Western North American Naturalist 81(2), © 2021, pp. 267–272

Courtship behavior of the meadow jumping mouse (*Zapus hudsonius*)

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Abstract.—We describe the first recorded observations of courtship behavior of the meadow jumping mouse (*Zapus hudsonius*) made in wild-caught and captive-reared animals. Male meadow jumping mice performed a series of courtship behaviors upon approach to the female, including rapid fanning of the muzzle with the forelimbs, self-grooming, muzzle fanning, retreat, and eventual mounting attempts. During courtship, female jumping mice may retreat, ignore the courting male, or bat at the male with forelimbs until the male retreats. Active rejection of the courting male by the female is suggestive of female mate choice in this species.

Resumen.—Describimos las primeras observaciones registradas de cortejo del ratón saltador de pradera (*Zapus hudsonius*). Se observaron animales tanto capturados como en cautiverio. Los ratones macho saltadores de la pradera realizaron una serie de comportamientos de cortejo al acercarse a la hembra que incluían la ventilación de aire por el hocico usando sus extremidades, el aseo personal, expulsión de aire por el hocico, retirase de la hembra, eventuales intentos de montaje. Durante el cortejo, la hembra puede retirarse, ignorar al macho que la corteja o golpear al macho con las extremidades inferiores hasta que el macho se retire. El rechazo activo por parte de la hembra hacia el macho que corteja sugiere que la elección de pareja es por la femina en esta especie.

The meadow jumping mouse (*Zapus hudsonius*) is a small, saltatory, hibernating rodent found throughout much of North America, with the northern extent of its range spanning the continent from Alaska to Newfoundland and Labrador (Krutzsch 1954). At the southwestern edge of the range, populations of Preble's meadow jumping mouse (*Zapus hudonius preblei*) exist on the eastern edge of the Rocky Mountains in Colorado and Wyoming (Malaney and Cook 2013). Populations of the New Mexico meadow jumping mouse (*Zapus luteus luteus*, formerly classified as *Zapus hudsonius luteus*) are found in limited areas of New Mexico, Colorado, and Arizona, and additional *Zapus* species range from the Intermountain West to the Pacific Coast (Frey and Malaney 2009, Malaney et al. 2017, Burgin et al. 2018). Some information about the timing and population structure of meadow jumping mouse reproduction is available for various localities (Quimby 1951, Whitaker 1963, Nichols and Conley 1982, Hoyle and Boonstra 1986, Frey 2015). However, despite strong conservation interest due to the federal listing of *Z. hudonius preblei* and *Z. luteus luteus* as threatened and endangered, respectively (United States Fish and Wildlife Service 2008, 2014), we are not aware of any previous documentation of courtship behavior for any Zapodinae. Knowledge of jumping mouse courtship behavior raises the probability of success of a potential captive breeding and reintroduction program using small numbers of animals, and it might lead to a better understanding of how anthropogenic factors may be influencing *Zapus* reproduction in critical habitats. A full understanding of the behaviors leading to successful copulation in *Zapus* would also help to reveal the role that mate choice plays in the reproduction and evolution of these small hibernators.

Among other members of family Dipodidae, the courtship behavior of the birch mice (*Sicista* spp.) has not been recorded, but some information is available about the courtship behavior of the jerboas, including *Jaculus* and *Allactaga* (Happold 1970, Eisenberg 1975). The courtship behavior of these Eurasian desert rodents may serve as a useful comparator to that of the meadow jumping mouse. The male courtship display of *Jaculus*, as reported by Happold (1970), begins with the male

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meeting the female, who crouches with belly close to the sand. The male stands on hind limbs facing the female and bobs the anterior part of the body up and down, up to around 12 times. The receptive female remains crouched while the male sniffs the genital region of the female, and then returns to face her. The female touches the nostril of the male with her snout; then the male moves behind the female, hops forward, and briefly copulates with the female, who has raised the hind part of her body. The entire encounter is reported to last 30–60 seconds and is broken off if the female chases the male away. Both *Jaculus* and *Allactaga* make a "courting sound," but the timing of this vocalization during the courting display has not been reported (Eisenberg 1975).

