



# The function and meaning of female rat paracopulatory (proceptive) behaviors



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## ABSTRACT

Female paracopulatory behavior is believed to incite the male to start copulation and to allow the female control over the pace of sexual interaction. It is also supposed to represent female sexual motivation. However, there is little direct experimental evidence for these presumed functions. In the present study, we determined the temporal relationship between female paracopulatory behavior, male pursuit of the female, and male copulatory acts. Groups of 4 intact female and 3 male Wistar rats were housed in a seminatural environment for 8 days. Sociosexual behavior during the entire period of behavioral estrus was analyzed. All episodes of paracopulatory behavior were identified, and the male behavior occurring up to 10 s before or after each episode was determined. Most paracopulatory behaviors were unrelated to male copulatory acts or male pursuit. To the contrary, 96% of copulatory acts occurred within 5 s of female paracopulatory behavior and 83% within 5 s of male pursuit of the female. Sexual interaction was initiated by a male as often as it was initiated by a female. The duration of an episode of paracopulatory behavior or male pursuit was an important determinant of the likelihood that a copulatory act would follow. Copulatory acts were a consequence of a subtle interaction between the male and the female, with the behavior of both being equally important. No support was obtained for the notion that sexual interactions are mainly controlled by the female.

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## 1. Introduction

When exposed to appropriate amounts of ovarian hormones, female rats will display a series of stereotyped motor patterns not present in the absence of these hormones (reviewed in Pfaff, 1980; Pfaff, 1999). The lordosis posture is the most well-known of these motor patterns. It is generally believed that male rats cannot achieve intromission, hence not ejaculation, if the female does not display lordosis in response to their mounts (Kow and Pfaff, 1977). The function of lordosis is, consequently, clear cut: making it possible for the male to achieve vaginal penetration and eventually ejaculation, thereby fulfilling the biological function of sexual behavior, the union of gametes.

Apart from lordosis, the sexually receptive female rat displays a few other motor patterns. One is ear wiggling, a lateral shaking of the head making the ears appear to quiver. Another is hop-darting, a behavior pattern consisting of a rapid hop with rigid legs combined with fast darting movements away from the male. A third is

the presenting posture, characterized by the female standing still and pressing the ventral body area against the floor with slightly spread limbs. Almost all hop-darts end with a presenting posture (Madlafousek and Hlinak, 1978). All these behavior patterns are frequently lumped together under the label solicitation (Erskine, 1989) or proceptive behaviors (Beach, 1976). In Beach's (1976), seminal paper a definition is provided: proceptivity connotes various reactions by the female toward the male which constitute her assumption of initiative in establishing or maintaining sexual interaction (p. 155). A few years later a similar definition was offered in another influential review (Erskine, 1989): solicitation behaviors may be defined as those species-typical behaviors displayed by the estrous female which encourage the male to mate and which regulate the pattern of copulation (p. 474). In both definitions, the function of these behaviors was primarily to incite the male to perform copulatory acts with the female. In the first definition, these behaviors should also make the male persist in his copulatory efforts, and in the second they should prevent the male from copulating too often, i.e., they should regulate pacing. Implicit in these definitions is the notion that proceptive behaviors somehow express the intensity of female sexual motivation.

Some time ago, it was suggested that the behavior patterns lumped together under the terms proceptive behavior or solicita-

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tion should be named by the more neutral term of paracopulatory behavior (Blaustein et al., 2009; Blaustein and Erskine, 2002). We have used that term in recent publications (Chu and Ågmo, 2014; Chu and Ågmo, 2015a) and it will be used in the present communication.

Experimental support for the notion that paracopulatory behaviors incite males to start copulation is, surprisingly enough, quite limited. In experienced heterosexual pairs tested in a standard observation arena there is no relationship between the amount of female paracopulatory behavior and the intensity of male sexual activity (Landau and Madden, 1983). In sexually inexperienced males, though, female paracopulatory behaviors determine the likelihood that the male will initiate copulation (Madlafousek and Hlinak, 1983). This is also the case in castrated males given low testosterone doses (Hlinak et al., 1979; Hlinak and Madlafousek, 1982). Furthermore, different kinds of central nervous lesions render male rat sexual behavior dependent on female paracopulatory behavior (Caggiula et al., 1976; Edwards and Maillard, 1988; Whishaw and Kolb, 1985). It would appear, then, that female paracopulatory behavior is important only in situations where male sexual activity either has been reduced by specific experimental manipulations or in animals lacking sexual experience. None of these circumstances are commonplace in nature. Most rats can be expected to have concentration of testicular hormones within the physiological range as well as an intact brain. The lack of sexual experience is a once in a lifetime situation, and although all males initially are sexually inexperienced most of them will acquire experience shortly after puberty. Thus, according to available data, paracopulatory behaviors will be of marginal importance in natural contexts. However, all studies mentioned so far have been made in heterosexual pairs of rats, subjected to a short test in a small arena.

