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VIDEO ARTICLE

Mating behavior in the Japanese badger *Meles anakuma*

Hiroshi Tanaka[1] · **Yukihiro Fukuda**[2] · **Etsuko Yuki**[2] · **Wataru Kojima**[3]

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Abstract

We describe the details of the mating behavior of the Japanese badger, *Meles anakuma,* using camera trapping. Similar to other mustelid species, the females copulated with multiple males (mean = 3.0). Repeated mounting with the same male was observed, occurring 3.4 times on average. The average duration of the mounting bout was approximately 70 min, which was much longer than that observed for the congener *M. meles*. Following the initial mounting bout, males constructed a rest site by gathering fallen leaves and branches close to the female sett. Males rested at these sites between mounting bouts, likely to guard their mates from rival males. The mating pairs displayed a preference for returning to the same location for copulatory activities, which resulted in the dispersal of fallen leaves and surface soil disturbance. We found that some males restored the copulation site by covering it with leaves, soil, and branches after all mating behaviors were completed. This action prevented rival males from locating females, especially if they relied on olfactory cues from the copulation sites. Our study reveals interspecific differences in mating behavior within *Meles* and the relationship between social systems and mating behavior. Digital video images related to this article are available at http://www.momo-p.com/showdetail-e.php?movieid=momo240213ma01a, http://www.momo-p.com/showdetail-e.php?movieid=momo240213ma02a, http://www.momo-p.com/showdetail-e.php?movieid=momo240213ma04a, http://www.momo-p.com/showdetail-e.php?movieid=momo240213ma05a, and http://www.momo-p.com/showdetail-e.php?movieid=momo240213ma06a.

Keywords Intrasexual competition · Mate guarding · Mating system · Multiple paternity · Mustelidae · Repeated mounting

Introduction

Mammalian females generally mate with multiple males, irrespective of their mating systems (Wolff and Macdonald 2004; Clutton-Brock and Isvaran 2006; Hoogland 2013), and are thought to gain benefits, such as increased access to high-quality sperm, foraging in better-quality habitats controlled by males, greater involvement in parental care, reduced risk of infanticide through paternity confusion, protection of both mothers and offspring provided by males, and avoidance of harassment from other males (Jennions and Petrie 2000; Kvarnemo and Simmons 2013; Qi et al. 2020). Males have evolved diverse adaptations to ensure paternity (i.e., mate guarding, Raveh et al. 2011; Girard-Buttoz et al. 2014). Mate guarding encompasses a range of behaviors, including the production of copulatory plugs (Ramm et al. 2015; Schneider et al. 2016), physical tracking of females after copulation (Girard-Buttoz et al. 2014), and scent marking on top of existing scent marks left by mates (Jordan et al. 2011).

As most species of mustelid carnivores are nocturnal and solitary (Lode 1995; Tanaka 2005; Zschille et al. 2010; Ross et al. 2017), observing their mating behavior poses considerable challenges (Thom et al. 2004; Hedmark et al. 2007). Microsatellite markers have revealed multiple paternity in the litter of some species (e.g., American minks *Neovison vison,* Thom et al. 2004; Yamaguchi et al. 2004; stoats *Mustela erminea*, Holland and Gleeson 2005). Moreover, given the male-biased sexual size dimorphism of most species (reviewed in Macdonald et al. 2017), intense male–male

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✉ Hiroshi Tanaka
h-tanaka43@nifty.com

[1] Laboratory of Zoology, Yamaguchi Prefectural Yamaguchi Museum, 8-2 Kasuga, Yamaguchi City, Yamaguchi 753-0073, Japan

[2] TopOutImages, Shibafuji, Kawaguchi City, Saitama 333-0854, Japan

[3] Graduate School of Sciences and Technology for Innovation, Yamaguchi University, 1677-1 Yoshida, Yamaguchi City, Yamaguchi 753-8511, Japan

competition is expected; however, mate-guarding behavior in mustelids remains to be elucidated.