We observed courtship behavior that was performed by 28 pairs of *Zapus* during our efforts to maintain a captive breeding colony of animals for studies of hibernation in the meadow jumping mouse. Animals were captured according to the Guidelines of the American Society of Mammalogists (Sikes and Gannon 2011) on the Bolton Flats Wildlife Management Area near Bolton, Massachusetts, in August–September 2014 and August 2015. Subsequent behavioral observations were made in the animal facility of the University of Texas Southwestern Medical Center, as approved by the Institutional Animal Use and Care Committee. One male and one female meadow jumping mouse were placed together in a large cage, typically used to house guinea pigs, which provided a food hopper, 2 water bottles, and an interior floor space of 54 × 37 cm. Two custom-built nest boxes were provided at opposite ends of the cage to provide a place of refuge for each animal; nest boxes were of the 2-chamber type previously reported by us, but without instrumentation (Kallmyer et al. 2019). Under captive conditions, we noted that meadow jumping mice remain hidden during the day and become active starting within a few minutes of the beginning of the dark phase in the animal room. We visually observed the behavior of the paired meadow jumping mice in the dark using handheld red LED illumination; the use of red light was expected to minimize disturbance to the animals because rodents lack red-sensitive photoreceptors (Jacobs 2009). The pairs were typically left together for 3 d, and in some cases the animals interacted during the day, which allowed observation under standard illumination.

Once paired, the male indicated interest in the female by performing a stereotypical series of core behaviors that typically lasted around 10–15 seconds (Fig. 1). The male (1) approaches and faces the female, usually within 10–15 cm; (2) fans muzzle briefly with forelimbs while standing on hind legs with body extended toward female, (3) briefly grooms forepaws and lower abdomen around prepuce, and then (4) fans muzzle with forelimbs in a continuous fashion; this muzzle fanning may be paused momentarily if the male uses his forelimbs while locomoting to adjust his position relative to the female. Muzzle fanning is an extremely rapid motion of both forelimbs, with paws passing to the side of and in front of the mouth, as revealed by slow motion videos (Supplementary Materials 1–4). In real time, the fanning motion appears somewhat reminiscent of the motion of paws at the mouth during rodent grooming behavior, but much faster and with different body posture. The postgrooming muzzle-fanning display typically continues until it is interrupted by the female.

The female is actively involved in the courtship behavior and may perform some combination of the following actions: she may (1) attentively observe the male while foraging/eating more slowly than normal or (2) watch the male with full attention; either activity can lead to the female (3) actively retreating by jumping away or (4) actively disrupting the male's display by batting at him with her front paws until contact is made, which causes the male to jump away. The active rejection of the male by the female suggests that female choice may play a role in mate selection in *Zapus*.

When the display is interrupted by the female, the male may simply resume the muzzle-fanning behavior, or if batted away he may reapproach and repeat the full series of core muzzle-fanning and self-grooming behaviors. In our captive conditions, the entire courtship encounter was usually brief (lasting from seconds to minutes) and was typically terminated by one of the animals seeking refuge in a nest box. We have never observed muzzle fanning exhibited by a female, but we have observed one additional behavior expressed by a single wild-caught male. When the courtship display

