



Ventro–ventral copulation in a rodent: a female initiative?

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This study reports a high rate of ventro–ventral (VV) copulation in 2 species of the African four-striped mouse—*Rhabdomys*—and explores its causes. VV postures were observed in 67% encounters with mating attempts, in both species and during intra- and interspecific trials, although discrimination between the species occurred (i.e., duration of sexual behavior or social investigation varied between intra- and interspecies encounters). Striped mice displayed more investigatory behavior during encounters with VV coitus postures than during encounters without mating attempts or with only dorso–ventral postures. Furthermore, mating solicitation was greater in females than in males exclusively when VV coitus occurred, suggesting that females' initiative could explain the high rate of VV postures in our model organism. We propose different hypotheses among which the role of pleasure through its supposed direct and indirect adaptive implications in triggering female initiative.

Key words: coitus postures, female proactivity, mating behavior, *Rhabdomys*, species discrimination

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Mating behavior, including coitus position, is complex and diverse among animals (Dewsbury 1972; Crews and Moore 1986; Huber et al. 2007). Although the evolution of duration, rate, and temporal patterns of copulation and genitalia morphology have been studied in a variety of species (Dewsbury 1967; Crews and Moore 1986; Birkhead et al. 1987; Magnhagen 1991; Eberhard 2004a; Simmons and Firman 2014), the evolution and functional significance of coitus position is rarely addressed (Acebes 2003; Huber et al. 2007).

Ventro–ventral (VV) coitus posture, where mates face each other, has been recorded in several groups, such as insects (Huber et al. 2007) and aquatic mammals (whales—Sauer 1963; dolphins—Norris 1977; seals—Harris 1991; dugongs—Adulyanukosol et al. 2007). However, it is generally considered to be particularly rare among terrestrial mammals other than apes (Beach 1976; Baker and Bellis 1995). Diversification of coitus postures may be influenced by different factors such as risk assessment and variation in vigilance in different environmental and social contexts. A dorso–ventral (DV) position would allow the individual that is above, or both sexes, to maintain visual contact with their environment to detect intruders (Huber et al. 2007). In contrast, VV coitus performed lying on a substrate, but possibly not when in a vertical position (Li et al. 2013), might expose the copulating pair to predators or intrusion of a competitor, suggesting that it would evolve in

environments that do not require high levels of vigilance (Ford and Beach 1951; Baker and Bellis 1995). Selective pressures on reproduction may also influence coitus position. For example, mechanical constraints would vary with genitalia shape and could favor either DV, VV, or other coital positions in insects (Huber et al. 2007), while constraints on sperm retention due to bipedalism might have favored VV coitus in primates (Gallup and Suarez 1983). Finally, sexual conflict over mating, e.g., control of timing of disengagement, could also influence coitus postures (Beach 1976; Huber et al. 2007).

Although the role of females in reproduction has long been considered to be confined to mate choice and maternal behavior (Trivers 1972), Beach (1976) argued that failure to recognize the importance of female initiative in reproduction had encouraged a biased view of feminine sexuality (for insects and arachnids, see Eberhard 1994, 2004b). In particular, female proceptivity (i.e., initiative to establish or maintain sexual interaction) and, to a lesser extent, receptivity (female's responses necessary for achieving intravaginal ejaculation) have been largely neglected in studies of mating behavior (Ford and Beach 1951; Beach 1976).

Our study provides evidence of VV coitus postures in 2 sister species of the African four-striped mice (genus *Rhabdomys*). *Rhabdomys* is a small diurnal rodent described as 5 different lineages (Rambau et al. 2003; du Toit et al. 2012). We studied

2 species, namely *Rhabdomys bechuanae* (sensu du Toit et al. 2012, hereafter *R. bechuanae*) and *Rhabdomys dilectus dilectus* (sensu Rambau et al. 2003, hereafter *R. d. dilectus*). We aimed to assess between-species discrimination comparing within- and between-species intersexual encounters in wild-caught striped mice housed in captivity for 5 months. To our surprise, VV mating postures were recorded in 67% of encounters with mating attempts, leading us to characterize this behavior in greater detail. Our observations suggest that female sexual arousal may lead to VV coitus posture in *Rhabdomys*.

