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COPULATORY PLUGS OF ROUND-TAILED GROUND SQUIRRELS (*XEROSPERMOPHILUS TERETICAUDUS*)

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ABSTRACT—Sperm competition, where sperm from more than one male competes to fertilize eggs within the reproductive tract of a female, is prevalent in mammals. In rodents, this competition often has led to copulatory plugs, a passive defense against further sperm competition. Copulatory plugs have been reported in many species of sciurids; however, not in round-tailed ground squirrels (*Xerospermophilus tereticaudus*). Here we report two observations of copulatory plugs in round-tailed ground squirrels and suggest they represent an indirect form of mate guarding in affording males a chance to seek additional mating opportunities as seen in other species of rodents.

RESUMEN—La competencia de esperma, en la que el esperma de múltiples machos compite por fertilizar óvulos en el tracto reproductivo femenino, es común en los mamíferos. En roedores, esta competencia comúnmente ha generado tapones copulativos, la cual es una defensa pasiva contra la posterior competencia de esperma. Los tapones copulativos han sido reportados en varias especies de sciúridos, pero no en las ardillas de cola redonda (*Xerospermophilus tereticaudus*). Aquí reportamos dos observaciones de tapones copulativos en *X. tereticaudus* y sugerimos que estos representan una forma indirecta para proteger a la pareja de otros machos y al mismo tiempo brinda a los machos la posibilidad de buscar adicionales oportunidades reproductivas como ha sido observado en otras especies de roedores.

Intrasexual competition for reproductive success by males can be divided into two categories: pre-copulation and post-copulation competition. Mechanisms that operate before copulation may lead to traits such as weaponry, dimorphism in size, increased ability to find a receptive female, increased endurance, conspicuous ornaments, and behavioral signals (Andersson, 1994). Post-copulatory mechanisms may include mate guarding, where a male guards the female to prevent her from mating with another male, and sperm competition, where sperm from more than one male competes to fertilize eggs within the reproductive tract of a female (Birkhead and Mller, 1998).

Sperm competition occurs when sperm from two or more males compete to fertilize eggs within the reproductive tract of a female (Birkhead and Mller, 1998). It favors mechanisms that allow males to increase number of sperm per ejaculate (Birkhead and Mller, 1998) or strategies that minimize risk of sperm competition, such as direct or indirect mate guarding (Voss, 1979; Dixson and Anderson, 2002). In many mammals (i.e., rodents, primates, marsupials, and bats), secretions from accessory glands form copulatory plugs, which are a coagulated mass of protein deposited in the vagina at

the end of copulation (Ginsburg and Huck, 1989). Suggested benefits of copulatory plugs include storage of sperm, prevention of leakage of sperm, pseudopregnancy, and transport of sperm (Voss, 1979). Copulatory plugs frequently are interpreted as a passive defense against sperm competition by preventing insemination by subsequent copulations, an indirect form of mate guarding (the chastity enforcement hypothesis; Voss, 1979).

Copulatory plugs have been reported in many species of sciurids (taxonomy follows Helgen et al., 2009): Abert's squirrels (*Sciurus aberti*; Farentinos, 1980), eastern fox squirrels (*S. niger*; Koprowski, 1992), eastern gray squirrels (*S. carolinensis*; Asdell, 1964; Koprowski, 1992), Arctic ground squirrels (*Xerospermophilus parryii*; Murie and McLean, 1980), Beechey's ground squirrels (*Otospermophilus beecheyi*; Tomich, 1962), Columbian ground squirrels (*Urocitellus columbianus*; Murie and McLean, 1980), Richardson's ground squirrels (*U. richardsonii*; Michener, 1984), thirteen-lined ground squirrels (*Ictidomys tridecemlineatus*; Schwagmeyer and Foltz, 1990), and white-tailed prairie dogs (*Cynomys leucurus*; Asdell, 1964). Despite the prevalence of copulatory plugs in sciurids, copulatory plugs in round-tailed ground squirrels (*X. tereticaudus*)

have not been documented. We have quantified high levels of multiple paternity in litters of round-tailed ground squirrels using microsatellite markers (K. E. Munroe and J. L. Koprowski, 2011), suggesting a likely role of sperm competition.

Round-tailed ground squirrels are small (125 g) ground squirrels that inhabit desert areas of the southwestern USA and northwestern Mexico (Hall, 1981). Males emerge first from torpor in late January and mating begins in late February or early March (Dunford, 1975; Ernest and Mares, 1987). Males with scrotal testes occur during mid-February to late April; motile spermatozoa were present in some males during early January to mid-April (Neal, 1965). Average size of litter is 6.5 young (range, 1–12; Reynolds and Turkowski, 1972).

While capturing individuals for another study during 2004–2007 at the Casa Grande Ruins National Monument in Coolidge, Pinal County, Arizona, we observed copulatory plugs in two female round-tailed ground squirrels. Daily trapping was conducted to determine timing of estrus. Upon handling of squirrels, copulatory plugs clearly were visible and firmly placed in the vagina, yet were removed easily by researchers. Both plugs were an opaque white with a greenish-yellowish tint and had a firm waxy consistency. The first plug collected on 29 February 2004 was 11.9 mm long and 3.6 mm wide, and the second plug collected on 12 March 2005 was 12.2 mm long and 3.8 mm wide. Both plugs were cylindrical but tapered toward the cervical end in a manner similar to those reported in Richardson's ground squirrels (Michener, 1984).

