Pitman III and Bastille-Rousseau
Animal Biotelemetry (2023) 11:24
https://doi.org/10.1186/s40317-023-00335-0

Animal Biotelemetry

METHODOLOGY

Open Access

Retention time and fix acquisition rate of glued-on GPS transmitters in a semi-aquatic species

John B. Pitman III[1*] and Guillaume Bastille-Rousseau[1]

Abstract

Background Movement is a core mechanism through which animals interact with their environment. GPS telemetry is a popular approach used to investigate animal movement, providing access to both the spatial and temporal behavioral patterns exhibited by an individual or population. However, while some species are easily tracked through traditional GPS attachment methods (such as GPS collars or backpacks), other species such as the North American beaver (*Castor canadensis*) present unique challenges given their fusiform shape and tapered neck.

Results We tested three different GPS transmitter attachment methods (tail-mounted, lower back glued-on, and upper back glued-on) for beavers over two seasons to determine which treatment was most effective in terms of retention time (RT, total number of days a transmitter remains attached) and GPS fix success rate (FSR, % of successful fixes vs. attempted) and investigated to what degree various factors (season, sex, and age class) affected these results. We then evaluated whether the data collected were sufficient for identifying home-ranging behavior (when an individual begins to display restricted space use and range residency). We found transmitters attached to the lower back during the fall to be the top performing treatment, having a similar mean FSR (51.59%) to upper back attachments in fall, but a significantly greater average RT (42.8 days). Of the 23 individuals included in the home-ranging behavior analysis, all but two had sufficient data for identifying home-ranging behavior.

Conclusions Our tests show that glued-on GPS tags can provide up to 2 months of fine-scale relocation data in a safe and effective manner. This allows the opportunity to answer novel questions regarding movement patterns of beavers and other semi-aquatic mammals.

Keywords *Castor canadensis*, GPS telemetry, Semi-aquatic animal movement

Background

Movement is one of the main mechanisms through which organisms interact with their environment and directly shapes many ecological processes. Movement impacts a multitude of phenomena including interspecific interactions such as competition and predation [3], how social networks propagate the spread of disease [22] or influence foraging behavior [32]. Given the wide impact of movement, understanding the implications of this behavior is critical for the conservation and management of species and the ecosystems they inhabit [51]. Global Positioning Systems (GPS) technology has become central to investigating movement, providing access to fine-scale relocation data required for understanding the intricacies of this behavior. Since its inception, the consistent improvement in GPS technology has led to an increase in the amount of relocation data that can be collected,

*Correspondence:
John B. Pitman III
brookspitman3@gmail.com
[1] Southern Illinois University, 1263 Lincoln Drive, Carbondale, IL 62901, USA

while also expanding on the diversity of species that may be tracked [21, 36, 49].

Despite GPS telemetry strengths, many species remain difficult to track. Semi-aquatic species (e.g., river otter (*Lontra canadensis*), mink (*Neovison vison*), Eurasian beaver *Castor fiber*) are a prime example where GPS telemetry is rarely used, though there have been attempts [34, 37, 41]. This is due to the fusiform shape and tapered necks commonly associated with most semi-aquatic species that prevents the use of typical collar-type devices. Conventional collar and backpack transmitters often used in other mammalian and avian studies are generally ineffective and potentially hazardous if the attachment prematurely slips off of the animal or becomes entangled with debris when an animal is submerged [1, 40]. In addition, the dense canopy cover commonly associated with the riparian habitat where these species are found can negatively impact the GPS fix success rate (FSR, percentage of successful fixes vs. total attempted fixes) due to the heightened chance satellite signals will be reflected or blocked during an attempted GPS fix [20]. Similarly, water submersion has been shown to negatively affect FSR due to the inability of GPS signals to properly propagate in water [34]. Lastly, long-term tagging or repeated captures of semi-aquatic animals can also have consequences on animal health, especially weight gain [30, 37, 44]. Temporary methods of transmitter attachment involving limited animal handling are therefore more suitable.