MATERIALS AND METHODS

Ethical note.—This study followed the American Society of Mammalogists guidelines (Sikes et al. 2011). All striped mice were trapped in nature and kept in the animal facilities of University of the Witwatersrand. A permit to trap and handle animals in the field was obtained from the Free State Province ethics authorities (n° 01/15700). The laboratory study was performed after authorization by the Animal Ethics Screening Committee of Witwatersrand University (ethics number AESC 2012/13/2A), and we were particularly careful to ensure the well-being of our mice.

Tested animals and laboratory conditions.—Striped mice were trapped in central South Africa (Sandveld Nature Reserve, 27°43'S, 25°45'E, Free State Province) during the austral spring (November 2011), in an area where the 2 species co-occur. Most striped mice trapped were sexually mature (38 out of 41) and, after transport to the laboratory (University of the Witwatersrand), they were maintained in same-sex groups (1–4 per group; $\bar{X} = 3$) under standardized laboratory conditions (LD 13:11 h, 24°C) and housed in breeding cages (42.5 × 15 × 27 cm) containing wood shavings and hay. Three months before being tested, the striped mice were housed singly. The tests were performed in May 2012 and lasted 2 weeks, after which the mice were housed in pairs or groups and involved in other experiments. Twenty males (14 *R. bechuanae* and 6 *R. d. dilectus*) and 21 females (10 *R. bechuanae* and 11 *R. d. dilectus*) participated in the tests (Table 1; Appendix I).

Experimental protocol.—The dyadic tests ($n = 31$) took place during the diurnal phase of the photoperiod (0800–1600 h, during peak activity of striped mice—Schradin 2006) in a different room from the colony. All females tested were in estrus (confirmed by vaginal smears taken at least 1 h before the tests).

The behavioral tests took place in a glass tank (50 × 34 × 35 cm), the floor of which was covered with a thin surface of clean wood shavings. The tank was separated into 2 equal triangular parts with a piece of cardboard. At the start

of a test, a male and a female were placed on either side of the cardboard partition for 10 min to acclimatize to the new environment and to the presence of the other mouse that they could hear smell on the other side of the partition. Recording started when the partition was removed and lasted for 20 min. Generally, after a few seconds of high activity, following the removal of the partition, the mice started to interact. At the end of each test, the mice were returned to their home cages. Some of the mice were tested once in intraspecific and once in interspecific encounters (randomized order), with at least 3 days between repeated use of individuals, to reduce potential influence of previous experience (Appendix I).

All experiments were video-recorded (HDR-CX130E, Sony, Puteaux, France) and the duration of 12 behaviors (Table 2) was scored using The Observer v3.0 software package (Noldus et al. 2000). We grouped different behaviors into 4 categories: “Agonistic” included avoid or reject advances from the opponent, threat, defense, attack, and fight; “Investigation” included approach and sniffing not followed by mating attempts; “Proactive” included intense allogrooming (a behavior that might be involved in courtship, e.g., Stopka and Graciasova 2001), acceptance of allogrooming or mating, and active participation in mating attempts; “Mating attempts” included either DV or VV attempts as well as copulation with thrusting movements (observed only once and during VV coitus) and acceptance of mating or of attempts (Table 2).

When mating attempts were observed, they were classified into VV when such a posture was observed at least once during the 20-min trials and classified as DV when all mating attempts during the trial were DV. Among the 12 dyads with mating attempts, 8 showed VV coitus postures. When a mouse was tested twice, it did not necessarily attempt mating twice, and the order of testing did not seem to influence the occurrence of mating attempts or the type of coitus posture displayed (Appendix I).

Data analysis.—To analyze the agonistic, investigatory, and mating behavioral categories, we summed the male and female values so as to obtain one value per dyad. In order to compare male and female sexual proactivity or investigation, we subtracted the male and the female values within each dyad so as to obtain a single value showing differences (or not) between the sexes.

Considering our relatively small sample size, we performed nonparametric tests with the R software (version 2.15—R Development Core Team 2012). For multiple testing, we adjusted the significance level (initial $\alpha = 0.05$) following the Bonferroni sequential procedure (Rice 1989).

Table 1.—Number of mouse pairs involved in intra- and interspecific encounters with reference to the coitus posture displayed. DV: when only dorso-ventral postures were displayed by the dyad. VV: when ventro-ventral posture was displayed at least once by the dyad.

