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Organization of Mating Behavior in Male Hamsters (Mesocricetus auratus)

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Abstract

Factor analysis was applied to standard measures of sexual behavior in 73 male hamsters as they interacted with hormone-primed females. The results suggest that five factors, or conceptual mechanisms, function in the organization of the behaviors observed in the first two copulatory series. Of these, the three that relate to the behaviors in the first copulatory series were compared to those emerging from prior analyses of other rodents. These comparisons revealed similarities and differences in factor structure across species. Whereas all of these analyses identify factors related to the initiation and efficiency of copulatory behavior, hamsters seem to differ from other species in the measures that best define these factors. In addition, the copulatory rate factor that has been prominent in previous analyses of rats seems to be absent in hamsters. These results suggest that male sexual behavior in hamsters is organized differently from that in other rodents. More generally, they suggest that even species with generally similar copulatory patterns can show significant differences in behavioral organization, in turn suggesting the need for additional factor analytic studies to better establish the extent of these species differences.

Keywords: conceptual mechanism, factor analysis, hamster, male copulatory behavior, male sexual behavior

Organization of Mating Behavior in Male Hamsters

The copulatory behaviors of male rodents have attracted much attention from behavioral scientists for many reasons including their biological importance, ease of elicitation and distinctive forms. Though muroid rodents vary considerably in their copulatory behaviors, the modal pattern seems to be one in which males show one intravaginal thrust per intromission but multiple intromissions prior to an initial ejaculation and multiple ejaculations in the course of an interaction (Dewsbury, 1972, 1975). In addition, this pattern is characterized by the failure to develop any mechanical lock between the penis and vagina during intromission or ejaculation.

Consistent with this pattern and the behavioral elements it stresses, the methods used to study the sexual behavior of male rodents typically begin by distinguishing mounts, intromissions and ejaculations. When multiple ejaculations are possible, scoring systems often distinguish copulatory series, each consisting largely of an ejaculation and the series of mounts and intromissions that immediately precedes it.

From frequency and temporal measures of the three basic behaviors, many studies derive at least a standard set of eight dependent variables (Table 1). This includes two that are considered to initiate the interaction as a whole and so are not tied to a copulatory series, i.e., mount latency (ML, the delay between the stimulus female's introduction and the first mount), and intromission latency (IL, the corresponding delay for the first intromission). In contrast, the remaining six measures typically are linked to specific copulatory series. These include ejaculation latency (EL, the interval separating the first intromission of a series from the ejaculation that concludes that series), mount frequency (MF, the number of mounts in a series), intromission frequency (IF, the number of

intromissions in a series), intromission ratio (IR, the proportion of all mounts and intromissions in a series that are intromissions, or IF/(MF+IF)), interintromission interval (III, the average interval separating successive intromissions in a series, or EL/IF), and postejaculatory interval (PEI, the interval separating the ejaculation of a focal series from the first intromission of the next series).

Researchers have long believed that these measures are not fully independent and that their interconnections go beyond the obvious cases, in which some measures enter into the calculation of others. Accordingly, several researchers have suggested processes that might integrate specific subsets of measures (e.g., Beach, 1956; also see review in Sachs, 1978). However, few studies have approached this issue by subjecting measures to factor analysis, a statistical method that should be well-suited to the task through its use of interindividual correlations among measures to identify the minimal set of processes required to explain most of the observed variations across individuals (Dewsbury, 1979b; Pfaus, Mendelson, & Phillips, 1990; Sachs, 1978).

Not surprisingly, much of the attention in early applications of factor analysis was focused on the behavior of male rats, especially in the first copulatory series. One striking aspect of these analyses is their high agreement. Emerging from each is an Initiation factor identified with ML and IL, a Copulatory Rate factor identified with III, EL, and PEI, and an Efficiency factor (termed Hit Rate in some early papers) identified primarily with MF and IR (see Tables 1 and 2 in on-line supplementary materials). The one disagreement seems minor by comparison and concerns the interpretation of IF: In several of the analyses this loaded on a separate Intromission Count or Mount Count factor (Pfaus et al., 1990; Sachs, 1978) whereas others found it to cluster with MF and IR in the Efficiency factor

(Dewsbury, 1979b).

These studies, then, showed that when male rats are studied in similar ways the resulting factor structures converge impressively. These studies also explored variables with the potential to alter factor structures. One of these is the test situation. Pfaus et al. (1990) tested their animals in bilevel chambers that expanded the range of male and female behaviors. The resulting factor structure also was more complex, most notably in suggesting a fifth factor related to the Anticipation of the behaviors that initiate the more standard copulatory sequence. A second variable with the potential to affect the results of factor analysis is the number of copulatory series observed. In one of his analyses, Dewsbury (1979b) observed male rats in five series. Most of the resulting factor structure was changed relatively little: For the most part, the Copulatory Rate and Intromission Count factors defined on the basis of the first series seemed to selectively "absorb" the corresponding measures from the subsequent series. The biggest change seemed to involve MF and IR, the measures previously identified with the Efficiency of copulatory performance. These continued to cluster together, but with separate clusters for successive copulatory series. This suggests that the processes controlling behavior in successive series differ in some respects and not others, and that the results of factor analysis can help to understand these outcomes.

Perhaps the most relevant and powerful of the variables with the potential to alter factor structure is species. In addition to laboratory rats, Dewsbury (1979b) applied factor analysis to the copulatory patterns of deer mice (*Peromyscus maniculatus bairdi*) and house mice (*Mus musculus*). The results revealed impressive similarities, but also suggested some differences in factor structure across these species (supplementary Tables 1

and 2). One similarity was the emergence from all three analyses of an Initiation factor identified with ML and IL. Beyond this, rats and deer mice differed in the prominence of a Copulatory Rate factor and possibly in the number and identity of the measures defining Efficiency (Dewsbury, 1979b; Pfaus et al., 1990; Sachs, 1978). But house mice seemed even more divergent. Some of the differences separating them from the other species seem possibly minor, involving the elaboration of familiar factors by additional measures, e.g., the loading of III on the Efficiency factor and of MF and EL on an Intromission and Thrust Count factor. Possibly more significant was the emergence of several new factors, most of which seem to reflect the fact that intromissions in house mice involve intravaginal thrusting and consequently are more prolonged than those in rats or deer mice. These differences are consistent with the fact that the intravaginal thrusting shown by house mice defines a pattern of male copulatory behavior that is fundamentally different from that in rats and deer mice (Dewsbury, 1972, 1975, 1979a).

These results show that species can differ in the basic processes identified by factor analysis as underlying mating behavior. Despite this, the range of species subjected to such analyses has not been extended in more than 30 years. We have taken a small step toward the expansion of this range by using factor analysis to describe the organization of male mating behavior in golden hamsters (*Mesocricetus auratus*).

