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# PRECOPULATORY FIGHTING AND OTHER AGGRESSIVE INTERACTIONS DURING MATING ENCOUNTERS IN THE CORN MOUSE, *Calomys musculinus* (MURIDAE, SIGMODONTINAE)

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**ABSTRACT**: Agonistic interactions and receptivity of females during mating encounters in the corn mouse (*Calomys musculinus*) were studied. Twenty nine couples were observed for copulatory behavior during postpartum estrus; 14 of them were composed of males and females that had bred together at least once (familiar male group), and 15 were composed of a male and a female each with reproductive experience, but were unknown to each other (strange male group). No significant differences between the familiar male and the strange male group were found in either the mount latency or the intromission latency. The strange male group showed a trend to have higher mount and intromission frequencies, both at the first and the second ejaculatory series, although some of these differences did not reach statistical significance. Also, males in the strange male group showed significantly higher ejaculatory thrust frequencies, both at the first and the second ejaculatory series, than males in the familiar male group. The post-ejaculatory interval was significantly longer in the strange male group. The incidence of all agonistic behaviors other than a stereotyped kind of fighting that precedes copulation ("precopulatory fighting") was higher in strange male group than in the familiar male group. In both groups, aggressive postures were more frequently seen in females than in males, and conversely, submissive postures were significantly more frequent in males than in females. Also, females in the strange male group made significantly more approaches than those in the familiar male group. Taken together, these findings suggest that *C. musculinus* is a non-monogamous species.

**Key words**: precopulatory fighting, aggression, mating behavior.

## INTRODUCTION

The available information on the patterns of copulatory behavior in South American sigmodontine rodents is rather scanty. However, *Calomys* is a comparatively well known genus, since three of its nine species (Musser and Carleton, 1993) have been studied in the laboratory, and were found to display both intravaginal penile thrusting and multiple ejaculations, in combination with either single or multiple preejaculatory intromissions, and with either rare or absent locks (*C. callosus*, Baumgardner and Dewsbury 1979; *C. musculinus,* Cutrera et al., 1988; *C. laucha*, Yunes et al. unpublished).

Besides those traits which are common to all studied species of the genus, *C. musculinus* shows a stereotyped precopulatory "fighting", which starts with a rapid alternation of nose and/or vibrissae contacts or with a rapid exchange of aggressive and submissive postures between both partners, that becomes progressively more rapid and is followed by a mutual

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pursuit within a close circle. This was interpreted as a ritual behavior serving as mate recognition, thereby contributing to the reproductive isolation of the species (Cutrera et al., 1988).

The present laboratory work was aimed to compare the behavior of couples in two treatments, i.e., a female with a strange male and a female with a familiar male. This seemed interesting since, in a field study it was shown that the females' home ranges are both penetrated by wandering males, and also, they are partially overlapped to those of residential males (Contreras and Rosi, 1980). In this paper, a special attention was laid on the occurrence of precopulatory fighting, and of the other aggressive interactions which precede or accompany copulation in this species, since it was hypothesized that the incidence of precopulatory fighting would not change with any of these treatments, while non-ritualized aggression would increase in the strange male situation.

## MATERIAL AND METHODS

The current study was done on adult laboratory bred animals. The original stock was captured in the Ñacuñán Biosphere Reserve (Mendoza, Argentina) in 1983; additional breeders of both sexes (captured in the same Reserve) were introduced in the colony in 1991, 1992, 1993 and 1994.

Taxonomy of the genus *Calomys* has been particularly unstable, and sometimes has led to confusion regarding the identity of the studied animals. In this, as well as in previous papers (Castro-Vázquez et al., 1987; Cutrera et al., 1988) we have followed the diagnosis of Massoia et al., (1968) that distinguishes *C. musculinus* from *C. laucha*. Sample specimens (the skull and skin of 5 adult females and 5 adult males) of our colony were deposited at the mammal collection of the Instituto Argentino de Investigaciones de Zonas Áridas, Mendoza, Argentina (the females were identified as # CM-03540 to # CM-03544, and the males as # CM-03545 to # CM-03549).

Our colony is always kept under standard conditions of lighting (14 light/10 dark) and temperature (24º C), and the animals have free access to water and to a commercial diet for laboratory rodents. For reproductive purposes, couples of a female and a male of similar age (6-9 weeks) are formed, and they remain together through the ongoing lactations until they retire as breeders (after 12 months or more). Mating partners are selected so as to avoid pairing of close relatives.

