

# On the function of the multiple-intromission, multiple-ejaculation copulatory patterns of rodents

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**Males of many rodent species attain both multiple intromissions before ejaculating and multiple ejaculations. It is suggested that an evolved function of the multiple intromissions may be the removal of sperm, vaginal casts, copulatory plugs, and plug fragments from the female's reproductive tract. By thus cleansing the female's tract before ejaculating, the male can both facilitate effective deposition of the plug in the cervix and benefit from reduced sperm competition. Multiple ejaculations are interpretable in relation to pregnancy initiation and sperm competition.**

The copulatory patterns of many small rodents are characterized by multiple, brief intromissions preceding ejaculation and multiple ejaculations within a single episode (Dewsbury, 1975b). To effect an intromission, a male mounts a female, gains vaginal penetration, and rapidly dismounts. In laboratory rats, the duration of intromissions is approximately 300 msec (Peirce & Nuttall, 1961), and about 10 intromissions typically precede ejaculation (Beach & Jordan, 1956). For other species, there is repetitive thrusting during each intromission (see Dewsbury, 1975b). Most species attain multiple ejaculations within a session (Dewsbury, 1975b); the mean number of ejaculations in laboratory rats is about seven (Beach & Jordan, 1956).

A fascinating problem for many theorists relates to the adaptive significance of the multiple-intromission pattern. Why should males display multiple, brief intromissions before ejaculation rather than either ejaculating quickly or displaying repetitive thrusting during a single intromission? It has been proposed that multiple intromissions are necessary for the male to attain sufficient stimulation for ejaculation (Beach, 1956). This explanation appears valid but leaves unanswered the problem of why brief intromissions are displayed rather than a single intromission with thrusting. Further, some species can indeed ejaculate on a single, brief intromission. A second proposal relates to pregnancy initiation in the female (Adler, 1969). Multiple intromissions are essential to trigger neuroendocrine reflexes and sperm transport in laboratory rats. It is possible that the threshold of females could not be lowered lest the system be triggered in the absence of copulation. However, single intromissions with repetitive thrusting could be as effective as multiple intromissions. Such longer intromissions might function in paternity assurance as a form of "mate guarding" (Ligon, 1981). A third alternative relates to risk of predation (Alcock, 1976; Dewsbury, 1975b). Brief,

rather than prolonged, intromissions may permit the animals to flee predators more effectively than longer copulations.

Perhaps the most powerful interpretation, although not incompatible with the three discussed above, relates to sperm competition (Parker, 1970). At the time of ejaculation, the males of most species of rodents deposit a plug in the female's vaginal tract (see Hartung & Dewsbury, 1978; Voss, 1979). Such plugs can prevent subsequent matings in guinea pigs (Martan & Shepherd, 1976); the role in murid rodents appears less absolute (Dewsbury & Baumgardner, in press). The surface of the glans penis of these species is covered with penile spines (e.g., Hooper, 1959). Milligan (1979) suggested that these spines may function in plug removal. Further, Parker (in press) has suggested that repetitive thrusting and Hart and Odell (1981) that intromissions may function in plug removal. It is likely that in many species several males copulate with a single female (e.g., Birdsall & Nash, 1973; Robitaille & Bovet, 1976). If a male is not the first to copulate with a given female, there might be an advantage to removing previous plugs before ejaculating. The combination of penile spines and deep thrusts would facilitate this. Further, separate intromissions should be more effective at producing complete removal than would be repetitive thrusting, although thrusting might be functional when plugs are lodged especially tightly. The proximal direction of penile spines makes sense in this context. This context may also provide the only framework within which to interpret observations that the males' inward thrusts are generally relatively subdued compared with the explosiveness of the dismount. The latter would relate to plug dislodgment.