Numerous previous studies have described aspects of sexual behavior in male hamsters (e.g., Beach & Rabedeau, 1959; Bunnell, Boland, & Dewsbury 1977; Reed & Reed, 1946). In the process, researchers have described at least three respects in which the sexual behavior of hamsters seems unusual. First and perhaps most striking is the female's posture of sexual receptivity, lordosis, which can extend for tens of minutes, much longer

than in other rodents (Dewsbury, 1972; Floody & Lisk, 1989). Second, though a focus on copulatory behavior is to be expected during sexual interaction, male hamsters seem unusual in the extent of this focus, showing little other than copulatory behavior during the period leading to ejaculation (Bunnell et al., 1977). Third, males approaching sexual exhaustion after many (typically 8-9) ejaculations depart from their normal copulatory pattern and begin to show "long intromissions" defined by prolonged (generally 4-24 sec) periods of intravaginal thrusting (e.g., Arteaga, Motte-Lara & Velázquez-Moctezuma, 2000; Beach & Rabedeau, 1959; Bunnell et al., 1977). All of these raise the possibility that the organization of copulatory behavior in male hamsters differs significantly from that in other rodents. Though the use here of a difference in female behavior to strengthen the case for a study focusing on males might seem out of place, it is important to recognize that copulation represents a product of social interaction, permitting the responses of each partner to help shape those of the other.

These results suggest that it may be fruitful to further examine the organization of copulatory behavior in male hamsters. To our knowledge, no published study has fully described this behavior on the basis of factor analysis. The elimination of this gap seems intrinsically worthwhile and also has the potential to advance our understanding of the processes that may mediate the impact of physiological and other manipulations on hamster mating behaviors.

Method

Animals and Housing

The data that are the focus of this report were collected from 73 adult male golden hamsters (LVG:Lak outbred strain) that were purchased from Charles River Laboratories

(Wilmington, MA) or bred from Charles River stock. Though we do not have weights for all of these animals, a representative subset of 43 averaged 144.0 g (*SEM* = 2.4) at the time of testing. Males varied in the extent of their prior sexual experience. However, minimal levels of experience and competence were ensured by the completion of at least one screening test requiring ejaculation within 15 min.

Each male was paired with one of 59 adult female hamsters. Each female was bilaterally ovariectomized at least one week before use and later treated with 10-15 µg of estradiol benzoate (EB) in 0.050-0.075 ml of peanut oil injected subcutaneously (sc) about 48 hr before testing, followed by a sc injection of 500 µg of progesterone (P) in 0.05 ml of oil at approximately 6 hr before use. This combination of treatments consistently ensured robust lordosis responses.

All animals were housed individually in 35 X 18 X 18 or 31 X 21 X 21 cm wire-mesh cages in a colony kept at 20-25°C and on a reversed 14:10 hr light:dark cycle. Behavioral tests were concentrated near the midpoint of the dark phase of the daily cycle. Food and water were freely available except during behavioral tests. Conditions of housing and all experimental procedures were approved by Bucknell University's Institutional Animal Care and Use Committee (IACUC).

Procedures

Behavioral tests began with the introduction of a male into a 40 X 20 X 25 cm glass aquarium. After 1-2 min of adaptation, a female was presented, the timing of the encounter beginning with the first social contact. Tests then continued through at least two copulatory series (including the first intromission after the second ejaculation).

In the course of these encounters, behaviors were viewed from the sides and above.

Accordingly, mounts, intromissions and ejaculations were distinguished on the basis of changes in the pattern of pelvic thrusting and movements of the hindlimb that was elevated off the floor. Specifically, intromissions were distinguished from mounts on the basis of the single deep thrust that accompanied just the former. Ejaculations were distinguished from intromissions partly on the basis of a change in the pattern of thrusting but primarily on the basis of spasmodic movements of the elevated hindlimb. Because we did not view encounters from below, we cannot confirm that penile insertion accompanied all of these intromissions. Instead, our definition of this behavior incorporates both the pseudo- and complete-intromissions of Rabedeau (1963), who suggested that these are equivalent in their impact on the male. It also is the case that we relied entirely on overt behaviors and did not confirm the exchange of sperm during ejaculations. However, the criteria we used to define this act draw upon previous studies that did provide such confirmation (Beach & Rabedeau, 1959; Bunnell et al., 1977). Though these earlier studies disagree on the value of hindlimb movements for the recognition of ejaculations, we have found such movements to be both distinctive and highly predictive of other behavioral markers of ejaculation (see further discussion in on-line supplementary materials).

The data collected in each test included the timing of the first mount and intromission within each copulatory series, the timing of each ejaculation, and the total numbers of mounts and intromissions in each series. From these scores we derived all of the standard measures defined in the introduction and Table 1, i.e., mount and intromission latencies for the test as a whole (ML, IL), the ejaculation latency for each of the 2 copulatory series (EL-1, EL-2), the interintromission and postejaculatory intervals for each series (III-1, III-2, PEI-1, PEI-2), the mount and intromission frequencies for each series (MF-1, MF-2, IF-1,

IF-2), and the intromission ratio for each series (IR-1, IR-2). Because of our focus on the first two copulatory series, we did not observe long intromissions and so excluded measures of this behavior from our analyses.

As suggested previously, most of these measures were defined in standard ways (e.g., Beach & Rabedeau, 1959; Bunnell et al., 1977). However, we did depart from the standard definitions in two ways. First, to decrease the chances of mistaking a failure to detect the female's presence for a disinclination to initiate copulation, both ML and IL were measured from the initiation of contact rather than the female's introduction. Second, we think that the orientation of a mount (from the rear or not) does not materially alter the information it provides about sexual motivation or performance: If mounts generally are viewed as decreasing the efficiency of performance, it makes no sense to excuse males for mounts that are especially inefficient. Therefore, we scored mounts without regard for a male's orientation rather than requiring initiation from the rear. Each of these changes does create a difference between this and many previous studies. At the same time, further analyses suggest that these changes are likely to have had little impact on these results (see details in on-line supplementary materials).

Each of the tests described here was included in one of six studies of the effects of cholinergic or dopaminergic drugs on hamster mating behavior. Each of these studies included 1-2 tests of responses to placebo treatments consisting of the intraperitoneal (ip) injection of 1 ml/kg of 0.9% NaCl at 15-45 min before the start of testing. These were incorporated in a counterbalanced order into series of 3-6 weekly behavioral tests. The focus here is on the behavior observed in each male's first control (placebo) test.