Mustelid social systems vary among species. Although most mustelids are solitary, European badgers (*Meles meles*) live in social groups of dozens of related and unrelated individuals of both sexes (Woodroffe and Macdonald 1992; Roper 2010; Dugdale et al. 2011). Unlike other mustelid species, the mating behavior of *M. meles* has been extensively studied (Christian 1995; Dugdale et al. 2011; Charlton et al. 2020). Females of *M. meles* mate with multiple males both within and outside the groups (Dugdale et al. 2007, 2011; Roper 2010). In instances where extra-group males attempt to mate with estrous females, within-group males that have previously mated with females engage in defense by biting and attacking the intruding males. Additionally, the males copulated repeatedly with females within a few days. Since social systems in mammals are generally associated with mating behavior, comparing mating behavior across species with varying social structures can provide valuable insights into the diverse patterns of mating behavior in mammals (Zamudio and Sinervo 2000).

Japanese badgers (*Meles anakuma*), in contrast to European badgers, are either solitary or form groups of females and their offspring (Tanaka et al. 2002, 2022; Kaneko et al. 2014). Japanese badgers use setts for resting, rearing offspring, and hibernation (Tanaka et al. 2002; Kaneko 2015; Tanaka 2015). The mating system of Japanese badgers is socially polygynous, with adult males establishing expansive territories that include two or more adult females (Tanaka et al. 2002; Kaneko et al. 2014). From mid-December to mid-February, these badgers hibernate within their setts (Tanaka et al. 2002, 2022; Tanaka 2005, 2006; Roper 2010). Parturition occurred after the hibernation period between late February and April. Following parturition, males visit female setts and engage in copulation. However, females do not undergo embryo implantation until January to February of the following year (i.e., delayed implantation). Offspring care is provided exclusively by females. Despite a previous study conducted on captive individuals (Chamura 1983), the mating behavior of Japanese badgers, including mate guarding and multiple matings, remains largely unexplored. Therefore, the primary objective of this study was to investigate the mating behavior of Japanese badgers under natural conditions.

Materials and methods

Study site and population

We studied two populations of Japanese badgers, one in Chino City, Nagano Prefecture, located in the central part of Honshu (35°58′N, 138°09′E) and the other in Yamaguchi City, Yamaguchi Prefecture, located at the western edge of Honshu (34°11′N, 131°29′E), Japan. The study area of Chino City is approximately 3 km^2, spanning elevations of 700–1000 m in an undulating mountainous range predominantly covered by Japanese red pine (*Pinus densiflora*) forests. The climate in this region is that of a temperate rainforest, with average summer temperatures of 24.1 °C (August), winter temperatures of −1.1 °C (January), and annual mean precipitation of 1301 mm (https://www.data.jma.go.jp/obd/stats/etrn/view/20230209). We identified 35 setts in this area and investigated the mating behavior of a single female in 2015. The study area of Yamaguchi is approximately 7 km^2, spanning an elevation of 50–250 m, and is predominantly covered by Japanese chinquapin (*Castanopsis cuspidate*) and ring-cup oak (*Quercus glauca*) forests. More than 200 badger setts are located in this area. We recorded the mating behavior of five females, with one female utilizing the same sett for three consecutive years and two females utilizing the same sett for two consecutive years. We determined the identities of the females based on their external physical characteristics. Tanaka et al. (2002, 2022) provide further details on the study sites and methods for individual identification.

Field methods

We used motion-triggered video cameras with an infrared flash (Bushnell Trophy Cam, USA; Ltl-Acorn 6210, China; Ltl-Acorn 6310 W, China) to monitor the behavior of Japanese badgers in their setts in Chino in 2015 and Yamaguchi from 2016 to 2018. The cameras were programmed to record 30- or 60-s video segments upon activation, with a subsequent 0–5-s delay before reactivation (Allen et al. 2014, 2017; Tanaka et al. 2022). Because copulation often occurred outside the camera's view at setts, we positioned one or two additional cameras in the vicinity to enable a wider angle of view. In some cases, motion-triggered video cameras were used to obtain clear images using a Canon 5D series camera equipped with video lights and multiple probes. During the mating season, we conducted direct daily observations of the study sites and searched for indicators of badger activity around the setts. We ensured that all copulation sites (characterized by conspicuously bare, well-trodden ground, as described in the "Results" section) were within the field of view of at least one camera.