Observations were conducted in a rectangular mating arena (104 cm x 60 cm) covered with wood shavings, under a dim red light, during the first 2 hours of the dark period, since april to september 1994. Couples of sexually experienced animals that had already bred two to six litters were used; each animal was observed once (couple-focal animal, Altmann, 1974). The male was removed 2-3 days before the expected day of parturition, to make sure that copulation would not occur without being observed. In all cases the litter remained with the dam throughout the study. The female and the nest with pups contained in a cylindrical can (11 x 7 cm) were put first in the arena. Fifteen minutes later, one sexually experienced male was introduced into the arena. In one group (familiar male group, n= 14 couples) the familiar male (with which the female had bred all her previous litters) was introduced in the arena. In the strange male group (n= 15 couples) a different male was put instead of the familiar one. Then the animals were observed for 30 min, and if copulation started, the observation was continued until a satiety criterion of 30 min without penile intromissions was met (Dewsbury, 1975). Total time spent in the observations was 50.9 ± 3.4 min and 47.0 ± 3.4 min, for the familiar and the strange male groups, respectively. Only those couples that displayed copulation sometime were included in this report. The observations were recorded with a microcomputer program that allows the simultaneous recording of the activities of two individuals.

### Behavioral categories

The present study is based on the description of behavioral patterns that were defined as mutually exclusive combinations of movements. This categorization was largely based on that of Dewsbury (1967, 1970, 1971) and Cutrera et al. (1988). Frequency of both interactive (i.e, those performed with, from or toward the partner) and non-interactive behavioral categories were recorded. However, only data of the interactive categories are presented in this paper. They were defined as follows:

**Approach:** Locomotion directed toward the partner and (in males) not aimed toward mounting was designated approach.

**Copulatory attempts:** The male approaches or follows the female attempting unsuccessfully to mount her while she runs away. This running away was explicitly excluded from escape run (see below).

**Precopulatory fighting:** The full performance may start with a rapid alternation of nose and/or vibrissae contacts or with a rapid exchange of aggressive and submissive postures between both partners. This alternation becomes progressively more rapid and is followed by a mutual pursuit within a close circle. The performance ends suddenly and is frequently followed by mounts with intromission or by copulatory attempts. All possible performances ranging from a mere rapid alternation of nose and/or vibrissae contacts to the full performance described above were recorded as precopulatory fighting.

**Mount with intromission:** The male jumps over the female's rump and clasps her flanks, making shallow, extravaginal pelvic thrusts and the female adopts the lordotic posture (see below). Once penile insertion is gained, a series of intravaginal thrusts ensues, although at a slower rate than during preinsertion thrusting. Vaginal insertion is sometimes lost during thrusting, but unless ventral viewing is used (Cutrera et al., 1988), this is only evident when intromission is alternated between both sides of the tail. The lordotic posture consists in the female making a concave arching of the back while she is standing on her four feet. The forelimbs are completely extended and the head points obliquely upward, while the hindlimbs are kept flexed (although some degree of extension may occur at deep thrusts). The female remains in this posture until the male dismounts. Then, the tenseness of the neck, back, and limbs is weakened, and the female usually lies flat on the floor, with her eyes half-closed.

**Ejaculatory reaction:** In most cases, the mount with intromission continues until ejaculation, without dismounting. Intravaginal thrusting is ended by a more profound and lasting insertion, during which the male ejaculates, as can be demostrated in the vaginal smear. Ejaculation is noted by a conspicuous tremor which is followed by a sudden loosening of the embrace and by dismounting in a more or less vertical position. Sometimes, a more marked relaxation is evident, and the male falls to one side. There is no intravaginal penile lock.

**Aggressive posture:** The animal stands on four feet and tenses its body toward the partner, pointing the nose at it. Sometimes this posture ends with a bite or a bite attempt.

**Submissive posture**: This posture is assumed in response to an approach or an aggressive posture of the partner. The animal bends its neck laterally, offering the concave side to the partner, sometimes with flexion of the contralateral forelimb.