This focus on control tests eliminates many, but not all, of the procedural differences

across the studies from which these data were drawn. One of those that could not be eliminated is the variability noted above in the timing of placebo injections. Another results from the fact that the subjects in four studies of cholinergic mechanisms were treated with methylscopolamine (scopolamine methyl bromide, Sigma; 1 mg/kg in saline injected sc or ip 15 min before placebo treatment) to reduce or cancel any peripheral responses to systemic treatment with cholinergic agonists. However, there are several reasons to think that these procedural differences are irrelevant to the present results. First, an unpublished study in our lab has found sexual behavior to be unaffected by treatment with methylscopolamine alone. Second, the same outcome has been reported in a study of male rats that included methylscopolamine doses much higher than any used here (Ahlenius & Larsson, 1985). Third, as a more comprehensive way of assessing the impact of these and other procedural differences, we ran analyses of variance (ANOVAs) comparing subgroups of subjects on each of the 14 measures specified above. In no case did a reliable difference across subgroups, or studies, emerge (see Table 3 in on-line supplementary materials).

Partly because these results emerged from separate studies scored by different sets of observers, the intra- and inter-observer reliabilities of the behavioral observations were assessed as detailed in the on-line supplementary materials. These analyses yielded average intra- and inter-observer correlations of 0.94 and 0.96, respectively, suggesting adequately high levels of each type of reliability.

Analysis

Means and 95% confidence intervals for each of the 14 measures specified above were calculated to describe male behavior in hamsters and to permit the comparison of

quantitative aspects of this behavior with those in other rodents. Interindividual correlations among these measures also were calculated, to extend this description and provide the correlation matrix required for factor analysis.

Principal components factor analysis with orthogonal rotation (varimax, SPSS) was applied to these data, duplicating the approach used in all previous studies applying factor analysis to patterns of male copulatory behavior (Dewsbury, 1979b; Pfaus et al., 1990; Sachs, 1978). In the interpretation of the resulting factor structure, attention was focused on the factors that individually accounted for at least 10% of the interindividual variance, as is standard practice. Each such factor was labeled and interpreted on the basis of the few variables that most heavily loaded on it, or were best accounted for by it.

The resulting factors and factor structures were then compared with those described previously for other rodents. These comparisons suggested differences in patterns of behavior that, in turn, highlighted specific correlations among measures. The reliability of differences in these key correlations was assessed (Chen & Popovich, 2002; Steiger, 1980) after having confirmed the existence of some reliable difference between the relevant correlation matrices (Larntz & Perlman, 1988). This approach was designed to follow the usual statistical method (e.g., in studies using ANOVA), in which the examination of specific effects is conditioned on the existence of some related but more global effect. In general, it may represent a less powerful way of comparing factor structures than the use of confirmatory factor analysis to test the fit between alternative hypothetical models and each of the critical correlation or covariance matrices (Kline, 1994; Thompson, 2004). However, with the exception of the rats described by Dewsbury (1979b), the samples available for comparison here are much too small for the latter approach.

These comparisons of factor structures across species focused on behavior in the first copulatory series, reflecting the restriction of most prior factor analytic studies to that period. They also focused on analyses of behavior in male hamsters, rats, and deer mice: House mice received less attention at this point in the analysis because of the unavailability of a full correlation matrix and the contrast between their basic copulatory pattern and that shared by the other species (Dewsbury, 1972, 1975). Among the several analyses of rats, that by Dewsbury (1979b) was emphasized because of its relatively large sample and comparable, relatively simple, test conditions.

All of the statistical analyses here used a probability of .01 to define significance, and considered probabilities between .01 and .02 to have approached significance. Most of these analyses were two-tailed. However, one-tailed tests were used in many of the comparisons of specific correlations because of their focus on differences in predicted directions.

Results and Discussion

Average Levels of Performance

Average levels of performance on each measure and for each of the two copulatory series are summarized for our hamsters at the top of Table 2. These data suggest changes across series for most of the measures that are tied to specific series (III, EL, PEI, MF, IR, IF). For all of these except PEI, these decreases (III, EL, MF, IF) or increases (IR) were found to be highly reliable by repeated-measures ANOVA, $F(1,72) \geq 15.04$ for the main effects of copulatory series, each $p < 0.001$).

These results resemble previous descriptions of male hamsters both in absolute levels and in the changes in III, EL, and IF exhibited across copulatory series (Arteaga-Silva et

al., 2005; Beach & Rabedeau, 1959; Bunnell et al., 1977; Dewsbury, Lanier, & Oglesby, 1979; Huck, Lisk, Allison, & Van Dongen, 1986; Lehman, Powers, & Winans, 1983; Miernicki, Pospichal, & Powers, 1990; Rabedeau, 1963). They extend previous descriptions by documenting changes over series in MF and IR, but disagree with some previous reports of progressive increases in PEI (Beach & Rabedeau, 1959; Bunnell et al., 1977). However, other results suggest that the emergence of consistent changes in this parameter may simply require more than two copulatory series (Arteaga-Silva et al., 2005).

These scores were compared with normative data for rats (Pfaus et al., 1990; Sachs, 1978), deer mice (Dewsbury, 1979a), and house mice (McGill, 1962; see Table 1 in on-line supplementary materials for some normative data on rats and deer mice). These comparisons suggest a separation of measures into at least four clusters. The first includes the measures (ML, IL) that seem most clearly to be species-specific, with average levels of performance that seem unique to each species. At the opposite extreme, the second category includes the one measure (IR) for which scores seem comparable across all four species. The third cluster includes measures (MF, IF) on which performance seems predicted by basic copulatory pattern (Dewsbury, 1972, 1975) in the sense that average scores are similar in the species (hamsters, rats, deer mice) that share a basic pattern but very different in the one that does not (house mouse). The most complex, and possibly interesting, category is the fourth, consisting of measures (III, EL, PEI) that exhibit only partial consistency with basic copulatory patterns. Here, the focus is on the three species that share a basic pattern: Whereas rats and deer mice seem to show comparable levels of III, EL and PEI, hamsters show much briefer intervals of each type despite the common basic pattern. As might be expected, house mice seem even more divergent on EL and PEI,

the second of which is so prolonged that it is rarely measured. On III, however, house mice resemble rats and deer mice, setting hamsters apart from all three of the other species.

These results suggest similarities and differences in quantitative indices of male copulatory behavior across rodent species. To a degree, relative levels of performance follow fluctuations in basic copulatory patterns. At the same time, it seems clear that the sharing of a copulatory pattern does not guarantee similar quantitative scores.