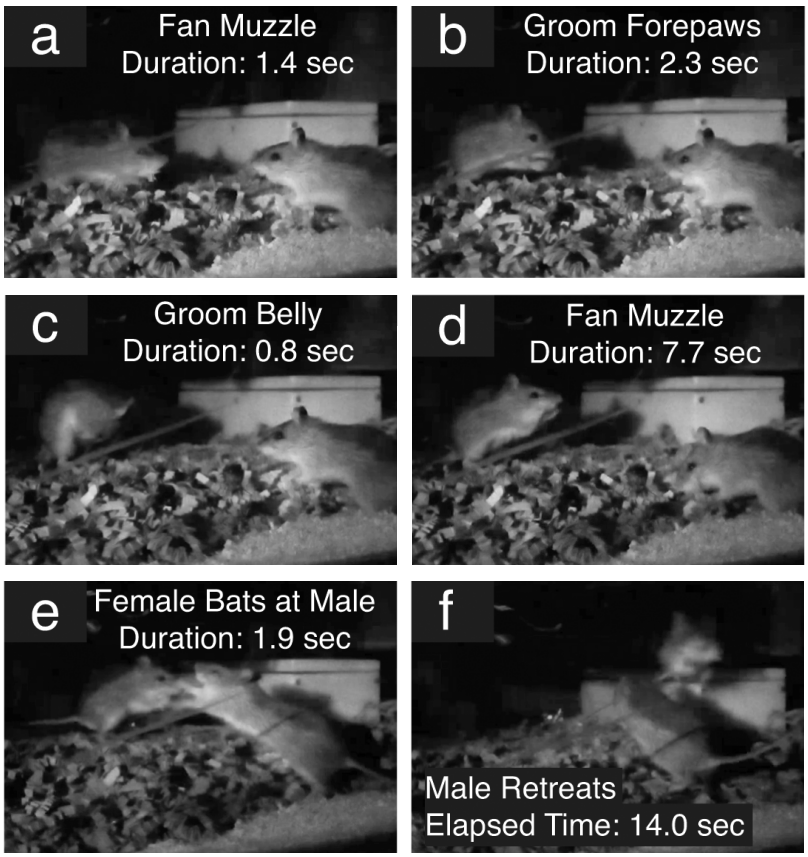

Fig. 1. An example of courtship behavior exhibited by male (left) and female (right) wild-caught meadow jumping mice (*Zapus hudsonius*). Upon approaching the female, the male (a) fans muzzle with forelimbs, (b) grooms forepaws, (c) grooms abdomen around prepuce, and (d) fans muzzle until (e) the female bats him with forelimbs, which (f) causes him to jump away. Video recordings of the courtship behaviors are available in the online Supplementary Materials 1–4. The duration (in seconds) of each part of the behavior is included in each panel, as determined from the video available as Supplementary Material 3.

of this particular male was interrupted by the female, he retreated for several hops, came to rest facing the female, and stomped with hind feet 2–3 times in rapid succession (i.e., within approximately 1 second) before reapproaching; each forceful stomp made a thumping noise that may have served to signal to the female. We have only very rarely observed attempts at mounting (all were unsuccessful) and have never observed copulation, although our captive animals have bred successfully. In cases where a successful mating was later determined to have occurred, we observed that the females often changed their behavior postcopulation from generally ignoring the male to repeatedly approaching him and batting at him as if to drive him away. We removed the male from the cage when this occurred to prevent any additional aggressive behavior, such as bites to the tail, which have been observed by us and others (Sheldon 1934). We suggest that pair bonding does not occur in these animals, as we have observed that failing to separate the sire from a pregnant female well before birth results in destruction of the litter.

The courtship behavior reported here occurred during 28 unique pairings of 14 males (5 wild-caught, 9 captive-reared) with 23 females (3 wild-caught, 20 captive-reared). Courtship behavior was noted during both dark and light phases and between pairs of wild-caught animals (3 pairings), pairs of a wild-caught male and a captive-reared female

(8 pairings), and pairs of 2 captive-reared animals (17 pairings). The age ranges of captive-reared animals at the time of pairing were 49–554 d for females (median = 237 d) and 122–754 d for males (median = 524 d). Given the ages of the captive-reared animals available for pairing, most males were older than females in the 17 pairs of captive-reared animals, with the greatest age difference being 497 d (male older). In 2 instances, the females were 53 d and 39 d older than the males. The 3 wild-caught females were paired at 285, 401, and 584 d postcapture, and the wild-caught males were paired from 267 to 691 d postcapture, with a median of 442 d. Of the 28 pairs, 6 pairs had to be separated within minutes to hours after pairing to reduce stress on nervous, jumpy animals; the remaining 22 pairings resulted in 5 litters of offspring, which suggests that female choice and/or the unnatural environment of captive housing limited the frequency of successful copulation.

To minimize inbreeding in the colony, we avoided pairing related animals, with the exception of one limited inbreeding attempt that was potentially informative in understanding mechanisms of inbreeding avoidance (if any) in this species. One of the 28 pairings that exhibited courtship behavior was the backcross of a wild-caught male with its captive-reared daughter; this pairing produced a litter of 1 male and 2 females. Subsequent pairings of the inbred male offspring with its female siblings resulted in one small litter from each female. Our captive meadow jumping mice thus did not appear to have used an odor-based kin-recognition mechanism of inbreeding avoidance like those employed by many mammals, including house mice (Pusey and Wolf 1996, Ferkin 2018); however, these limited observations of captive animals are only suggestive of the natural behavior in wild populations. Perhaps inbreeding avoidance in *Z. hudsonius* species occurs via male dispersal, as has been reported for the Pacific jumping mouse (*Z. trinotatus*) (Vignieri 2007).