**Cutting-off acts:** These acts are also performed after an approach or an aggressive posture. One of them is similar to the submisive posture, except that the animal offers the convex side of the neck to the partner, instead of the concave side, while both forelimbs remain equally extended. The other behavior included in this category was the half-closing of the eyes, performed after an approach or an aggressive posture of the partner. Both acts may have the meaning of suppressing an aversive stimulus.

**Upright/lying-down fighting:** Both partners first adopt upright postures oriented toward each other, and then make sparring movements of their forepaws in the upright position. Afterwards, both partners may fall on their side or on the back of one of them (usually the male). Biting and injuries may also occur after falling down.

**Escape run:** This includes the running away after an approach or an aggressive posture of the partner or after the performance of upright/lying down fighting or of precopulatory fighting. It does not include the running away of the female from male's attempts to mount her.

**Sniffing and grooming partner:** Two distinct behaviors were recorded under this category, since they frequently occurred in a rapid and continuous succession: (a) the animal either stands close to or follows the partner, while sniffing the genitals or any part of the partners body, and (b) the animal grooms or manipulates the partner's body with mouth or forepaws.

## Measurements of copulatory behavior

Measures are derived from the behaviors listed above and include the 'standard' measures of copulatory behavior (Beach and Jordan, 1956; Dewsbury, 1967 and 1974; Cutrera et al. 1988): (1) mount latency, time in seconds (sec) from the start of a test until the first mount; (2) intromission latency, time from the introduction of the male to the first penile intromission; (3) ejaculatory thrust frequency, number of intravaginal pelvic thrusts during an ejaculatory series; (4) ejaculation latency, time from the first intromission of an ejaculatory series to the respective ejaculation; (5) intromission frequency, the number of mounts with intromissions in a series; (6) mount frequency, the number of mounts, with or without intromissions, in a series; (7) postejaculatory interval, time from the occurrence of an ejaculation to the next mount with intromission; (8) ejaculation duration, duration of the ejaculatory reaction; and (9) ejaculation frequency, number of ejaculations attained before meeting the satiety criterion.

Also, a receptivity index was calculated as the sum of intromissions and ejaculations, divided by the sum of intromissions, ejaculations and mounts without intromissions. This index provides a measure analogous to the "lordosis quotient" that has

been widely used as a parameter of female receptivity in laboratory rats, and it equals one when all the attempts from the male result in lordosis and intromissions.

### Statistics (Siegel, 1956)

Kruskal-Wallis ANOVA by ranks test (followed by two-tailed Mann-Whitney U test as a post hoc analysis) was used for multigroup comparisons, that is, when both sexes and both treatments (familiar male and strange male group) were compared. The two-tailed Mann-Whitney U Test was used when the incidence of a category by both sexes together (e.g., precopulatory fighting) was compared between animals in the familiar male and strange male groups. The same test was used when either the receptivity index or the standard measurements were compared between two groups. Statistical level of significance was fixed at $p < 0.05$.

## RESULTS

Twenty one (72 %) out of 29 observed couples engaged in copulation during the first hours of the dark period following parturition. Four of the 8 couples that did not copulate were of the familiar male group and 4 of the strange male group (Fisher's Exact Probability Test p=0,616). All couples that engaged in copulation displayed at least an episode of precopulatory fighting, and also, 6 (75%) out of the 8 non copulating couples showed at least an episode of "precopulatory" fighting (3 of these couples were of the familiar male group and 3 of the strange male group).

### Standard measures of copulatory behavior

They are presented in **Table 1**. A single ejaculatory series occurred in 6/10 tests in the familiar male group and in 3/10 tests in the strange male group; two complete series occurred on 2/10 tests in the familiar group and in 7/10 tests in the strange male group; three complete series occurred in 2/10 tests in the familiar group, and four complete series occurred in 1/10 tests in the strange male group. No significant differences between the familiar male and the strange male group were found in either the mount or the intromission latency nor in either the mount or intromission frequencies (Mann-Whitney U Test), although the strange male group showed a trend to have higher mount and intromission frequencies, both at the first and the second ejaculatory series (Mann-Whitney U Test). Males in the strange male group showed significantly higher ejaculatory thrust frequencies, both at the first and the second ejaculatory series, than males in the familiar male group. The post-ejaculatory interval was significantly longer in the strange male group (Mann-Whitney U Test).