♀\♂	No mating attempt		Mating attempt (only DV/VV)	
	<i>R. d. dilectus</i>	<i>R. bechuanae</i>	<i>R. d. dilectus</i>	<i>R. bechuanae</i>
<i>Rhabdomys dilectus dilectus</i>	0	8	5 (2/3)	2 (1/1)
<i>Rhabdomys bechuanae</i>	4	7	2 (1/1)	3 (0/3)

RESULTS

The sequence of behavior leading to a DV coitus posture was initiated by the male after approaching, investigating and allogrooming the female. VV coitus posture was always observed to start with insistent allogrooming by the female, pushing the male, crawling under it while adopting a ventral position and sniffing its genitalia, the male keeping the same posture as in DV (Fig. 1; Supporting Information S1).

Encounters with mating attempts (12 out of 31 trials) were observed both in intra- and interspecific dyads (Table 1) but tended to be more frequent than expected during intraspecific *R. d. dilectus* encounters (binomial test $P = 0.06$; Table 1). Further, the duration of mating attempts differed between encounter types (Kruskal–Wallis, $\chi^2 = 13.32$, $d.f. = 2$, $P = 0.001$) and was higher among intraspecific *R. d. dilectus* dyads ($\bar{X} \pm$

SE : 125.8 ± 44.19 s) than among intraspecific *R. bechuanae* dyads (15.3 ± 10.36 s) and interspecific dyads (9.85 ± 7.80 s; Mann–Whitney post hoc tests, $W = 3$, $P < 0.001$ and $W = 48$, $P = 0.004$, respectively), with the latter 2 groups not being statistically different ($W = 67$, $P = 0.42$; Fig. 2).

Interspecific dyads were not more agonistic than any of the 2 intraspecific types ($\chi^2 = 2.91$, $d.f. = 2$, $P = 0.23$). However, the duration of investigation varied between encounter types ($\chi^2 = 7.73$, $d.f. = 2$, $P = 0.02$) due to higher values during intra-*R. bechuanae* dyads (465.9 ± 71.96 s) as compared to interspecific dyads (207.7 ± 29.49 s; $W = 34$, $P = 0.014$). The duration of investigation during intra-*R. d. dilectus* encounters (329.9 ± 59.51 s) was intermediate and did not differ significantly from the 2 other categories (compared to *R. bechuanae*, $W = 16$, $P = 0.31$; compared to interspecies dyads, although a

Table 2.—Description of behavioral items recorded and merged into 4 behavioral categories.

Behavioral categories	Behavioral items	Description
Agonistic/dyad	Refuse	The mouse leaves, avoids, flees during an action of the other
	Threat, defense	The mouse is in semi-upright posture with open mouth, or rattles, or vocalizes
Sexual proactivity/individual	Attack	Attack and pursuit
	Fight	Both mice fight and bite
	Allogroom	Grooms, scratches, and pushes the other
	Accept allogroom	The mouse exposes its neck and/or lays down on its side while the other allogrooms
Mating attempt/dyad	Accept mating attempts	The mouse participates in the pelvic movement or does not move when the other tries or performs copulation
	Accept mating attempts	The mouse participates in the pelvic movement or does not move when the other tries or performs copulation
	Dorso–ventral mating attempts	The male mounts the female from the rear and attempts coitus
	Ventro–ventral mating attempts	The female exposes its ventral parts and approaches the male genitalia from above, the male attempts ventral mounting
Investigation/dyad and individual	Ventro–ventral coitus	Copulation with pelvic movement
	Investigation	The mouse sniffs the body and nose of the other individual
	Accept investigation	The mouse does not move when the other investigates