In turn, these results suggest that both similarities and differences in behavioral organization will emerge from the factor analytic descriptions of these animals. Further, this may be nearly as true for the three species that share a basic copulatory pattern as it is for the entire set. Finally, for these three focal species, it might be expected that some of the most interesting differences in factor structure will revolve around the measures that seem to set hamsters apart from the others and that, in the latter, sometimes cluster to define a Copulatory Rate factor, i.e., III, EL, and PEI (Dewsbury, 1979b; Pfaus et al., 1990; Sachs, 1978).

Interindividual Correlations

Correlations among the standard measures of male behavior in hamsters are detailed in the lower half of Table 2. The corresponding matrices described by Dewsbury (1979b) for rats and deer mice are reproduced in Table 2 of the on-line supplementary materials (also see matrix for house mice in Dewsbury (1979b) and those for rats in Pfaus et al. (1990) and Sachs (1978)).

The matrix for hamsters includes correlations that may be of interest, both on their own and as determinants of the relationships that will be highlighted by the factor analysis that is the focus of this report. Four clusters of correlations seem noteworthy. First, ML,

IL, and PEI-1 (but not PEI-2) are highly intercorrelated. The correlation of the first two is common and expected, but the correlation of each of these with PEI-1 represents a point of departure of these results from many of those previously reported for rats and other species (Dewsbury, 1979b; Pfaus et al., 1990; Sachs, 1978). Second, essentially all of the other reliable correlations are grouped by copulatory series, so that measures of performance in the first series correlate almost exclusively with other measures from the first series and vice versa. This suggests that the processes that control copulation in male hamsters differ across series, a point consistent with the distinct patterns of correlation involving PEI in the two series. It also confirms the value of including more than one copulatory series in analyses of this sort. Third, MF, IR, III, and EL all are highly intercorrelated within each series, but perhaps more strongly in the first than the second. These close relations probably are due partly, but only partly, to the facts that MF enters into the calculation of IR and EL does the same for III. Fourth, in addition to its involvement in the preceding cluster, EL correlates reliably with IF, but more strongly in the second copulatory series.

Factor Analysis

Application to data describing mating in male hamsters.

The application of factor analysis to the full correlation matrix in Table 2 resulted in the identification of five factors, together accounting for 81.2% of the interindividual variance. Table 3 identifies these factors and specifies for each the measures that loaded most strongly on it and the percentage of variance that each explains. It also suggests labels for each factor on the basis of the major loadings. Table 4 describes the results of a similar analysis limited to the data from the first copulatory series. As previously mentioned, these results will be emphasized in the later comparisons of male patterns across species.

The first two factors in the more complete analysis reflect two of the trends previously identified in the intercorrelations. First, each is identified most strongly with the measures MF, IR, III, and EL. Second, these factors differ from each other primarily in their identifications with the first or second copulatory series. The labeling of these factors reflects this distinction. Beyond this, the suggestion that both of these factors relate to the efficiency of copulatory performance follows from the definition of IR, the partial determination of IR by MF, and the fact that some earlier reports have identified a factor associated with MF, IR, and III or EL with hit rate or efficiency (Dewsbury, 1979b).

The third factor is closely associated with ML and IL, obvious measures of how quickly males initiate copulatory behavior. The fact that PEI-1 also loads strongly on this factor suggests that it relates not just to the initiation of copulation but also to its resumption at the end of the pause that typically follows the first ejaculation. The label suggested for this factor follows directly from these observations, especially the first.

The last two factors both relate most closely to IF and EL, but again for one or the other copulatory series. The identification of these factors with intromission follows earlier reports in which similar factors were suggested to relate to the counting of thrusts, mounts or intromissions (Dewsbury, 1979b; Pfaus et al., 1990). In turn, it seems likely that these labels were based in part on the common suggestion that ejaculation (and thus EL) is determined by the summed excitation derived from a series of intromissions that meets a numerical threshold that can vary over copulatory series (e.g., see discussion of "copulatory mechanism" in Sachs, 1978).

Comparison of factor structures across species.

The factor structures described in Tables 3 and 4 parallel the results of prior factor

analytic studies (Dewsbury, 1979b; Pfaus et al., 1990; Sachs, 1978; see Table 2 in on-line supplementary materials) in suggesting the existence of (a) a factor defined in part by ML and IL, (b) one or more factors defined in part by MF and IR, and (c) one or more factors defined in part by IF. Of these, the last has the least support. Such a factor is evident in four studies of rats by other authors, but only on one of the three observations of these animals in Dewsbury's (1979b) sample. It also appeared on just one of the two tests administered to the deer mice described by Dewsbury (1979b).

The interpretation of some of these factors is complicated by the partial determination of IR by MF and by the identity of ML and IL whenever the first copulatory act in a series is an intromission. Nevertheless, these parallels and factors suggest that the minimal set of processes required to understand male copulatory behavior in rodents includes one revolving around the initiation of the behavior, at least one revolving around its efficiency, and at least one focusing on the impact of intromissions. Each of these seems to represent a potentially important cross-species similarity supported and extended by these results.

At the same time, these factor analytic results suggest at least four ways in which the processes that control copulatory behavior in male hamsters differ from those in other rodents. First, hamsters seem unique or nearly so among the few species examined in the loading of PEI (albeit for just the first copulatory series) on the factor relating to the initiation of sexual behavior (cf., Dewsbury, 1979b; Pfaus et al., 1990; Sachs, 1978). This difference is quite clear in most comparisons of hamsters and rats or deer mice. However, as suggested previously, it does not extend to house mice, in which an extremely long postejaculatory refractory period typically excludes the collection of data on PEI (Dewsbury, 1979b; McGill, 1962).

Second, hamsters seem unusual in some aspects of the factor(s) related to the efficiency of copulatory performance. Here, the fact that measures clustered by copulatory series is unusual, but possibly only because few studies have varied series: In the one previous study to make this distinction (Dewsbury, 1979b), the factor structure for rats included series-specific "hit rate" factors consistently loaded by MF and IR, as in the present results. More interesting and suggestive of species differences is the loading on the Efficiency factors here by the relevant III and EL (those for the corresponding copulatory series). This pattern in hamsters extends a similar one in house mice, in which MF and IR combined with III to define Efficiency (Dewsbury, 1979b). In contrast, such patterns have appeared weakly or not at all in studies of rats (Dewsbury, 1979b; Pfaus et al., 1990; Sachs, 1978) and on only one of the two tests of deer mice by Dewsbury (1979b).