### Interactive behavioral categories

Changes in the frequency (episodes/hour) of these categories (except precopulatory fighting) according to sex and group are shown in **Figure 1**.

In both groups, aggressive postures were more frequently seen in females than in males (Kruskal-Wallis ANOVA by ranks test: H=31.09, p=0.000; followed by Mann-Whitney U Test, familiar male group: U=0, p=0.00007, and strange male group: U=13, p< 0.005 ), and conversely, submissive postures occurred more frequently in males than in females (Kruskal-Wallis ANOVA by ranks test: H=18.78, p<0.0003; followed by Mann-Whitney U Test, familiar male group: U=10, p=0.0009, and strange male group: U=23, p=0.04).

When both groups are compared, the incidence of behaviors such as submissive posture, upright/lying down fighting and escape runs was significantly lower in the males of the familiar male group than in the strange male group (Mann-Whitney U Test, U=10, p=0.05, U=22.5, p=0.03, U=23.5, p=0.04, respectively). Also, females in the familiar male group made significantly less approaches and aggressive postures than those in the strange male group (Mann-Whitney U Test, U=23.5, p=0.04 and U=17.5, p=0.01, respectively).

The mean frequency of sniffing and grooming partner was always higher in males than in females, although the differences were not statistically significant (**Fig. 1**). The mean frequency of precopulatory fighting was slightly higher in the strange male than in the familiar male group, as it is shown in **Figure 2**, although the difference was again not significant (Mann-Whitney U Test). Other measures of this behavior were also examined (percent

of the observation time invested in precopulatory fighting, and the mean episode duration of this behavior) and no significant differences were found between both groups (Mann-Whitney U Test).

### Receptivity index

Female receptivity during the first ejaculatory series was lower (as estimated by this index) in the familiar male than in the strange male group (0.69 ± 0.08, n=10, and 0.81 ± 0.06, n=11, respectively, mean ± SEM), and the difference was not statistically significant (Kruskal-Wallis test). During the second ejaculatory series there was no significant difference between the familiar and the strange male group (0.79 ± 0.13, n=4 and 0.79 ± 0.11, n=7, respectively).

## DISCUSSION

Precopulatory interactions in *Calomys musculinus* are composed mostly of agonistic behaviors in which the female and the male play the aggressive and submissive roles, respectively. However, during the kind of fighting that Cutrera et al., (1988) labelled as "precopulatory", both partners alternate the aggressive and submissive roles (see the description of this category under Methods). Its stereotyped performance, the lack of injuries, and the constancy of its occurrence in situations in which the frequency of aggression is changed (Cutrera et al., 1988 and **Figs. 1** and **2**), may suggest that *C. musculinus* acquired this kind of fighting through ritualization.

Behaviors that appear homologous to the

**Table 1**. Mean (± standard error) of standard measures of copulatory behavior.

| Measure | Familiar male group | n | Strange male group | n | p |
|---|---|---|---|---|---|
| Mount latency | 172 ± 42.5 | 10 | 195.3 ± 85.2 | 10 | NS |
| Intromission latency | 384 ± 160 | 10 | 208 ± 84.6 | 10 | NS |
| Mount frequency | | | | | |
| 1st. series | 4.1 ± 1.1 | 10 | 10.2 ± 6.3 | 10 | NS |
| 2nd. series | 3.2 ± 1.6 | 4 | 7.8 ± 2.4 | 7 | NS |
| Intromission frequency | | | | | |
| 1st. series | 2.3 ± 0.7 | 10 | 6.0 ± 3.3 | 10 | NS |
| 2nd. series | 1.5 ± 0.5 | 4 | 4.8 ± 1.3 | 7 | U=16.5, p=0.05 |
| Ejaculatory thrust frequency | | | | | |
| 1st. series | 14.2 ± 3.9 | 10 | 46.36 ± 8.42 | 10 | U=14.5, p=0.007 |
| 2nd. series | 16.4 ± 5.6 | 4 | 64.80 ± 18 | 7 | U=22,5, p=0.03 |
| Ejaculation latency | | | | | |
| 1st. series | 312.3 ± 144.4 | 10 | 296.3 ± 159 | 10 | NS |
| 2nd. series | 293.6 ± 126.1 | 4 | 193.4 ± 63.4 | 7 | NS |
| Ejaculation frequency | 1.6 ± 0.26 | 10 | 1.9 ± 0.27 | 10 | NS |
| Ejaculation duration | | | | | |
| 1st. series | 7.6 ± 2.6 | 10 | 9.6 ± 5.4 | 10 | NS |
| 2nd. series | 5.8 ± 1.5 | 4 | 7.5 ± 1.5 | 7 | NS |
| Postejaculatory interval | 211.6 ± 114 | 4 | 765.5 ± 166 | 7 | U=2, p=0.02 |