As territorial and central place foragers, beavers present an interesting system to study movement in a semi-aquatic species [15, 38]. Beavers generally engage in multiple foraging excursions per day, generally returning to the original central place (the lodge). Inside the lodge, beavers often engage in social grooming where individuals will nibble portions of fur that are out of reach for another individual [33]. However, it has been documented that beavers can also use multiple dens and lodges within their core home range depending on foraging intensity (possibly using alternative lodges and dens during increased foraging in the fall) or to accommodate fluctuations in water depth [5, 19]. Beavers also actively engage in territorial behavior including patrolling and scent marking, with some studies documenting a strong propensity to monitor and maintain these territorial markers through several revisits over a short period of time [38, 39].

Furthermore, a better understanding of beaver movement is also warranted given their ecological and economic impacts. Described as both a keystone species and ecological engineer, their damming behavior results in the development of pond and wetland complexes that strengthen spatial heterogeneity and geomorphic complexity, thereby promoting an increase in species and habitat diversity [11]. Furthermore, the reduced flow of streams and increased storage of surface and groundwater may improve climate resiliency at the landscape scale by supplying a reservoir for riparian vegetation during dry periods of the year [12]. Agricultural workers and civilians benefit from this reduced flow and storage of water as well, where it aids in the prevention of catastrophic flooding during periods of high precipitation and mitigates the cost of water during periods of drought [31]. Conversely, beaver activity also has the potential to cause extensive damage to agricultural crops [23] infrastructure such as roads and culverts, and commercial timber stands [2].

To date, the traditional method for tracking beavers has been with VHF transmitters bolted to the tail, which has been implemented in multiple geographic regions with good success [1, 4, 26, 50]. Alternative attachment methods have also been tested including VHF collars mounted on the neck [1] or at the base of the tail [40], however these methods have yielded low retention times (RT, number of days a transmitter remains attached) limiting the total tracking period. Likewise, subcutaneous implants have also been used with limited success [25]. While tracking animals via VHF telemetry can provide information on behavior such as home ranging or dispersal, it is generally impractical to collect numerous locations per day throughout the entire tracking period. Without insight into the daily activity patterns of an animal, the ability to evaluate other aspects of the movement process such as foraging strategies (i.e., trapline foraging, central place foraging), or quantifying the degree to which abiotic and biotic factors influence home range structure is limited. There have been several studies investigating beaver movement using GPS telemetry [9, 16–18, 20, 25, 29, 30, 37, 45]. Average retention time in these studies ranged from 5 to 22 days with GPS fix acquisition success rates around 80–86%. However, the goals of these studies were not centered on specifically testing and improving upon the longevity of the attachment method or the fix success rate (but see [20]).

The main objective of this study was to identify the most effective method for attaching GPS transmitters to beavers to investigate fine-scale spatial movement patterns. We evaluated each method to ascertain which provided the greatest RT and FSR, and then analyzed the location data collected to determine whether the total number of locations acquired, and length of tracking period were sufficient for identifying home-ranging behavior in beavers. Moreover, we evaluated how some methods may differ among seasons (spring and fall). We predicted that tail-mounted transmitters would have the highest RT based on previous studies using this same attachment method with VHF units. Upper back mounts would follow tail-mounts, while transmitters glued to the lower back would have the shortest RT due to the lower back being the widest point of the body. We assume this would lead to more aggravation of lower back attachments as they would be more prone to catch on debris as a beaver moves through tight spaces. We predicted that FSR would be highest for transmitters glued to the lower back, followed closely by transmitters glued to the upper back. Since the lower back protrudes slightly more from the water while swimming, we believe this will provide an increased chance for successful GPS fixes. We predicted that tail-mounted transmitters would have the lowest FSR since the tail tends to remain submerged while swimming. Lastly, we predicted that lower- and upper-back glued-on tags will provide a sufficient number of relocations to estimate home-ranging behavior.