How soon a plug forms after copulation is unclear because round-tailed ground squirrels were never seen copulating above ground. Copulatory plugs in most rodents form in <15 min (Michener, 1984) and may form in <1 min (Dewsbury, 1988; Koprowski, 1992). However, as traps were checked hourly during the period of receptivity by females and only two copulatory plugs were observed, we suggest that length of time plugs persist is short; plugs were deeply imbedded and not visible or females promptly groomed plugs out, similar to other sciurids (Murie and McLean, 1980; Michener, 1984; Koprowski, 1992).

In conclusion, copulatory plugs may represent an indirect form of mate guarding in round-tailed ground squirrels. This would allow males a chance to seek additional mating opportunities, as round-tailed ground squirrels show an asynchronous estrus, which may last several weeks, allowing males multiple mating opportunities. Although the function of copulatory plugs in round-tailed ground squirrels is uncertain, we suggest a role in reducing the likelihood of fertilization by subsequent males as seen in other taxa (Ginsburg and Huck, 1989). We make this suggestion due to observed plugs completely filling the vagina and not adhering tightly to vaginal walls, in conjunction with a lack of

observations of long-term presence of the plug in the vagina. It appears there may be a conflict between the sexes: females want the advantages of multiple mates, whereas males attempt to fertilize as many eggs as possible. Male round-tailed ground squirrels do not have dramatic dimorphism in size, weaponry, conspicuous ornaments, or above-ground behavioral signals; therefore, passive mate guarding may be a successful competition strategy (Dunham and Rudolf, 2009). Future studies should establish empirically that plugs either prevent subsequent copulations or reduce passage of sperm in subsequent inseminations.

Research was conducted under permits from the University of Arizona Institutional Animal Care and Use Committee (protocol 04-009), Arizona Game and Fish Department, and the National Park Service.

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SIPHONAPTERA OF *PEROMYSCUS* IN THE NIOBRARA CHALK BARRENS, COLORADO

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ABSTRACT—We collected 327 *Peromyscus truei* (pinyon deermice), 211 *P. maniculatus* (North American deermice), and 38 *P. leucopus* (white-footed deermice) on Fort Carson Military Reservation, Pueblo County, Colorado, during May–June 2007. The deermice hosted 408 fleas including 238 *Aetheca wagneri*, 169 *Orchopeas leucopus*, and 1 *Meringis parkeri*. Both *A. wagneri* and *O. leucopus* were on all species of deermice. Prevalence of fleas was 42.1% for *P. leucopus*, 36.4% for *P. truei*, and 35.1% for *P. maniculatus*. Prevalence of *O. leucopus* was significantly greater for *P. truei* (43.1%) than for *P. maniculatus* (13.7%) and *P. leucopus* (13.2%). Conversely, *P. maniculatus* (52.1%) had a significantly greater prevalence of *A. wagneri* than either *P. leucopus* (47.1%) or *P. truei* (33.6%).

RESUMEN—Colectamos 327 *Peromyscus truei* (ratones piñonero), 211 *P. maniculatus* (ratones ciervo), y 38 *P. leucopus* (ratones de patas blanca) durante mayo a junio del 2007 en la Reserva Militar de Fort Carson, condado de Pueblo, Colorado, USA. Los ratones albergaron a 408 pulgas, incluyendo a 238 *Aetheca wagneri*, 169 *Orchopeas leucopus*, y 1 *Meringis parkeri*. Ambos *A. wagneri* y *O. leucopus* fueron encontrados en todas especies del ratón. La prevalencia de infestación de pulgas fue el 42.1% en *P. leucopus*, el 36.4% en *P. truei*, y el 35.1% en *P. maniculatus*. La prevalencia de *O. leucopus* fue significativamente mayor en *P. truei* (43.1%) comparado con *P. maniculatus* (13.7%) y *P. leucopus* (13.2%). Inversamente, *P. maniculatus* (52.1%) tuvo la prevalencia de *A. wagneri* significativamente mayor que *P. leucopus* (47.1%) o *P. truei* (33.6%).

In central and southern Colorado, the Niobrara Chalk Barrens consist of small exposed islands of shale that overlie a layer of chalk. The barrens are sparsely vegetated, with 30–50% coverage, and consist of shale (70%), silt (30%), and occasionally, rocks and sand (R. Leyva and R. Bunn, in litt.). They comprise about 405 ha at the southern end of Fort Carson Military Reservation, Pueblo County, or 2% of the reservation (Peyton, 2008). Although small, the area represents ca. 30% of the extant

Niobrara Chalk Barrens in south-central Colorado; the remainder of the barrens is on privately owned lands in the Arkansas River drainage.

Predominant species of plants in the barrens include the pinyon pine (*Pinus edulis*), one-seed juniper (*Sabina monosperma*), mountain mahogany (*Cercocarpus montanus*), Indian rice grass (*Achnatherum hymenoides*), New Mexico feather grass (*Hesperostipa neomexicana*), and several species of cactus (Kelso et al., 2003), which provide