The presumption that paracopulatory behavior is an expression of the degree of female sexual motivation also lacks direct empirical support. Since these behaviors do not involve the genitals, they cannot be considered sexual behaviors (see Ågmo 2007, 2011 for a discussion) and are, consequently, not necessarily dependent on sexual motivation. Furthermore, paracopulatory behavior is very stereotyped, and can be considered as entirely reflexive. It has, therefore, been argued that it is not adequate as measure of sexual motivation (Cummings and Becker, 2012). Notwithstanding, the amount of paracopulatory behavior displayed has frequently been used as indicator of the female's level of sexual motivation (e.g., Montoya et al., 2010; Santoru et al., 2014; Ventura-Aquino and Fernández-Guasti, 2013).

In the wild, rats copulate in groups rather than in pairs. As soon as a female enters into estrus, several males will pursue and copulate with her (Calhoun, 1962; Robitaille and Bouvet, 1976). The possible importance of paracopulatory behaviors in this context is entirely unknown. However, data from a seminatural environment housing 1 male and 1 sexually receptive female show that most intromissions (90%) occur shortly after that the female displays paracopulatory behavior (McClintock and Adler, 1978). Furthermore, 84% of all female approaches were followed by male pursuit of the female and eventually by intromission. These and other observations (e.g., Bermant, 1961; Peirce and Nuttall, 1961) have led to the widespread belief that the female almost exclusively controls sexual interaction when given the opportunity to do so. In more recent studies of copulatory behavior in a seminatural environment, we confirmed the strong association between the intensity of female paracopulatory behavior and the number of male mounts (Chu and Ågmo, 2014; Chu and Ågmo, 2015b). Interestingly, there was no relationship between paracopulatory behavior and the number of intromissions and ejaculations performed with the females. Likewise, the number of lordoses displayed by a female is strongly correlated with the amount of paracopulatory behavior but not with the number of intromis-

sions or ejaculations received. The robust correlation between male mounting and female paracopulatory behaviors as well as between number of lordoses and amount of paracopulatory behavior could suggest that these behaviors cause the male to mount, thereby stimulating female lordosis. It could also suggest that paracopulatory behaviors are activated by male pursuit of the female, a behavior that almost always precedes mounting, with or without intromission/ejaculation (Ågmo, 1999; Chu and Ågmo, 2015a; Shimura et al., 1994; Shimura and Shimokochi, 1990).

It is not impossible that observations of sexual interactions between a pair of opposite sex rats in a small cage are inappropriate for an ecologically valid determination of the importance of paracopulatory behavior. In the present study, we determined the temporal relationship between displays of female paracopulatory behavior and male pursuit of the female in a seminatural environment housing multimale and multifemale groups of rats. Likewise, the association between these behaviors and copulatory acts were established. This would make it possible to determine whether female paracopulatory behavior incites the male to pursue the female and eventually perform a copulatory act or whether female paracopulatory behavior is a response to male pursuit. Furthermore, these data would illuminate the issue of the role of the female vs. the male in the control of sexual interactions. Finally, we collected data relevant to the issue of whether female paracopulatory behavior enhances male sexual motivation (encourage the male to mate) and if they represent female sexual motivation or not. The procedure employed here should have external validity, thus, allowing us to reach reasonably well-founded conclusions.

## 2. Methods

### 2.1. Subjects

Male (300 g) and female (250 g) Wistar rats were obtained from Charles River (Sulzfeld, Germany) and they were housed in same-sex pairs in Macrolone IV cages in a room with lights on from 0800 to 2000. Room temperature was  $21 \pm 1$  °C, and humidity was  $55 \pm 10\%$ . Commercial rodent pellets and tap water were freely available.

### 2.2. Apparatus

The seminatural environment has been described in considerable detail elsewhere (see Fig. 1 and Chu and Ågmo, 2014; Chu and Ågmo, 2015b). Briefly, it consists of an open area ( $2.1 \times 1.4$  m) joined to a burrow made up of several tunnels and 4 nest boxes. Four openings between the open area and the burrow allow the experimental subjects to move freely within the setup. There is a 12/12 h light/dark cycle in the open area with a light intensity at floor level of 180 lx during the light period and of 1 lx during the dark period. The burrow is kept in constant darkness for the rats, but infrared (820 nm) lamps provide light for a video camera installed in the ceiling 2.4 m above the center of the burrow. Another video camera is installed above the center of the open area.

### 2.3. Procedure

Five groups of 7 rats each were used in this study. Each group consisted of 4 females and 3 males. On the morning of the first day of the study, a rectangle measuring  $2 \times 3$  cm was shaved on different parts on the back of the animals. They were also marked on the tail with thick stripes of black ink. These two marks made it easy to identify the subjects on the video record throughout the observation period.

The floor of the entire environment was covered by wood shavings to a depth of 2 cm. Three plastic huts and 12 short wood sticks

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