Methods

Study system

We conducted our research on the Union County Conservation Area, hereafter referred to as the UCCA, which encompasses 25.1 km^2 in the Lower Mississippi River bottomlands division of southwest Illinois, USA. Acquired by the Illinois Department of Natural Resources (IDNR) in the late 1940s, the UCCA is primarily managed to provide an overwintering site for Canada geese (*Branta canadensis*) and other waterfowl. The topography is relatively flat with numerous shallow sloughs and other scattered bodies of water making up ~ 4.5 km^2 of the property. Of the ~ 21.5 km^2 of land area, approximately 10 km^2 are cultivated including crops such as corn, sunflower, wheat and clover, portions of which are left standing for overwintering waterfowl. The remaining acreage on the UCCA consists of timber, brush, or grass cover.

The dominant aquatic vegetation consists of buttonbush (*Cephalanthus occidentalis*), elodea (*Elodea* spp.), and water lily (*Nymphaea* spp.). The bottomland hardwood forests that make up this region include tree species such as green ash (*Fraxinus pennsylvanica*), black willow (*Salix nigra*), and cottonwood (*Populus deltoides*) in wet areas, with sweetgum (*Liquidambar styraciflua*), pecan (*Carya illinoensis*), and pin oak (*Quercus palustris*) in the drier areas [5]. Fauna that may interact with beavers in the study area include river otter, mink, muskrat (*Ondatra zibethicus*), bobcat (*Lynx rufus*), and coyote (*Canis latrans*). Due to low trapping levels and highly suitable habitat, beaver density on the UCCA was determined to be one of the highest reported in wildlife literature, estimated at 3.27 colonies/km^2 [4]. Mild winters and hot summers characterize the climate of southern Illinois. Mean temperature during the spring tracking period was 14.3 °C with an average daily precipitation of 0.16 inches. During the fall tracking period, the mean temperature was 11.2 °C with an average daily precipitation of 0.13 inches [47].

Field methods

Beaver capture and processing

Beaver capture and handling protocols were approved by the Institutional Animal Care and Use Committee at Southern Illinois University (No. 21–002). Beavers were captured during March–May and October–November 2021 using cable snares [27]. Each snare was built using steel aircraft cable and fitted with a loop stop ~ 34 cm from the end of the cable, preventing the snare from closing past a 12.5 cm diameter and limiting the capture of non-target species. Snares were secured to the trapping location using earth anchors that were connected to the snare with stainless-steel swivels to reduce the chances of injury. Snares were also equipped with a relaxing slide-lock to prevent the snare from continually tightening down on a captured animal. Trap locations included dams, den entrances, beaver runs, haul-out slides, and along beaver trails. Each snare was baited with commercial lures or local vegetation such as twigs and branches. All trap locations were cleared of any debris that may cause entanglement of the snare cable and snares were checked twice daily.

During captures, beavers were restrained using a catchpole and anesthetized with an intramuscular injection of ketamine hydrochloride (10 mg/kg) and xylazine hydrochloride (0.125 mg/kg). Once anesthetized, each beaver was fitted with an ear tag (Model: 1005–1, National Band & Tag Company, Newport, KY), sexed, weighed, and assigned an age class based on weight: kits (< 1 yr; < 11 kg), juveniles (1 yr; 11–16 kg), subadults (1–2 yr; 16–19 kg), and adults (> 2 yr; > 19 kg) [28].

Transmitter attachment

Customized GPS transmitters (Q4000ER LS17500, Telemetry Solutions, Concord, CA, Fig. 1A) were attached by one of 3 methods: (1) traditional tail-mount [26, 50]; (2) glued to lower back via mid-cure epoxy [16, 17, 37]; and (3) glued to upper-back via mid-cure epoxy. For transmitters attached via the tail-mount method, a sterilized stainless-steel drill bit was used to punch an 8 mm hole through the tail, approximately 2.5 cm left of the center of the tail to ensure no muscle or bone was damaged in the process. Prior to puncturing the tail, the site was sterilized with betadine solution and received an injection of 250 mg/mL 0.5% bupivacaine (< 1 CC's) to act as a topical anesthetic. The transmitter was then secured to the tail with a stainless-steel machine bolt, washer, and lock nut (Fig. 1B). Once the transmitter was

Fig. 1 Picture including custom-designed transmitters and various attachment methods. Pictures displaying **a** the customized tail-mount (transmitter with white colored end and hole to facilitate bolting the transmitter to the tail) and back-mount transmitters (the red tape was used to fasten magnets to the transmitters, temporarily disabling the GPS and VHF until deployment), **b** a tail-mounted transmitter successfully secured to the tail of a captured beaver, **c** transmitter adhered to the lower back using mid-cure epoxy, and **d** transmitter adhered to the upper back using mid-cure epoxy

attached, Vetbond™ was applied around the attachment area to help prevent any infection.