We determined the parturition date based on changes in female behavior. During parturition, females typically remained inside the sett for half a day to 1 day and began to gather bedding materials (e.g., fallen leaves) close to their sett after parturition. Additionally, we cross-validated the date by counting back approximately eight weeks from when the cubs initially emerged from the sett (Roper 2010). We determined the identity of the males that visited the focal females based on body shape, overall coat color, facial contours, color, twin-stripe patterns on the face, and facial scars (Tanaka et al. 2022). However, we did not differentiate between the identities of males who visited different females.

We recorded the arrival and departure times of males visiting the female sett, as well as the initiation and termination times of the mounting bouts. We defined a 'mounting bout' as an event where the male mounted the female and subsequently left. These mounting bouts included instances of short duration (< 10 min; see "Results" section), during which ejaculation might not have occurred. However, because we could not identify the timing of ejaculation from the video recordings, our classification of a 'mounting bout' was based on criteria unrelated to mounting duration. This definition of "mounting bout" was used in a previous study of European badgers (Dugdale et al. 2011), facilitating the comparison of mounting duration between the two species.

Results

Sequence of mating

Although we monitored the behavior of badgers around their setts throughout the seasons, mating events were exclusively observed following parturition between February and April. A few weeks before parturition, males visited the setts within female territory. Positioned at the setts, they emitted alluring "churring" mating calls to attract the female from within. Additionally, males were scent-marked in the vicinity of sett entrances. Females occasionally emerged from setts in response to mating calls. However, they consistently rejected mating attempts.

Following parturition, the behavior of the emerged females changed; they displayed active pursuit by the males, emitting barking calls, and subsequently returning to their setts (Fig. 1a; http://www.momo-p.com/showdetail-e.php?movieid=momo240213ma01a, Video 1). This sequence was typically repeated multiple times. Upon emergence from the sett, she lowered her head. However, in some cases, the male entered the female sett and pulled the female out by biting her body. Subsequently, the male grasped her neck with his mouth, held her between his paws in a mounting posture, and copulated (Fig. 1b, c; http://www.momo-p.com/showdetail-e.php?movieid=momo240213ma02a and http://www.momo-p.com/showdetail-e.php?movieid=momo240213ma04a, Videos 2, 3). During mounting, the males emit intermittent mating calls. The mean duration of mounting bout was 70.2 ± 4.4 SE min (range = 1–198, N = 98) (Table S1; Fig. 2). Females engaged in copulation with the same males over 1–2 days, with an average of 3.4 ± 0.4 SE mounting bouts (range = 1–8, N = 30) (Table S1; Fig. 3). We observed