Third, hamsters departed from some previous analyses in the structure of the factors loaded by IF. The analysis of hamsters revealed IF-related factors tied to each copulatory series. Much as was the case above, this finding is unique but hard to judge since the role of copulatory series has been examined in just one other study (Dewsbury, 1979b). Hamsters also differ from most prior analyses of rats (Dewsbury, 1979b; Pfaus et al., 1990; Sachs, 1978) in the loading of this intromission-centered factor by EL as well as IF, a combination that may emphasize the number of intromissions as a determinant of ejaculation. But this joint loading on an IF-related factor is not unique, having been reported in at least one previous study of rats (Pfaus et al., 1990) and in one of two tests of deer mice (Dewsbury, 1979b). Perhaps most importantly, this pattern seems to resemble that described just above in being characteristic of house mice as well as hamsters (Dewsbury, 1979b).

Fourth, possibly as a consequence of some of the differences discussed earlier, the organization of copulatory behavior in male hamsters seemed to differ from that in some of the other rodents subjected to factor analysis in *not* exhibiting a Copulatory Rate factor identified with the combination of III, EL, and PEI. This factor has been one of the most consistent outcomes of previous analyses of rats (Dewsbury, 1979b; Pfaus et al., 1990; Sachs, 1978). At the same time, it is not evident in house mice and seems weak, if present at all, in deer mice (Dewsbury, 1979b).

Statistical analysis of species differences in factor structure.

The description of possible species differences in factor structure raises the issue of the reliability of these differences. As explained previously, we addressed this issue through statistical comparisons of correlation matrices and specific correlations. The availability of the relevant correlation matrices limited these analyses to the first copulatory series and to comparisons of hamsters with rats and deer mice. To limit the number of specific correlations undergoing analysis, these analyses also were limited to each animal's first test and to the largest of the available samples of rats (Dewsbury, 1979b; see previous results summarized in supplementary Tables 1 and 2).

The first step in this analysis involved the comparison of entire correlation matrices using the method of Larntz and Perlman (1988). In particular, we compared the matrix describing interindividual correlations in hamsters (Table 2) with those for rats and deer mice (Dewsbury, 1979b; supplementary Table 1), in each case considering only results for the first copulatory series of the first test. These analyses confirmed the existence of highly reliable differences across these correlation matrices without specifying their sources (the specific correlations most responsible for them) or implications, $T_3(28) \geq 4.34$, $p \leq .001$.

The remaining steps in the analysis involved the assessment of specific correlation coefficients, tailored to the species differences in factor structure suggested in the preceding section. Thus, we next revisited the initiation of copulatory behavior by more carefully examining the strength of the link between PEI and the measures that most consistently define the Initiation factor, ML and IL. To be supported, the species difference in initiation suggested previously requires significantly higher correlations of PEI with each of ML and IL in hamsters than in rats or deer mice. Such a difference was confirmed for each of the four relevant comparisons, $Z(132 \text{ or } 379) \geq 2.43$, $p \leq .008$, 1-tailed (Chen & Popovich, 2002; Steiger, 1980). A specific illustration is provided by the correlation of PEI with ML, which amounts to .535 in hamsters (Table 2) but .17 in rats (Dewsbury, 1979b; supplementary Table 1). These correlations differ significantly ($.535 > .17$), $Z(379) = 3.21$, $p = .001$, 1-tailed. The results of these analyses suggest that hamsters do differ from rats and deer mice in the factor or conceptual variable most closely identified with the initiation of male copulatory behavior. More specifically, these results suggest that, in hamsters but not these other rodents, a single process controls initial sexual arousal and recovery from the refractory state that immediately follows an initial ejaculation. This presents an interesting contrast with previous factor analytic results as well as many other data on male rats (see brief review in Sachs, 1978).

The second of the suggested species differences concerns the process controlling the efficiency of male copulatory performance. In many, though not all, analyses of data from rats and deer mice, the Efficiency (or "Hit rate") factor is identified much more closely with MF and IR than with any other measure. In contrast, our results suggest that the efficiency of performance in male hamsters relates nearly as strongly to III and EL as to MF and IR,

at least in the first copulatory series. These differences suggest that correlations of MF and IR with each of III and EL should be significantly higher in hamsters than in rats or deer mice. This assessment requires the consideration of four pairs of correlation coefficients in each comparison of species, or eight pairs of correlation coefficients in all (four to compare hamsters and rats, four to compare hamsters and deer mice; see Table 2 here and Table 1 in the on-line supplementary materials). Among these, five differences between correlations were found to be reliable and in the expected direction, $Z(132 \text{ or } 379) \geq 2.33$, $p \leq .010$, 1-tailed (Chen & Popovich, 2002; Steiger, 1980). Another two were found to be nearly reliable, $Z(132 \text{ or } 379) = 2.11 \text{ or } 2.19$, $p \leq .017$, 1-tailed. The only clear exception reflects the similar correlations of IR and EL that were observed in hamsters and rats.

Taken together, these results support the suggestion that a factor identified with the efficiency of copulatory performance is organized differently in hamsters as opposed to other rodents with generally similar mating patterns. Efficiency in hamsters seems to involve a wider range of parameters than in the other species considered here. These measures could be linked by a dependence of ejaculation (EL) on the spacing of intromissions (III), which in turn is affected by the intrusion of mounts (MF, IR). The species difference in factor structure could reflect a greater prominence of these links in male hamsters. Alternatively, it is possible that at least some of the species differences that factor analysis reveals in the organization of measures of male performance reflect differences in female behavior, specifically the unusually prolonged lordosis responses characteristic of female hamsters (e.g., Bunnell et al., 1977; Dewsbury, 1972). It is possible that complete immobility on the part of the female increases a male's ability to pace and integrate elements of his behavior, in the process revealing relations among

behaviors that can be obscured by a more complex pattern of male-female interaction.

Though we commented above on possible differences between hamsters and other species in the structure of the factors loaded by IF, these differences seemed relatively subtle and consequently were not subjected to statistical analysis. Thus, the last suggested difference that seemed to merit further analysis is that revolving around the rate at which copulatory behavior unfolds. As noted previously, a Copulatory Rate factor identified with III, EL, and PEI has been one of the most consistent outcomes of previous analyses of rats (Dewsbury, 1979b; Pfaus et al., 1990; Sachs, 1978; supplementary Table 2). At the same time, it is not evident in house mice and seems weak or absent in deer mice (Dewsbury, 1979b). Our data suggest that this factor is weak or absent in hamsters as well: Though III and EL did cluster, the net effect of their affiliation with MF and IR, and of their separation from PEI, was to modify the Initiation and Efficiency factors rather than create a Copulatory Rate factor.