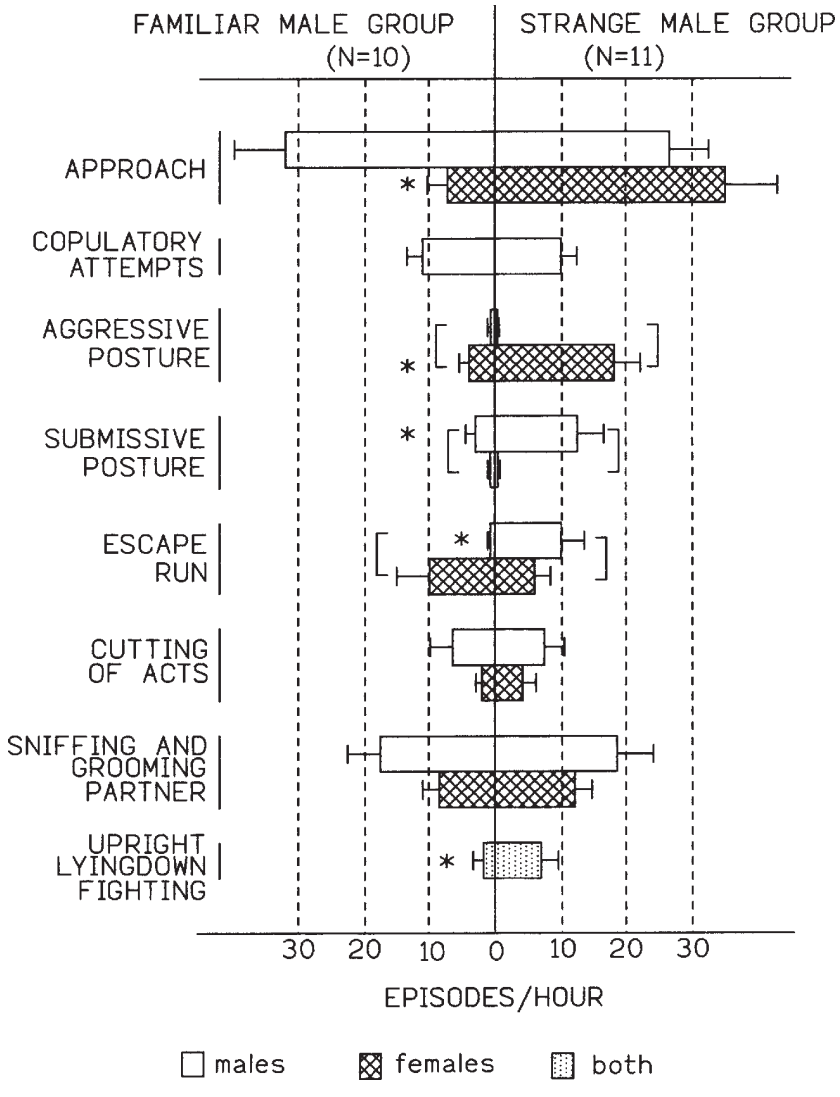


**Fig. 1**. Mean frequency (episodes/hour ± SE) of the interactive behavioral categories in couples composed of either a familiar male (on the left) or a strange male (on the right). Mean values (± SE) for males are indicated by open bars, while criss-cross bars indicate those of females. Asterisks indicate statistically significant differences between familiar male and strange male groups (Mann-Whitney's U Test). Also, statistically significant differences by gender are indicated with square brackets (Mann-Whitney's U Test).