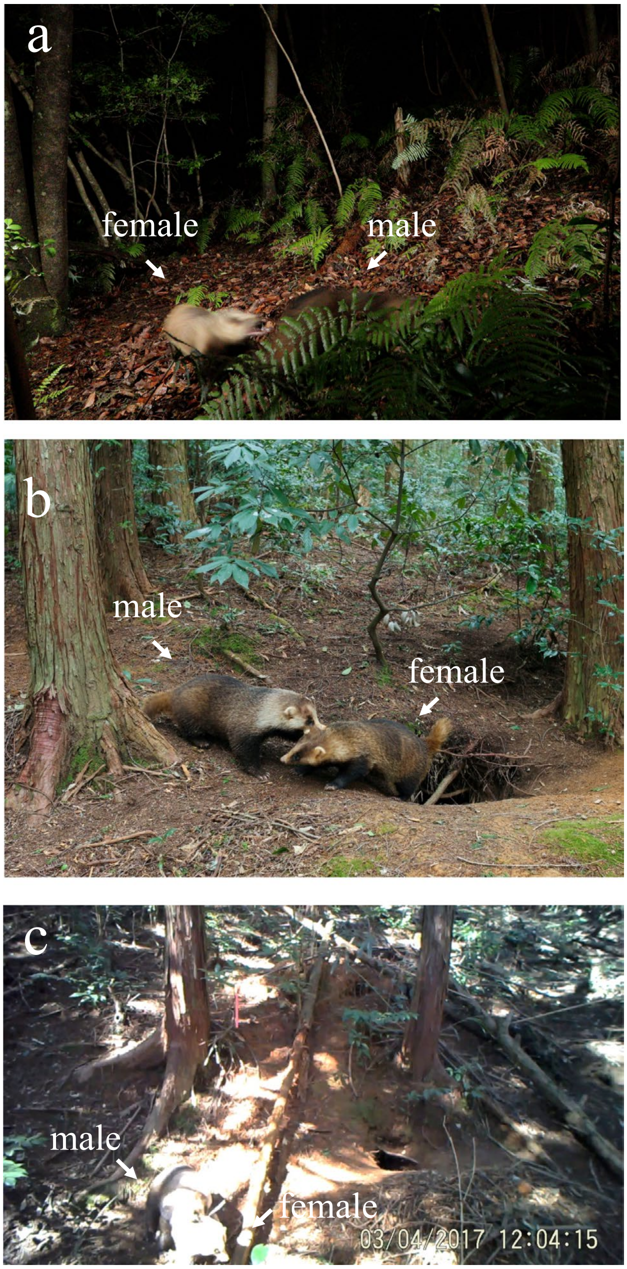

Fig. 1 Female refusal behavior before mounting (**a**) and two examples of copulation (**b**, **c**) of the Japanese badger *Meles anakuma*. In **a**, a female emerges from the sett and is chasing a male (http://www.momo-p.com/showdetail-e.php?movieid=momo240213ma01a, Video 1). In **b**, a male is pulling a female from her sett with biting her ear before mounting (http://www.momo-p.com/showdetail-e.php?movieid=momo240213ma02a, Video 2). In **c**, a male is holding a female between his paws with a mounting posture (http://www.momo-p.com/showdetail-e.php?movieid=momo240213ma04a, Video 3)