The plugs of laboratory rats contain a "plug cup" that is filled with sperm for some time after ejaculation (Matthews & Adler, 1977). Thus, in removing a plug, a male might also be removing the sperm of a competing male. The male's postejaculatory refractory condition

would prevent his removing his own plugs until plug cups were appreciably emptied and interfering with his own transport (Matthews & Adler, 1977). In this context, the spine-thrust complex appears analogous to the adaptations of damselflies, in which an intromittent organ and copulatory behavior are mutually adapted to remove sperm from the female's sperm storage organs (Waage, 1979).

Even if a female is unmated, the tract may contain a "vaginal cast" composed of epithelium sloughed by the female (e.g., Yasukawa, Michael, & Christian, 1978) that may serve as an impediment to effective deposition of sperm and plug.

In order for transport of sperm to the uterus to be maximally effective, there must be a precise and tight fit of the plug in the cervix (Matthews & Adler, 1977, 1978, 1979). For this to be effected, the female must remain still and the male must retain pelvic contact with the female for at least 1 sec after the final ejaculatory thrust. Thus, copulatory behavior has evolved in part to ensure tight plug fit. All research relating to this phenomenon has been done on the first ejaculation for a male and female. It would seem reasonable, however, that if the vaginal tract is cluttered with plugs or plug fragments from previous matings, the necessary plug fit in the cervix will be difficult to attain. Thus, it would be advantageous to remove such material.

In general, then, the multiple-intromission pattern can be seen functioning to cleanse the female's reproductive tract of sperm, casts, plugs, and plug fragments. It is suggested that this may be an evolved function, rather than a mere incidental consequence of the multiple-intromission pattern (cf. Matthews & Adler, 1977). Thus, the copulating male can reduce competition of previous sperm with his own and secure the proper placement of sperm and plug for effective insemination. Multiple intromissions thus prepare the female tract for effective insemination. That intromissions are effective in this respect is suggested by the data of Mosig and Dewsbury (1970) on laboratory rats. Sixty-nine percent of 162 copulatory plugs were removed by subsequent copulation; 82% of these were removed after only three or fewer intromissions (see also Lisk, 1969; Matthews & Adler, 1977).

One difficulty with this interpretation lies in the observation that the species of muroid rodents that have the most fully developed spines are those that display a lock, or mechanical tie between penis and vagina, during copulation and also deposit no plug (Dewsbury, 1975b). It is likely that penile spines evolved in the context of plug removal and served as a pre-adaptation for the evolution of a locking pattern by providing a mechanical basis for the lock. Another difficulty is that multiple-intromission/multiple-ejaculation patterns are displayed by some monogamous species, such as *Peromyscus polionotus* (Dewsbury, 1971). It is likely that either mating systems are more evolutionarily labile than copulatory patterns, and thus the copulatory

patterns lag behind changes in mating system, or there is a nontrivial amount of mating outside of the pair bond in such species. Finally, the directional dominance for low intromission frequencies, found by Dewsbury (1975a), remains unexplained.

Like the multiple-intromission pattern, multiple ejaculations have several functions. The multiple ejaculations of most species of muroid rodents appear necessary for pregnancy initiation (Dewsbury, 1978). Further, by attaining multiple ejaculations, males can be more effective in a sperm-competition situation than if they attain only a single ejaculation and search for other females (Dewsbury & Baumgardner, in press; Lanier, Estep, & Dewsbury, 1979; Oglesby, Lanier, & Dewsbury, 1981). The issue of one large ejaculation vs. many smaller ones is addressed admirably by Parker (in press). The most convincing argument is that with multiple, small ejaculations, the male gains flexibility to apportion his sperm either to one female or to spread them out among many, depending on the operational sex ratio. Males are limited in the number of ejaculations they can produce, and thus, such prudent allocation of ejaculates would be favored (Dewsbury, Note 1).

Obviously, the functions of the multiple-intromission/multiple-ejaculation pattern are multiple. Viewing the pattern in the context of sperm competition helps elucidate the full richness of these multiple functions.

#### REFERENCE NOTE

1. Dewsbury, D. A. *Ejaculate cost and male choice*. Manuscript submitted for publication, 1981.

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