precopulatory fighting of *C. musculinus* may also occur in other related species. In particular, the congeneric species *C. laucha* also displays a similar, but frequently less conspicuous, precopulatory fighting (Yunes et al., unpublished). Usually, performance of precopulatory fighting ends suddenly, and it is followed by mounts with intromission (Cutrera et al., 1988). Because of this immediate relation to copulation, it is possible that this kind of fighting may serve functions generally attributed to courtship behavior, i.e., (1) to bridle intraspecific aggression and to overcome the female's reluctance to copulate, and (2) to reciprocally assess the potential partner, so as to avoid interspecific mating (Immelmann, 1980). Indeed, as a ritualized behavior, precopulatory fighting may help to redirect

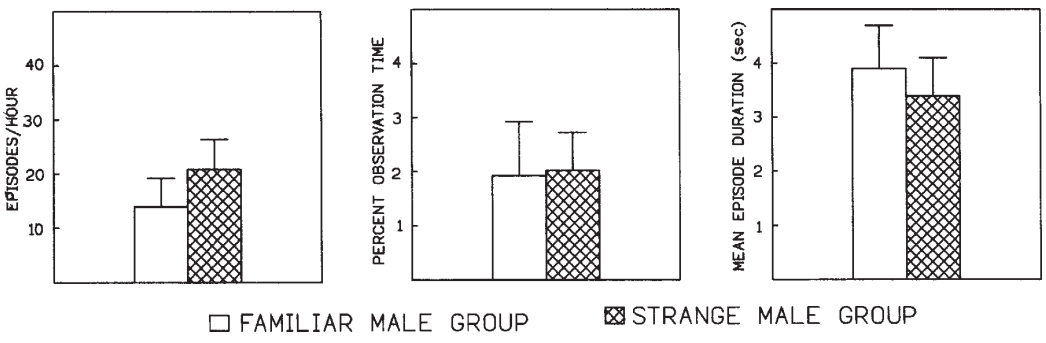


**Fig. 2.** Frequency of precopulatory fighting (episodes/hour), percent of observation time invested in the category, and mean episode duration in couples composed of either a familiar male (open bars) or a strange male (criss-cross bars). Results are expressed as means ± SE. No significant differences were observed (Mann-Whitney's U Test).

(Lorenz, 1963) aggression, and also, the accelerations and sudden arrests that occur during precopulatory fighting may increase female's receptivity by means of a vestibular mechanism similar to that described for the laboratory rat (Modianos and Pfaff, 1977). Besides that, precopulatory fighting may be the occasion for the female to assess the potential partner, particularly for his able performance of the ritual. Courtship behavior in the previously studied species of murid rodents seems practically restricted to non-ejaculatory intromissions (Dewsbury, 1988) and, in this perspective, this rather elaborate courtship in *C. musculinus* is puzzling. Also, since precopulatory fighting was also observed in tests in which copulation did not occurred, it should be considered that this kind of fighting may also serve functions other than the immediate preparation to copulation.

The strange males of *C. musculinus* show mount, intromission and ejaculatory thrust frequencies that were higher than those of the familiar male controls, which might be due to differences in female's behavior toward the strange male or it might be indicating a higher ejaculatory threshold as a consecuence of inhibition by a novel situation. The strange male group also showed a significantly longer post-ejaculatory interval.

It is worthnoting that the receptivity index was the same during the first and the second ejaculatory series for females in the strange and the familiar male group. These observations suggest that *C. musculinus* females may not show any preference for the familiar males, as one would expect in a non-monogamous species. However, this should be stated with caution, since mate choice studies have not yet been conducted, and since differences in female's behavior toward strange males (more frequent aggressive postures, less approaches, and less upright/lying down fighting, **Fig. 1**) are indicating that there is a recognition of something different.

Another fact which is consistent with a non-monogamous mating system is that *C. musculinus* starts copulation after a rather short intromission latency, and that this latency is not shortened between familiar partners (Dewsbury, 1979). Also, *C. musculinus* shows at least three elements that are useful in a context of sperm competition, as one would expect in promiscuous species, namely, deposition of a seminal plug at ejaculation (Castro-Vázquez, unpublished findings) and the occurrence of both multiple intromissions and ejaculations (Cutrera et al., 1988, and this paper). A field study in this species (Contreras and Rosi, 1980) has shown that the individuals live in only partially overlapping home ranges and that a female overlaps her home range with more than one male. Taken together, all these findings may suggest that *C.*

*musculinus* does not develop sexual bonds, and that a female in the field may copulate with more than one neighboring male.

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