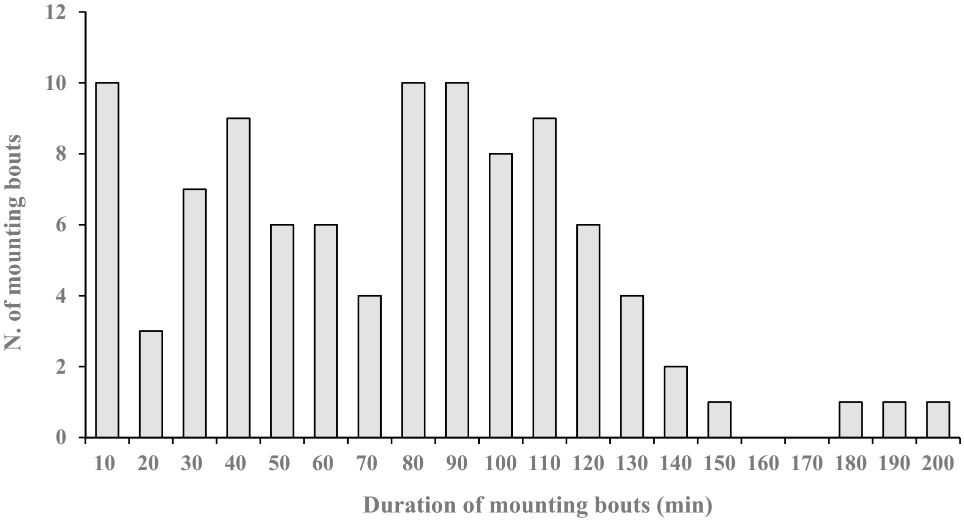

Fig. 2 Histogram of observed mounting duration (min) of Japanese badgers

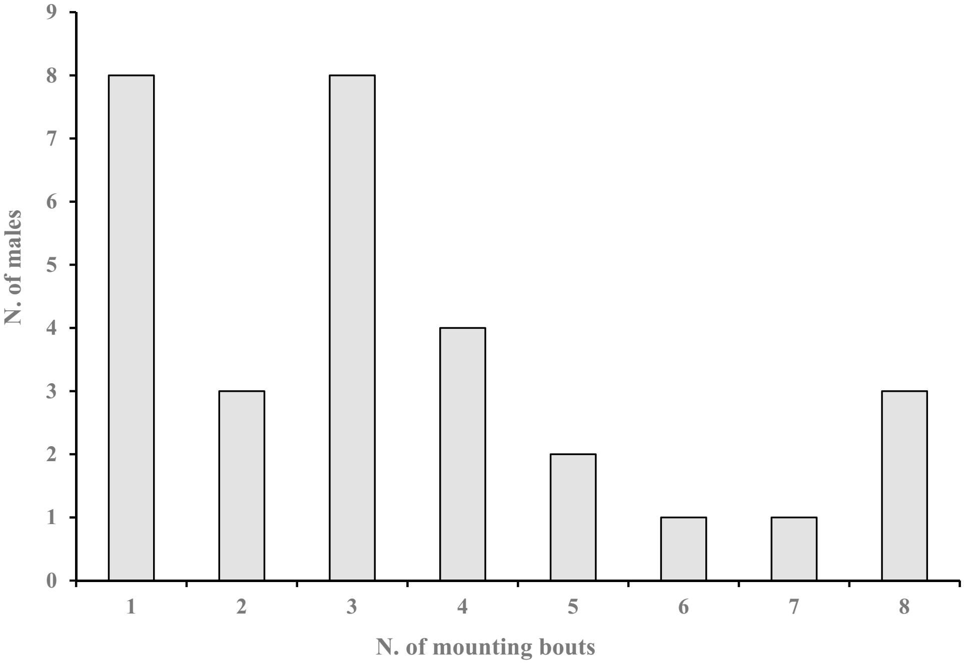

Fig. 3 Histogram of the number of mounting bouts for each pair of Japanese badgers

allogrooming only once between mounting bouts involving females (F6) and males (M30) (Table S1).

After the initial mounting bout, the female returned to her sett, whereas the male retreated to its resting nest. This resting nest was constructed by a male who collected fallen leaves and debris within approximately 20 m of his mate's sett either between mounting bouts or before the first mounting bout. If unoccupied setts were available within this 20 m radius from the female sett, one of these unoccupied setts was used as a resting site. Between 2 min and 18 h later (313.5 ± 35.0 SE min), the male returned to his mate's sett to entice her for another mounting bout at the same mating sites. The pairs repeated this behavioral pattern of movement between the resting sites and female setts. The sequence was sometimes terminated by female refusal. The time that the male spent between his initial visit to the female's sett and his departure from the sett after a series of mounting bouts (i.e., attendance duration) was 26.6 ± 3.5 SE h (range = 1.4–74.2, N = 29) (Table S1). The duration from the start of the first mounting bout to the end of the last mounting bout was 16.5 ± 2.7 SE h (range = 0.07–50.3, N = 30) (Table S1). Given the repeated use of the same mating site, the copulatory activities of badgers tended to disperse fallen leaves and disturb the surface soil. Consequently, the bare, well-trodden ground at these sites became particularly conspicuous to the human eye (Fig. S1).