Ultrasonic communication is used by various rodent species in the context of courtship (Hooper and Carleton 1976, Barfield et al. 1979, Musolf et al. 2010). The meadow jumping mouse male makes no sound audible to the human ear during muzzle fanning, but we suspect that this behavior may be accompanied by ultrasonic vocalization, for the following reasons. First, we observed an instance when the courting male initially approached the female from behind and was ignored until the instant muzzle fanning began, at which point the female whirled to face him. This suggests that the female reacted either to an auditory signal or to motion at the extreme edge of her visual field. Second, we have observed instances wherein the female retreated into a nest box during courtship by the male. When this occurred, the male remained outside of the nest box but continued to direct the muzzle-fanning behavior toward the female either through the nest box wall or at the outer nest box entrance, neither of which offer a direct line of sight to the female. This behavior suggests that the male may have expected a response despite lack of visual stimulus being presented to the female. Attempts to record ultrasonic vocalizations of paired animals using an ultrasonic bat detector (Echo Meter Touch 2, Wildlife Acoustics, Maynard, MA) were unsuccessful, either due to lack of vocalization from the animals, or due to the lower volume of sound putatively produced by the jumping mouse in close quarters relative to bat echolocation calls. While we have heard the high-pitched squeaks produced by *Zapus* neonates (Quimby 1951), we have only heard an adult animal produce an audible vocalization in a single instance; this sound was the "clucking noise" or series of "cho" notes previously described by others (Sheldon 1934, Edwards 1945, Quimby 1951). Adult *Zapus* have also been reported to squeak audibly in various contexts, including while fighting, while occupying a nest with more than one individual, or if a nest is uncovered when the animals are about to hibernate (Svihla and Svihla 1933, Sheldon 1934). We can therefore not rule out the possibility that other jumping mice are more vocal than our particular animals. It is conceivable that the typical male *Zapus* produces a "courting sound" analogous to those of related jerboa species (*Jaculus* spp. and *Allactaga* spp.; Eisenberg 1975), either in the audible range or at an ultrasonic frequency due to its smaller size. If the male *Zapus* does indeed produce ultrasonic vocalizations during the courtship display, we propose that the rapid movement of paws in front of the mouth during muzzle fanning may serve to modulate the sound that is produced. Further investigation is needed to understand the

use of vocalization, if any, in the courtship behavior and social interactions of meadow jumping mice.

Courtship among rodent species can be elaborate and may range over some distance (Ewer 1968). For example, male courtship display in the Sudanese jerboa (*Jaculus jaculus butleri*) involves the male hopping around the female and performing a bobbing display of the anterior body (in a posture similar to that of *Zapus* while muzzle fanning), with courtship encounters often ending in a chase (Happold 1970). Given the locomotive ability of the meadow jumping mouse, we expect that the courtship behaviors employed by *Zapus* in the wild are more expansive than those observed in the limited space available to our captive animals, and courtship in wild populations might more routinely include additional behaviors, such as the stomping behavior exhibited by one of our males. We observed the same stereotyped sequence of muzzle-fanning and self-grooming behaviors in both wild-caught and captive-reared male meadow jumping mice, but observations of free-ranging animals may be required to fully understand the interactions between potential mates in wild populations. For example, if a female breaks off a courtship encounter in the wild by jumping away for some distance, does this end the encounter? Or does this lead to pursuit by the male?

To conclude, we have presented here a first description of the behaviors exhibited by male and female meadow jumping mice during courtship in a captive setting. The active rejection of a courting male by the female is suggestive of female mate choice, and we propose that a better understanding of the behaviors necessary for successful reproduction in *Zapus* may inform conservation efforts and will increase the feasibility of a captive breeding program involving endangered or threatened populations.

Supplementary Material

Four online-only supplementary files accompany this article (https://scholarsarchive.byu.edu/wnan/vol81/iss2/11).

Supplementary Material 1. Slow-motion video of courting display from male *Zapus hudsonius* (left); the female (right) bats at the male and then jumps away.

Supplementary Material 2. Slow-motion video of courting display from male *Zapus hudsonius* (left); female (right) makes contact while batting the male, causing him to retreat.

Supplementary Material 3. Slow-motion video showing courting interactions between male (starts on left) and female *Zapus hudsonius*.

Supplementary Material 4. Real-time version of Supplementary Material 3, showing courting interactions between male (starts on left) and female *Zapus hudsonius*.

Acknowledgments

We acknowledge support for this work from NIH grant DP5OD021365 and the Sara and Frank McKnight Fund for Biochemical Research.

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Received 31 July 2020
Revised 14 December 2020
Accepted 5 January 2021
Published online 26 May 2021