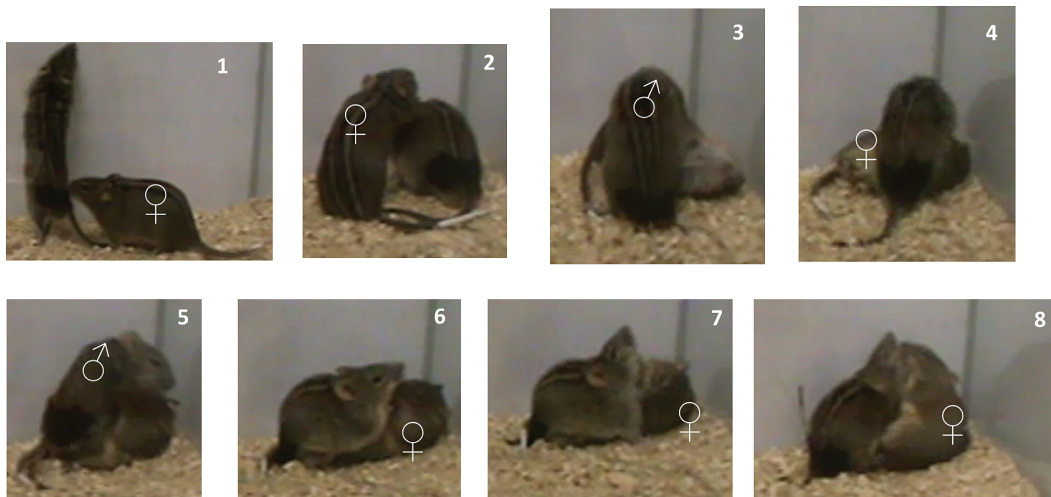


Fig. 1.—A sequence of a mating attempt with a ventro–ventral posture. 1) The female (*Rhabdomys*) approaches and sniffs the male. 2) The female initiates allogrooming of the male. 3) The male grooms the female, which lay on her back. 4) Male and female groom each other. 5) The male mounts the female which faces the male ventrally. 6, 7, 8) Both the male and the female show active pelvic movements. In other instances, the male may attempt a dorso–ventral mount while the female would twist her body to face the male ventrally.

trend was observed ($W = 17$, $P = 0.06$). After checking that species identity did not influence aggressiveness and investigation when considering encounters with and without mating attempts separately (Table 3; all within-species comparisons $P > 0.05$), we pooled the data across species and specifically assessed differences in behavior patterns displayed during encounters with mating attempts ($n = 12$) and without mating attempts ($n = 19$). Striped mice displayed the same level of agonistic behavior in both encounter types ($W = 114$, $P = 1$), while the level of investigatory behavior was higher during encounters with mating attempts ($W = 64$, $P = 0.04$).

Mating attempts and VV coitus postures were observed in both species and encounter types (intra- and interspecific). Again, we checked for species influence on our results and did not detect significant differences (Table 3, all comparisons $P > 0.05$). Therefore, we pooled the data across species to explore the potential causes of VV postures by comparing behaviors displayed during encounters where mating attempts were displayed with ($n = 8$) and without ($n = 4$) VV postures. We did not detect differences in agonistic behaviors between dyads displaying or not displaying VV ($n = 8$ and 4, $W = 24$, $P = 0.19$). The duration of mating attempts did not differ between VV and

DV encounters ($W = 14$, $P = 0.81$), yet, interestingly, individuals in dyads displaying VV postures spent more time investigating each other than those not displaying VV postures ($W = 3$, $P = 0.03$), and the females were found to be more sexually proactive than the males during encounters with VV postures ($W = 28$, $P = 0.05$; Figs. 1 and 3), while they were not during encounters with mating attempts not showing VV postures.

DISCUSSION

This study reveals the occurrence of VV coitus postures in 2 species of striped mice *Rhabdomys*, suggesting that this rarely described copulatory behavior may occur in a wider range of species than previously thought. The sequence of copulatory behavior was consistent in all dyads with VV copulation, indicating an inherent ability of several females of the 2 species to solicit copulation with VV postures. Our observations involved wild-caught striped mice housed in captivity for a few months, but it is improbable that the VV copulation and female proactivity are laboratory artifacts (Wolff 2003) since VV was not observed by all mice and the females actively solicited copulation only in dyads involving VV coitus.

Our results indicate that this VV behavior may not be species-specific and could involve heterospecific dyads, although our small sample size precludes testing for fine differences between encounter types. Yet, the 2 species could discriminate between each other: *R. bechuanae* displaying more investigation during intraspecific encounters and *R. d. dilectus* more sexual behavior during encounters between conspecifics, than during interspecific encounters. None of the few earlier studies addressing sexual behavior in *Rhabdomys* reported VV postures (Dewsbury and Dawson 1979; Willan 1982). These studies generally involved laboratory bred animals (*R. d. dilectus*—Dewsbury et al. 1984), hormonally induced estrous females (*R. d. dilectus*—Dewsbury and Dawson 1979), or a relatively small number of mice (6 *R. dilectus chakae* dyads—Willan 1982). Further, none of these studies described female behavior in any detail or compared behavior between the sexes. Males were reported to initiate mating, culminating in the classical DV coitus position. Within a 15-min laboratory observation, a full effective copulation was observed, characterized by multiple intromissions (up to 17—Willan 1982). In our study, females were housed separately from males for a long period, which could have enhanced their sexual arousal.