Male concealing behavior of mating sites

Following a series of copulations, we recorded two instances in which the males covered bare ground with fresh soil and fallen leaves. The initial occurrence of this behavior was recorded in Chino in 2015 (Fig. 4, http://www.momo-p.com/showdetail-e.php?movieid=momo240213ma05a, Video 4). The final mounting bout was completed at 15:06 h on April 16. The female subsequently returned to her sett. The mating site was bare and devoid of fallen leaves. Subsequently, the male was observed sniffing the mating site, and 2 min after completing mating (15:08), he began to rake up the surrounding fallen leaves and soil and covered the bare site. Within 4 min, the site was completely covered and was no longer discernible to the human eye. Subsequently, the male left the vicinity and was not observed returning.

Multiple mating by females

Eighty percent (8/10) of the females mated with multiple males (Table 1). The mean interval between the end of the last mounting bout with a preceding male and the initiation of the first mounting bout with a subsequent male was 24.7 ± 7.8 SE h (range = 0.5–164.6, N = 19). The mean number of mates per female was 3.0 ± 0.4 SE (range = 1–5, N = 10) (Table 1). The mean period from the onset of the first mounting bout with the initial male to the termination of the last mounting bout with the final male was 5.1 ± 0.7 SE days (range = 2–9, N = 10) (Table 1). In only one case was a female engaged in copulation with a male 7 days after the previous mounting, although the duration of this mounting was notably shorter than the standard duration, lasting just 4 min (Table S1). We encountered two instances in which a male was physically attacked during mounting and was taken over by a rival male (Table S1; Fig. 5; http://www.momo-p.com/showdetail-e.php?movieid=momo240213ma06a, Video 5).

Discussion

We found that female Japanese badgers mated with multiple males and were repeatedly mounted by the same male. Although we did not examine the genetic fathers of the Japanese badgers, it is plausible that individual litters could exhibit multiple paternities. This behavior aligns with the mating behavior of a congener, the European badger. In European badgers, multiple males sired a single litter (Dugdale et al. 2007, 2011). Many solitary species of mustelids, including the American mink, stoat, and wolverine *Gulo gulo*, have multiple paternities within their litter (mink, Thom et al. 2004; Yamaguchi et al. 2004; stoat, Holland and Gleeson 2005; wolverine; Hedmark et al. 2007). Multiple