In view of these similarities and differences across species, our statistical analyses focused on the relative prominence of a Copulatory Rate factor in hamsters and rats. All of the earlier comparisons of these species are relevant here, since they support correlations of measures in hamsters *other than* those associated with a Copulatory Rate factor (i.e., of PEI with ML and IL, of III with MF and IR, of EL with MF). In addition, this species difference would seem to require that correlations of PEI with each of III and EL be significantly weaker in hamsters than in rats. Reliable or nearly reliable differences were confirmed for each of these two comparisons, $Z(379) \geq 2.15$, $p \leq .016$, 1-tailed (Chen & Popovich, 2002; Steiger, 1980). This supports the inference that the Copulatory Rate factor evident in previous analyses of rats is significantly altered or absent in hamsters.

Conclusions

Taken together, these analyses identify several significant ways in which male hamsters differ from other rodents in the organization of their copulatory behaviors. In the process, they add to the dimensions on which rodents vary in their patterns of mating behavior. Previous researchers established that rodents differ in their basic copulatory patterns (Dewsbury, 1972, 1975) and on a variety of latency and frequency measures of copulatory performance (e.g., Sachs & Dewsbury, 1978). But the few species subjected to factor analysis seemed more similar than different, showing factor structures with few differences other than those required to accommodate differences in basic copulatory pattern (Dewsbury, 1979b; Pfaus et al., 1990; Sachs, 1978). The present results depart from this pattern in two major respects, by suggesting new species differences in factor structure and in suggesting that these are largely orthogonal to any differences in basic copulatory pattern: Hamsters seem possibly to be more similar in factor structure to house mice than either rats or deer mice, despite the fact that house mice are the outliers here in terms of basic copulatory pattern.

Factor analysis obviously represents just one of many ways of describing behavior. Further, it is neither sufficient in itself nor perfect, being subject to a variety of limitations, especially when applied to small samples (Dewsbury, 1979b). Nevertheless, factor analytic descriptions can extend and improve our analyses of reproductive behavior in at least two ways. First, they can identify conceptual variables that may correspond to distinct physiological processes or subsystems (Sachs, 1978). Though such processes should not be considered to be indivisible (Pfaus et al., 1990; Sachs, 1978), the measures that define them presumably cohere for a reason and consequently can tell us potentially useful things

about the forces and mechanisms that cause behavior to be organized as it is. At the same time, however, the conceptual variables suggested by a factor analysis will be useful only if the factor analytic solution extends to the species at hand, something that cannot simply be assumed on the basis of similarities across the earliest such descriptions.

Second, the consideration of factor analytic descriptions can improve the statistical analysis of behavioral data (Pfaus et al., 1990). For example, many studies of male behavior consider many individual measures. In their analyses, however, many of these studies treat these measures as independent. Unfortunately, to assume this inappropriately can increase the risk of experiment-wise error, thus possibly distorting one's inferences and conclusions. An obvious implication of most factor analytic solutions is that measures can cluster and relate, possibly requiring appropriate adjustments in their statistical analysis. Again, effective adjustments require knowledge of the behavioral organization that actually operates in the species under examination, which may require further factor analytic studies of any species other than rats, deer mice and hamsters.

Finally, the existence of significant species differences in the factor structure of mating behavior raises the question of how these differences might arise. Unfortunately, we know very little about the responsiveness of factor structures to experimental manipulation. Dewsbury (1979b) considered differences in strain, sample size, number of tests, and copulatory series and concluded that these had relatively little impact on factor structure in rats. Pfaus et al. (1990) tested their animals in multi-level compartments that seemed to foster more complex social interactions than observed in the simpler chambers used in most studies of male behavior. The assessment of these interactions required the use of new measures that, in turn, altered factor structure. But these alterations were

limited in scope, with most contained within a novel factor defined by the new measures: The more standard factors described by earlier studies of rats were largely preserved in spite of the environmental and behavioral changes.

These observations suggest that factor structure, like basic copulatory pattern, is quite stable and resistant to change. At the same time, it is important to recognize how little work has addressed this issue. In this regard, we think that Pfaus et al. (1990) were very much on the right track in recognizing the facts that mating requires an interaction of two animals and that critical influences structuring male behavior may be derived from the behavior of their female partners (also see Dewsbury, 1972, 1975). Such influences may be especially relevant to the differences suggested here between the behavior of hamsters and other rodents. For example, though the basic elements of male behavior in hamsters may differ from those in rats, any such difference probably pales in comparison to the contrast between the prolonged lordosis responses of female hamsters and the pattern characteristic of female rats, in which instances of lordosis represent brief reflexive responses to individual mounts and are separated by periods of activity that can include hopping, darting and other species-typical forms of proceptive behavior (e.g., Bunnell et al., 1977; Dewsbury, 1972; Pfaff, 1980). This contrast raises the possibility that any departures of hamsters from rats in the organization of male mating behavior are products of species differences in female, rather than male, behavior: In effect, these differences may not originate in the males but instead be imposed on them by differences in the behavior of their female partners. This suggests that it may be especially interesting to determine the extent to which manipulations of behavior in female hamsters can alter the organization of behavior in males, perhaps in the process reducing or erasing some of the

species differences described in this report.

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Table 1

Standard measures of male copulatory behavior

Measure	Abbreviations	Units
Mount latency	ML	sec
Intromission latency	IL	sec
Ejaculatory latency	EL-1, EL-2	sec
Interintromission interval	III-1, III-2	sec
Postejaculatory interval	PEI-1, PEI-2	sec
Mount frequency	MF-1, MF-2	per copulatory series
Intromission frequency	IF-1, IF-2	per copulatory series
Intromission ratio	IR-1, IR-2	none

Note. Listed in order of appearance in Methods. The numbers in some abbreviations designate a copulatory series for measures that are specific to series.

Table 2:

Means, 95% confidence intervals, and correlations for standard measures of male behavior

	ML	IL	MF-1	IF-1	IR-1	III-1	EL-1	PEI-1	MF-2	IF-2	IR-2	III-2	EL-2	PEI-2
M	69.1	100.1	3.5	7.1	0.71	16.4	108.5	31.9	0.5*	2.1*	0.87*	10.4*	22.2*	34.6
CI	18.4	21.4	0.8	0.7	0.05	2.7	18.8	3.0	0.2	0.4	0.05	1.4	5.3	2.6
ML	-													
IL	**.902**	-												
MF-1	.099	**.355**	-											
IF-1	.074	.083	-.026	-										
IR-1	-.086	**-.315**	**-.857**	**.370**	-									
III-1	.235	.272	**.597**	-.255	**-.627**	-								
EL-1	.257	.292	**.617**	**.387**	**-.325**	**.671**	-							
PEI-1	**.535**	**.497**	.066	.001	-.082	.185	.115	-						
MF-2	-.066	-.076	.011	.051	.048	-.067	-.057	.161	-					
IF-2	-.055	-.040	.180	**.313**	-.051	.011	.166	.008	.089	-				
IR-2	.011	.034	.041	-.038	-.050	.082	.094	-.281	**-.860**	.049	-			
III-2	-.124	-.096	.065	-.041	-.009	-.022	-.024	-.162	**.683**	.035	**-.485**	-		
EL-2	-.131	-.077	.239	.148	-.100	.031	.115	-.089	**.508**	**.731**	-.278	**.653**	-	
PEI-1	.208	.264	.253	-.015	-.236	.235	.170	.185	.162	.244	-.057	.193	**.318**	-