A VV coitus posture was reported on one occasion in the European hamster *Cricetus cricetus* during mating attempts

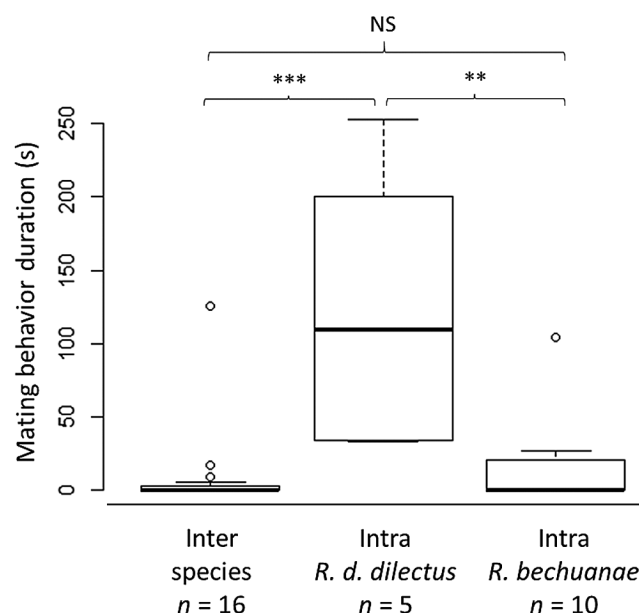


Fig. 2.—Variation in mating behavior duration across 3 encounter types. Results of post hoc Mann–Whitney tests are indicated (NS: not significant, $**P < 0.01$, $***P < 0.001$). Box-plots show the median (thick line), 1st, and 3rd quartiles.

Table 3.—Results of Wilcoxon (Z and W) and Kruskal–Wallis (KW) tests evaluating the influence of encounter type (interspecies, intra-*Rhabdomys dilectus dilectus*, intra-*Rhabdomys bechuanae*, see Table 1) on 4 behaviors within the 4 categories of dyads: not showing or showing mating attempts and, among the latter, showing or not showing VV (ventro–ventral) positions (NA: when not applicable). DV = dorso–ventral.

Behavior	Dyads without mating attempts	Dyads with mating attempts	Dyads with only DV coitus postures	Dyads with VV coitus postures
Investigation	$Z = 1.73$, $P = 0.08$	$KW = 1.91$, $P > 0.6$	$W = 5$, $P = 1$	$KW = 2$, $P > 0.6$
Agonistic	$Z = -1.63$, $P = 0.10$	$KW = 0.85$, $P > 0.6$	$W = 4$, $P > 0.6$	$KW = 0.02$, $P > 0.6$
Mating attempts	NA	NA	$W = 3$, $P > 0.6$	$KW = 1.05$, $P > 0.6$
Sexual proactivity	NA	NA	$W = 3$, $P > 0.6$	$KW = 3.15$, $P > 0.6$

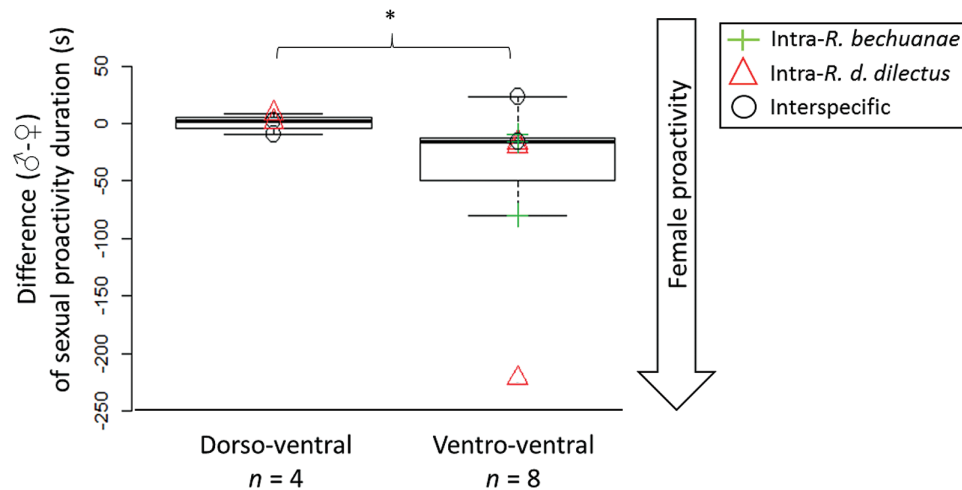


Fig. 3.—Difference in duration of sexual proactivity between dyads with dorso-ventral versus ventro-ventral coitus postures. Values are differences between a male and a female (*Rhabdomys*) in a given dyad. Negative values indicate female proactivity (* $P < 0.05$, Mann-Whitney test). Box-plots show the median (thick line), 1st, and 3rd quartiles.