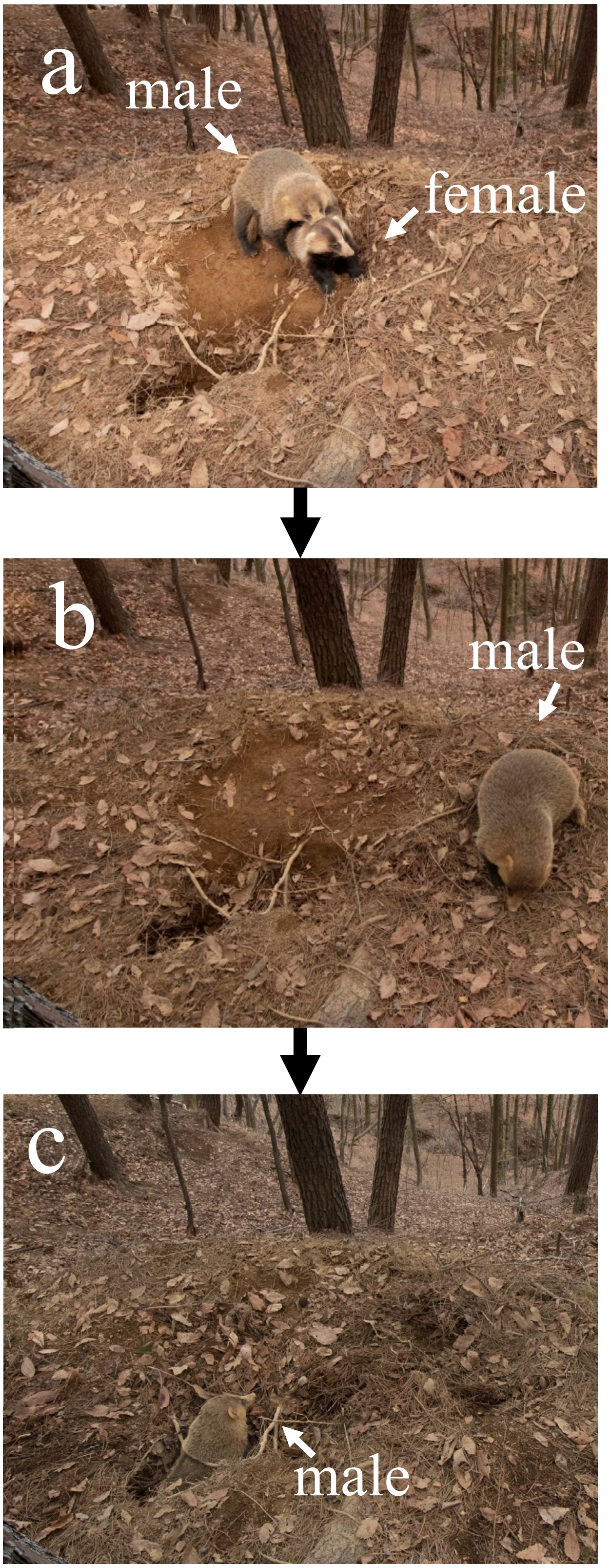

Fig. 4 Concealing behavior of a mating site by a male Japanese badger. Time-lapse image taken at Chino City, Nagano on April 16, 2015. A male copulated with a female at a mating site (**a**). After copulation, he began to rake up surrounding fallen leaves and soil, covering the mating site (**b**). The mating site was completely concealed (**c**) (http://www.momo-p.com/showdetail-e.php?movieid=momo240213ma05a, Video 4)

Table 1 Copulation behavior of *Meles anakuma* females. Mating period is the period females engage in mating throughout the focal mating season. No. of mounting bouts is the sum of the number of mountings throughout the focal mating season

Area	Female ID	Year	Mating period (day)	No. of mates	No. of mounting bouts
Nagano	F1	2015	3	2	7
Yamaguchi	F2	2016	6	5	19
Yamaguchi	F3	2016	6	4	12
Yamaguchi	F2	2017	6	4	12
Yamaguchi	F3	2017	5	4	12
Yamaguchi	F4	2017	9	2	4
Yamaguchi	F5	2017	2	1	2
Yamaguchi	F2	2018	6	4	18
Yamaguchi	F5	2018	6	3	9
Yamaguchi	F6	2018	2	1	6
Mean ± SE			5.1 ± 0.65	3.0 ± 0.42	10.1 ± 1.68

Fig. 5 Interruption of copulation by an intruding male (http://www.momo-p.com/showdetail-e.php?movieid=momo240213ma06a, Video 5)

paternity may be prevalent among mustelid families, regardless of whether they are solitary or group-dwellers.

The following are possible hypotheses: females benefit from multi-male mating and repeated mounting with the same male, similar to Japanese badgers. The first was to devalue the sperm of previous males. This hypothesis has been rejected in European badgers, where females are subjected to dual mounting by a single male, with an intermediate mounting event involving a different male (Dugdale et al. 2011). However, this mounting pattern was not observed in Japanese badgers, suggesting that this hypothesis cannot be dismissed for this species. The second hypothesis states that females gain genetic benefits by obtaining compatible genes and increasing the genetic diversity of their offspring (Dugdale et al. 2011). The third hypothesis posits that females disrupt paternity and reduce their risk of male infanticide (Dugdale et al. 2011). Unlike European badgers, who occasionally engage in cub predation as a potential competition reduction strategy, there are no documented instances of infanticide among Japanese badgers. Further studies are required to identify the benefits females gain.