Note. *M* = mean; *CI* = 95% confidence interval; the other abbreviations that appear across the top and along the left margin refer to standard measures of male behavior that are defined in the text. In the table's upper section, asterisks indicate measures showing reliable changes from the first copulatory series, $F(1,72) \geq 15.04$, $p < .001$, partial eta squared $\geq .173$, ANOVA. The

Table 3

Major loadings emerging from factor analysis of data from both copulatory series

	Factor				
	Efficiency-1	Efficiency-2	Initiation	Intromissions-2	Intromissions-1
	MF-1, .899	**MF-2, .953**	**ML, .916**	**IF-2, .860**	**IF-1, .915**
	III-1, .850	**IR-2, -.907**	**IL, .874**	**EL-2, .812**	**EL-1, .599**
	IR-1, -.847	**III-2, .771**	**PEI-1, .775**	**PEI-2, .582**	IR-1, .348
	EL-1, .721	EL-2, .463	PEI-2, .332		
% variance	20.9	18.5	17.5	13.7	10.5

Note. Total variance accounted for = 81.2%. The percentage of variance accounted for by each factor is indicated at the bottom of that column (row labeled % variance). Factors are ordered so that the percentage of variance accounted for decreases from left to right. To emphasize the measures most closely associated with factors, loadings of less than .300 are omitted and those of .500 or greater are bolded.

Table 4

Major loadings emerging from factor analysis of data from the first copulatory series

	Factor		
	Efficiency	Initiation	Intromissions
	MF-1, .917	**ML, .937**	**IF-1, .941**
	IR-1, -.874	**IL, .890**	**EL-1, .626**
	III-1, .837	**PEI-1, .764**	IR-1, .325
	EL-1, .695		
% variance	36.2	28.9	17.7

Note. Total variance accounted for = 82.7%. The percentage of variance accounted for by each factor is indicated at the bottom of that column (row labeled % variance). Factors are ordered so that the percentage of variance accounted for decreases from left to right. To emphasize the measures most closely associated with factors, loadings of less than .300 are omitted and those of .500 or greater are bolded.

Supplemental materials to appear on-line in support of

Organization of Mating Behavior in Male Hamsters

by

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Validity of distinction between intromissions and ejaculations

Studies of male copulatory behavior in hamsters and other rodents consistently have documented a postejaculatory pause that exceeds the average separation between intromissions (e.g., Sachs & Dewsbury, 1978). Any tendency to confuse intromissions and ejaculations should reduce the extent and consistency of this difference.

To estimate the extent to which our methods created such confusions, we directly compared the durations of the intervals separating ejaculations from the intromissions just before and after them in a separate, supplementary, set of 30 encounters (including 60 copulatory series) that was videotaped for analyses of the reliability of our behavioral methods (see later section of this supplement).

This comparison revealed a highly reliable difference between the intromission-to-ejaculation and ejaculation-to-intromission intervals (for I-to-E interval, M = 7.1 sec, 95% CI = 0.6; for E-to-I interval, M = 23.2 sec, 95% CI = 1.6; $F(1/29) = 282.49$, $p < .001$, partial eta squared = .907). Consistent with the reliability of this effect was a near absence of overlap between these distributions of scores. For example, 56 of the 60 I-to-E intervals were 10 sec or less whereas no E-to-I interval this brief was observed. Conversely, just two of the I-to-E intervals exceeded 15 sec whereas all of the E-to-I intervals did. These data support the ability of our behavioral definitions and methods to consistently distinguish intromissions and ejaculations.

Impact of changes in criteria used to initiate encounters and define mounts

As indicated in our full report, we considered encounters to begin at the time of the initial social contact rather than upon the female's introduction. Further, we defined mounts without regard to their orientation rather than following the more standard practice

of scoring only mounts that are oriented from the female's rear. To assess the impact of these changes, we relied on the new set of 30 encounters that was videotaped for analyses of the reliability of our behavioral methods and is described in greater detail later in these on-line supplementary materials.

For the purposes of this assessment, each of the videotaped encounters was scored using both of the alternative definitions of initiation and distinguishing mounts that were properly and improperly oriented. These analyses revealed, first, that the mean time separating the female's introduction from the initiation of contact was 3.0 sec, which represents just a small fraction of the mean mount latency, intromission latency and total encounter duration (of 54.7, 73.2 and 208.5 sec, respectively). Second, we found that the typical encounter in this supplementary set included no improperly oriented mount (mode and median = 0), possibly reflecting both a high quality of orientation and a relatively low frequency of mounts (median total mounts/encounter = 2). From these results, we infer that our definitional changes are likely to have had at most a minor impact on our analyses of male hamster mating patterns and on the results emerging from these analyses.

Analyses of intra- and inter-observer reliabilities

To assess the reliability of the methods used to train observers and score sexual interactions, we videotaped 32 male-female encounters, each through two copulatory series. Despite the use of a rotating platform to increase the visibility of the hindleg that was elevated during mounts, it was necessary to exclude two encounters in which this leg was completely obscured at critical times.

The remaining 30 encounters were scored carefully by the principal investigator, using multiple and frame-by-frame viewings to ensure the accuracy of all scores. Based on

these results, two measures (MF-2 and IF-2) were excluded from further consideration on the basis of their highly restricted ranges. The nine measures selected for analysis included the latencies of the first mount and intromission in each copulatory series, the latency of each ejaculation, the latency of the first intromission after the second ejaculation, and the frequencies of mounts and intromissions in the first copulatory series. All latencies were measured from the time at which the male initiated social contact.

From this set of 30 encounters, eight were selected for use in tests of reliability. These were selected so as to best represent the distributions of each of the nine measures identified above. With just one exception, these eight encounters included those that most closely approximated the first quartile, median and third quartile of each of these distributions.

Fourteen observers were recruited to view and score these videotapes. Of these, four had limited prior experience viewing such encounters whereas 10 had none at all. Each volunteer received two hours of training that was adjusted to the current focus on videotaped encounters but otherwise was similar to that routinely provided to student researchers in our lab, including the observers responsible for the data subjected to factor analysis and described in the companion full report.