(Petzsch 1986). In that study, the mechanistic constraint hypothesis was proposed, considering the fact that the short legs in that species hindered direct mounting from the rear (Petzsch 1986; but see Reed 1946). This is not the case in striped mice, since the male maintained the same position as when involved in DV copulation, and was observed sometimes to attempt DV copulation while the female presented its ventral part and took an active part in the copulation attempt.

Comparing the behaviors of dyads showing VV versus exclusively DV coitus postures, our results indicate greater mutual investigation as well as higher female proactivity and/or mating solicitation as compared to their male counterparts during VV. Allogrooming was described in intersex encounters in *Rhabdomys* (Willan 1982) and in other rodent species in which this behavior was proposed to be involved in courtship behavior (Stopka and Graciasova 2001; Fernandez-Vargas et al. 2011). Greater mutual investigations may suggest greater acceptance and a form of mate assessment, which might in turn contribute to triggering female initiation of mating. Moreover, actively seeking mating by females could function as a courtship cue, signaling to males their eagerness and possibly commitment to mate. Finally, female initiation of mating could also be at least partly driven by rewards such as sexual pleasure (Balcombe 2009). Indeed, VV coitus posture (when the penis rubs the clitoris), unlike the DV posture, is considered to facilitate clitoral stimulation and hence sexual pleasure in apes (Ford and Beach 1951; Dixon 1998). Pleasure has long been a taboo in human society in general and science in particular (Balcombe 2009), resulting in the neglect of its potential reinforcing and driving role in animals in general and females in particular (Lloyd 2005). If true, and if sexual pleasure derived from coitus results in a positive feedback in female response (Balcombe 2009), we may expect females to initiate VV coitus postures. Female sexual pleasure could be directly targeted by selection or may have evolved as a by-product of male sexual pleasure, alternatives that are still under debate in human evolutionary biology (Lloyd 2005; Puts and Dawood 2006; Zietsch and Santtila 2011, 2012; Zietsch

et al. 2011). Notwithstanding, besides its potential reinforcing effect, female orgasm may maximize sperm transport (Puts and Dawood 2006) and retention thanks to muscular contractions of the vagina that produce a stopper-like effect and slight cervical dilatation (Gallup and Suarez 1983), benefiting both males and females. The presence of a clitoris is reported in many mammal species (including rodents), and female orgasm has been described in a variety of monkeys (Dixon 1998; Balcombe 2009). Recently, sexual pleasure in a rodent was reported in a study revealing that a stimulation of the clitoris in estrous female rats resulted in enhanced levels of melanocortin and, to a lesser extent, of oxytocin in the brain, indicating female's sexual pleasure and possibly orgasm (Gelez et al. 2010). These 2 hormones are the main inducers of uterus contractions and increased seminal fluid transport (Puts and Dawood 2006), and hence female sexual pleasure could enhance fecundity. More recently, studies on the evolution of the baculum in the house mouse showed that males with a thicker baculum sired embryos with increased viability, suggesting that a thicker baculum might induce the strongest stimulation of the female during mating, resulting in greater fecundity or/and embryos surviving (Stockley et al. 2013; Simmons and Firman 2014). Finally, the adaptive value of pleasure is further suggested by studies showing that it could reinforce social networks in bonobos *Pan paniscus* and chimpanzees *P. troglodytes* (Wrangham 1993) and have a positive effect on the individual's immune system (Haake et al. 2004).

If female *Rhabdomys* derive pleasure through VV mating, as suggested by their proactivity, and VV resulted in greater female fitness, such behavior could be favored by selection. We hence propose that female solicitation of mating, possibly reinforced by pleasure, could explain VV postures in our study model. Future studies could test this proposition and specifically address: i) whether female initiation of mating could act as a courtship signal; ii) whether pleasure is involved and how it may reinforce female sexual behavior; and iii) the adaptive value of such behavior, and if any, whether it benefits both or only one of the sexes.

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SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmmammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—Video of an encounter showing a pair of striped mice displaying VV (ventro–ventral) coitus postures. For more details, see “Materials and Methods” and legend of Fig. 1.

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APPENDIX I

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