We found that female Japanese badgers engaged in mating activities spanning only a few days in all instances except for one (7-day interval). This pattern suggested an estrous period similar to that documented in European badgers (Dugdale et al. 2011). However, the mating schedules were largely different between the two species. While copulation frequently occurs outside the estrus period, even during summer and autumn, in European badgers (Roper 2010), all mating instances were confined to the period between February and April in Japanese badgers. These findings imply that Japanese and European badgers are monoestrus and polyoestrus, respectively (Yamaguchi et al. 2006). However, physiological analyses are required to determine the reproductive cycles of these species.

We observed female Japanese badgers barking and chasing away males that attempted to copulate. However, in nearly all cases, the females eventually accepted mating. This consistent pattern implies that the initial refusal behavior of females could be "ritualized behavior" preceding copulation, in which females assess the conditions and physical traits of males. Although female European badgers also exhibit refusal behavior, their behavior differs from that of Japanese badgers. European badger females refuse males by flattening their bodies on the ground, turning their sides, or backing sett entrances to prevent copulation (Roper 2010; Dugdale et al. 2011).

The mean duration of mounting bout of the Japanese badger was 70.2 min, which was much longer than that of European badgers (230 s; Dugdale et al. 2011), as well as the durations recorded in a few other mustelid species including Japanese marten (15 min, Tatara 1994) and the American pine marten (4–14.5 min, Grant and Hawley 1991). Although the ovulation type (induced or spontaneous) of badgers remains unknown, European badgers are assumed to be induced ovulators (Yamaguchi et al. 2006).

If Japanese badgers exhibit induced ovulation, then prolonged mounting may trigger ovulation (Yamaguchi et al. 2006).

Between mounting bouts, the male badgers rested close to their mates to guard them against their rival males. Some males attended their mates for approximately 2 days, a duration that accounted for approximately 40% of the mean mating period of females (5.1 days). This protracted attendance limits the mating opportunities for females, thereby increasing their paternity. However, as copulation and attendance are sometimes terminated by female refusal, prolonged copulation and attendance may be costly for females. Male European badgers build neither resting nests nor guard females from within-group males. The intense mate guarding of Japanese badgers may be attributed to stronger intrasexual competition. This interpretation is supported by the greater sexual size dimorphism observed in Japanese badgers (1.3–1.4; Kaneko 2015; Tanaka 2015) compared to European badgers (1.1; Roper 2010). Notably, we observed two instances of physical contests between the males during copulation (Table S1), with the intruding male successfully displacing the resident male on both occasions. Males with facial scars were frequently observed during the mating season (Tanaka unpublished data), and it is highly likely that male–male aggression occurs frequently.

We observed that some males covered their copulating sites with fresh soil and fallen leaves immediately before leaving the mating sites. This intriguing behavior in male badgers may enhance their paternity by obscuring the presence of estrous females in potential rival males. The scent of the females likely permeated the soil during copulation, because they were pressed against the ground during this process. The olfactory cues left behind by badgers at these mating sites are potent and even discernible by human senses. If male badgers rely on olfactory cues absorbed in the soil to locate their mates, concealing mating sites from leaves and soil may impede the ability of rival males to locate females. A similar phenomenon of scent concealment has been reported in male bamboo lemurs, *Hapalemur meridionalis* (Eppley et al. 2016). Males of *H. meridionalis* scent-mark latrines directly on top of a previous mark made by females to disguise the presence of females in the territory of rival males.

This study revealed substantial disparities in mating behavior between Japanese and European badgers. The high relatedness among within-group individuals in the European badger may reduce competition between males compared with that in the solitary Japanese badger, which may account for the differences in mating behavior between the two species. This study provides important insights into the intricate interplay between social structures and mating behaviors within the mustelid family.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10164-024-00810-y.

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Author contributions HT designed the study. HT, YF, and EY collected the data. HT and WK analyzed the data. HT and WK prepared the manuscript.

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Data availability Nothing applicable.

Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval All applicable international, national, and institutional guidelines for animal care and use were followed. This article does not contain any studies with human participants performed by any of the authors.

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