Following this training, the 14 observers were divided into seven pairs, reflecting our routine practice of always scoring encounters in groups of two-three. Each pair independently scored each of the eight selected encounters in the course of a single continuous viewing. Approximately one week later, this exercise was repeated, but after the males had been relabeled and their order of presentation scrambled.

To assess levels of intra-observer reliability, the scores provided by each team in its first and second viewings were used to calculate Pearson correlation coefficients for each of the nine measures of male copulatory behavior. These then were averaged across measures and teams, yielding a mean correlation coefficient of 0.94, suggestive of very high levels of intra-observer reliability.

The standard way of assessing levels of inter-observer reliability would require the calculation, for every measure, of every possible correlation across teams. However, a much simpler method for the estimation of the average correlation coefficients by analysis of variance (ANOVA) is described by Rosenthal and Rosnow (1991). This yielded estimates of the average inter-observer (inter-team) reliability that ranged between 0.90 and 0.99 across measures, with a grand mean of 0.96. To confirm the accuracy of these estimates, all possible correlations were calculated for the one measure that ANOVA identified as being least reliable, and possibly most likely to be problematic (MF-1). This yielded an average inter-team correlation of 0.90, essentially identical to the ANOVA-based estimate. The net effect of these analyses is to suggest that our methods of training and scoring are highly reliable, both within and across observers.

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Table 1

Descriptive data and correlations for standard measures of male behavior in rats and deer mice

	ML	IL	MF	IF	IR	III	EL	PEI
Weighted means and SEMs for combined sample of 41 rats described by Sachs (1978)								
M	18.7	24.2	3.3	8.9	0.75	49.5	372.8	421.1
SEM	3.5	3.7	0.4	0.5	0.03	6.9	46.4	19.2
Means for 16 deer mice described by Dewsbury (1979a)								
M	1255	1295	1.5	6.4	0.81	71.6	300.1	534.9
Correlation matrices for rats (below horizontal) and deer mice (above horizontal)								
ML	-	.98	.03	.07	.03	-.09	.10	-.07
IL	.72	-	.12	.10	-.02	-.10	.09	-.06
MF	-.09	.20	-	.41	-.70	.03	.25	.13
IF	-.12	-.12	.30	-	.20	-.35	.44	-.05
IR	.04	-.25	-.86	.01	-	-.34	.03	-.19
III	.30	.32	.25	-.11	-.34	-	.39	.20
EL	.21	.23	.39	.41	-.29	.82	-	.02
PEI	.17	.22	.18	.03	-.18	.44	.42	-

Note. *M* = mean; *SEM* = standard error of the mean; the other abbreviations that appear across the top and along the left margin refer to standard measures of male behavior that are defined in the text. All correlations are from Dewsbury (1979b), which reports the results of factor analyses of 312 rats and 65 deer mice. However, average levels of behavior are not included in that report, requiring the use of other sources for the descriptive results in the upper half of this table. The report by Dewsbury (1979a) omits the measure IR, so that the value for deer mice provided here was estimated using the average values of MF and IF.

Table 2

Factors and major loadings emerging from factor analyses of rats and deer mice

Factor structure for rats

	Copulatory rate	Initiation	Hit rate
	EL, .93	**ML, .80**	**IR, .96**
	III, .78	**IL, .80**	**MF, -.61**
	PEI, .64	**IF, -.61**	
	IF, .42		
	ML, .31		
% var	37	15	22

Factor structure for deer mice

	Copulatory rate	Initiation	Hit rate	Intromission count
	III, .95	**ML, .99**	**MF, .90**	**EL, .85**
	IF, -.45	**IL, .99**	**IR, -.90**	**IF, .84**
	EL, .44			MF, .36
	PEI, .33			
% var	15	27	24	19

Note. Summary of results reported by Dewsbury (1979b). Total variance accounted for = 74% (rats) or 85% (deer mice). The percentage of variance accounted for by each factor is indicated at the bottom of that column (rows labeled % var). To emphasize the measures most closely associated with factors, loadings of less than .300 are omitted and those of .500 or greater are bolded.

Table 3

Performance differences across subgroups included in factor analysis

	Subgroup # (*N*)					
Measure	1 (11)	2 (19)	3 (15)	4 (10)	5 (8)	6 (10)
ML	54.7 (47.5)	73.7 (36.1)	44.8 (40.6)	95.8 (49.8)	106.3 (55.7)	56.3 (49.8)
IL	90.6 (55.8)	107.6 (42.4)	75.5 (47.7)	136.3 (58.5)	122.3 (65.4)	79.4 (58.5)
III-1	22.5 (6.9)	16.5 (5.3)	16.2 (5.9)	19.7 (7.2)	11.7 (8.1)	10.6 (7.2)
III-2	12.3 (3.8)	10.1 (2.9)	11.4 (3.2)	9.3 (3.9)	7.9 (4.4)	10.4 (3.9)
EL-1	111.9 (48.1)	142.9 (36.6)	100.9 (41.2)	98.6 (50.4)	74.5 (56.4)	88.1 (50.4)
EL-2	24.9 (13.8)	23.8 (10.5)	20.1 (11.9)	29.2 (14.5)	14.4 (16.2)	18.8 (14.5)
PEI-1	27.4 (7.5)	29.9 (5.7)	33.1 (6.5)	38.0 (7.9)	38.5 (8.8)	27.5 (7.9)
PEI-2	32.3 (6.3)	37.3 (4.8)	36.1 (5.4)	40.6 (6.6)	27.0 (7.4)	29.6 (6.6)
MF-1	4.2 (2.0)	4.4 (1.5)	2.7 (1.7)	4.5 (2.1)	2.3 (2.3)	2.5 (2.1)
MF-2	0.7 (0.6)	0.5 (0.5)	0.5 (0.6)	0.2 (0.7)	0.4 (0.8)	1.0 (0.7)
IF-1	6.1 (1.7)	8.3 (1.3)	6.5 (1.5)	6.1 (1.8)	6.8 (2.0)	8.4 (1.8)
IF-2	1.9 (1.0)	2.4 (0.7)	1.8 (0.8)	2.8 (1.0)	1.9 (1.1)	1.7 (1.0)
IR-1	0.60 (0.13)	0.72 (0.10)	0.77 (0.12)	0.59 (0.14)	0.78 (0.15)	0.77 (0.14)
IR-2	0.80 (0.13)	0.89 (0.10)	0.92 (0.11)	0.92 (0.14)	0.87 (0.16)	0.75 (0.14)

Note. Mean (and 95% *CI*) scores for the standard measures of male copulatory performance as observed in each of the six subgroups of males contributing data to the factor analysis described in the companion full report. Each of these measures was subjected to ANOVA using subgroup as a between-subjects variable. None of these analyses revealed a group effect that achieved our criterion level of significance.