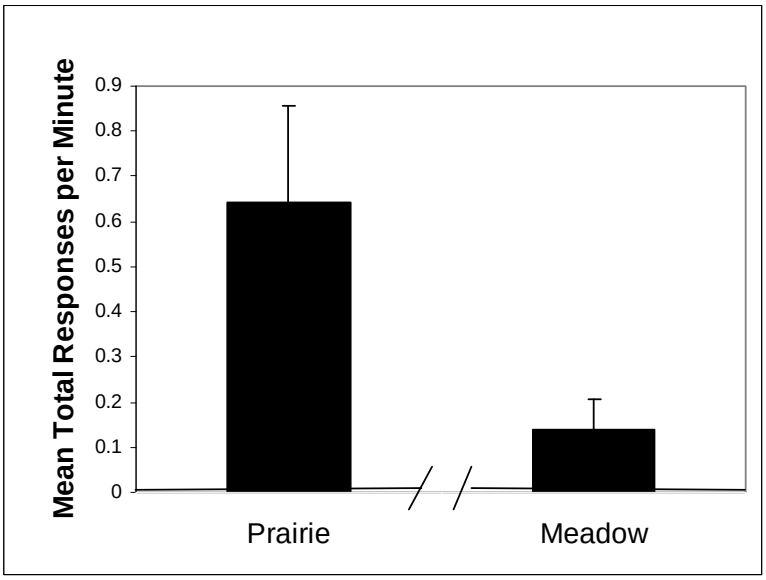

Fig. (5). Mean responses per minute over all subjects during the last four days of training for Prairie and Meadow Voles. Error bars represent the standard error of the mean.

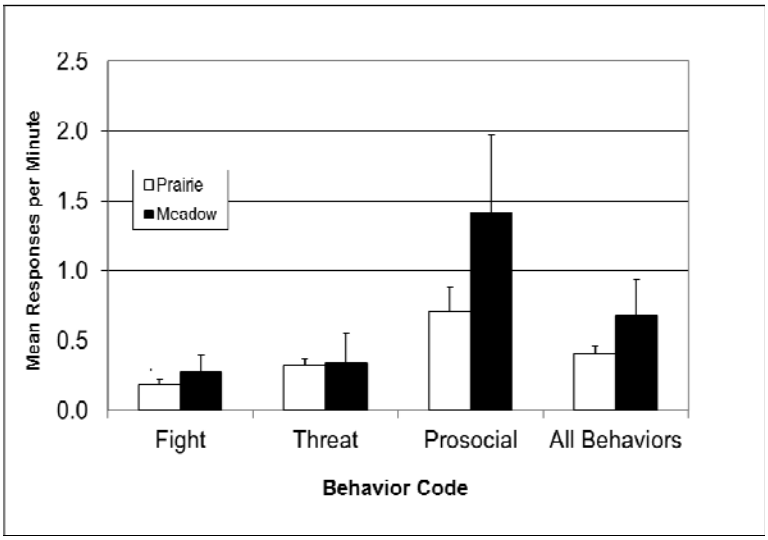

Fig. (6). Mean responses per minute across all test conditions and sessions for each behavior code and for Prairie and Meadow voles. Error bars represent the standard error of the mean.

DISCUSSION

It was expected that because meadow voles have a more solitary residential pattern, they may also be less motivated by access to a conspecific. Indeed, as the initial training procedure showed, there was virtually no evidence that access to a conspecific had any reward value whatsoever for meadow voles in territorial mode. This, however, was not because these animals lack social behavior. In fact, it appeared that their overall level of prosocial behavior during the test phases was, if anything, slightly more frequent than seen with the prairie voles. Thus, the distinction between the prairie and meadow voles that may be most instrumental in determining their residential style is their motivation for social contact.

A reservation that could undermine the above conclusion is that while the preparations for the learning of the operant response was identical for the two species, differences in their performance may result from their differential sensitivity to some other aspect of the learning paradigm than the motivational strength of the potential social reinforce. For example, the social motivation of meadow voles may actually be identical to that of prairie voles but their cognitive capacity to appreciate the reinforcement contingency is less. This is, of course, quite possible but unfortunately it cannot be experimentally demonstrated. Testing the learning speed of the two species with a different reinforcer, such as food, might show that the meadow voles were indeed less responsive to a positive reinforcement contingency. But this could not be used to undermine our interpretation of the current result because it could as well be that food, like social contact, is a weaker reinforcer for meadow voles. In the end, we must trust to the vast body of literature that shows that organisms across the animal kingdom are broadly responsive to immediate reinforcement contingencies when provided with an effective reinforcer. Likewise, we should trust to the equally large body of literature that shows that motivational processes are highly specific to species.

In sum, the proposition that residential pattern in rodents may be in large part attributable to differential levels of social motivation in species that show distinctive residential patterns is supported. On a physiological level, it has been demonstrated already that these species differ in the distribution of oxytocin receptors in a way that is consistent with this interpretation [17], the colonial residential style is mediated by high levels of social motivation, and, therefore, a strong reward value of social stimuli, it would be expected that there would be a strong association between the social hormone oxytocin and neural circuitry associated with reward. Indeed, as has been shown, oxytocin receptors are concentrated in the Nucleus Accumbens and other regions associated with the dopaminergic reward system. Correspondingly, low levels of oxytocin receptors are found in the reward areas in the meadow vole [3, 32].This convergence of results encourages an interpretation of residential style as being the product in part of differential distribution of oxytocin receptors.

While the neural correlates of residential style support the conclusion that a behavioral mechanism is responsible for the observed species difference in affinity, this result does not independently point to social motivation as the causal mechanism. Rather, the identification of social motivation as the primary behavioral factor in the emergence of differential affinity rests more squarely on the observation here that the species did indeed respond differently to tests of motivation but did not differ in the type and frequency of pro-social behavior. Thus, these data favor a motivational rather than explicit behavioral interpretation of residential style.

ACKNOWLEDGEMENTS

The authors wish to thank C. Sue Carter, University of Illinois, Chicago and Robert S Zucker, University of California, Berkeley, for supplying the prairie and meadow voles respectively. We also thank Phillip Caffrey, Brian Delaney, Maeve Gerety, Alexander Hogan, Meghana Komati, Blair March, Lauren Morales, and Vaughan Wilkins for assistance in the conduct of the experiment and Vikki Papadouka for assistance with preparation of the manuscript.

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Received: August 06, 2012 Accepted: September 01, 2012