For transmitters attached to the upper and lower back with adhesives, the transmitter was first glued using cyanoacrylate super glue to a neoprene interface (2–3 mm); each piece of neoprene was cut so that approximately 1–2 cm of the neoprene was visible around the transmitter. The beaver's fur was then cleaned using acetone to ensure removal of any dirt and debris. Once the fur was completely dried, mid-cure epoxy (Bob Smith Industries, Paso Robles, California, USA) was then applied to the attachment location and the transmitter was placed on either the upper or lower part of the back, centered along the spine. A two-part resin epoxy was then applied over the top of the unit to fully encase the transmitter and neoprene in epoxy (Fig. 1C, D).

After completing the processing event, each beaver was placed in a recovery crate to allow for the immobilization drugs to fully metabolize and to allow sufficient time for the epoxy to completely cure. Tagged individuals were closely monitored via VHF telemetry for one week following the capture event, after which they were tracked every two weeks to remotely download GPS data for the remaining life of the transmitter. GPS schedules were set to acquire a location every hour, resulting in a maximum battery life estimation of approximately four months. To preserve battery life of the transmitters and reduce bias in the GPS fix success rate analysis, each transmitter was programmed to skip up to six scheduled fixes in a row if there was little to no activity detected via the accelerometer. This helped to avoid GPS fix attempts while a beaver was in its lodge or den where the transmitter would be incapable of acquiring a successful fix [20].

During the spring (March–May), we intended to deploy eight transmitters using the tail-mounted approach and eight transmitters to the lower back using the adhesive mounted approach. However, following early results showing extremely low GPS acquisition rates with the tail-mounted units (see results), we deployed the remaining transmitters on the lower back using adhesives. During fall (October–November), we divided transmitter deployments evenly between adhesive attachments to the upper back and to the lower back to determine whether there was any difference in RT or GPS FSR between the two locations.

Data analysis

Due to the complications experienced with the tail-mount approach (see results), that attachment method was excluded from analysis. The remaining transmitter deployments were then categorized as one of three treatments including lower back/spring (LS), lower back/fall (LF), and upper back/fall (UF). We used a one-way ANOVA [52] to determine whether there were differences among the treatments for both RT (total number of days a transmitter remained attached to a beaver) and FSR (% of successful fixes acquired vs. attempted) ($\alpha = 0.05$ throughout). We visually inspected that variables respected the normality assumption and did not need to be transformed [52]. We then used Tukey's HSD post hoc test [52] to provide pairwise comparisons of each treatment and identify the top performing treatment. While not the main focus of our work, we also used a T-test [52] to determine whether there was a difference between fall vs. spring, or male vs. female on RT and FSR. In addition, we analyzed the data with respect to age class (adult, sub-adult, juvenile) using a one-way ANOVA to determine whether there was a difference among the three groups and their effect on FSR and RT. We then performed a Tukey's HSD post hoc test to determine which age class was associated with the greatest RT and FSR. Lastly, we also evaluated FSR over time to evaluate for temporal bias in fix acquisition.

We used the package ctmm [7] in program R [35] to evaluate if the locations acquired were sufficient for identifying home-ranging behavior of each individual (i.e., the temporal period required for an individual to begin displaying restricted space use and range residency). Variograms showing the autocorrelation in the movement data were produced and used to estimate the home range crossing time (τ position parameter) (Fig. 2A, D). The estimated home range crossing time represents the time lag at which the variogram reaches 63% of its asymptote, with the asymptote indicating the time lag at which an

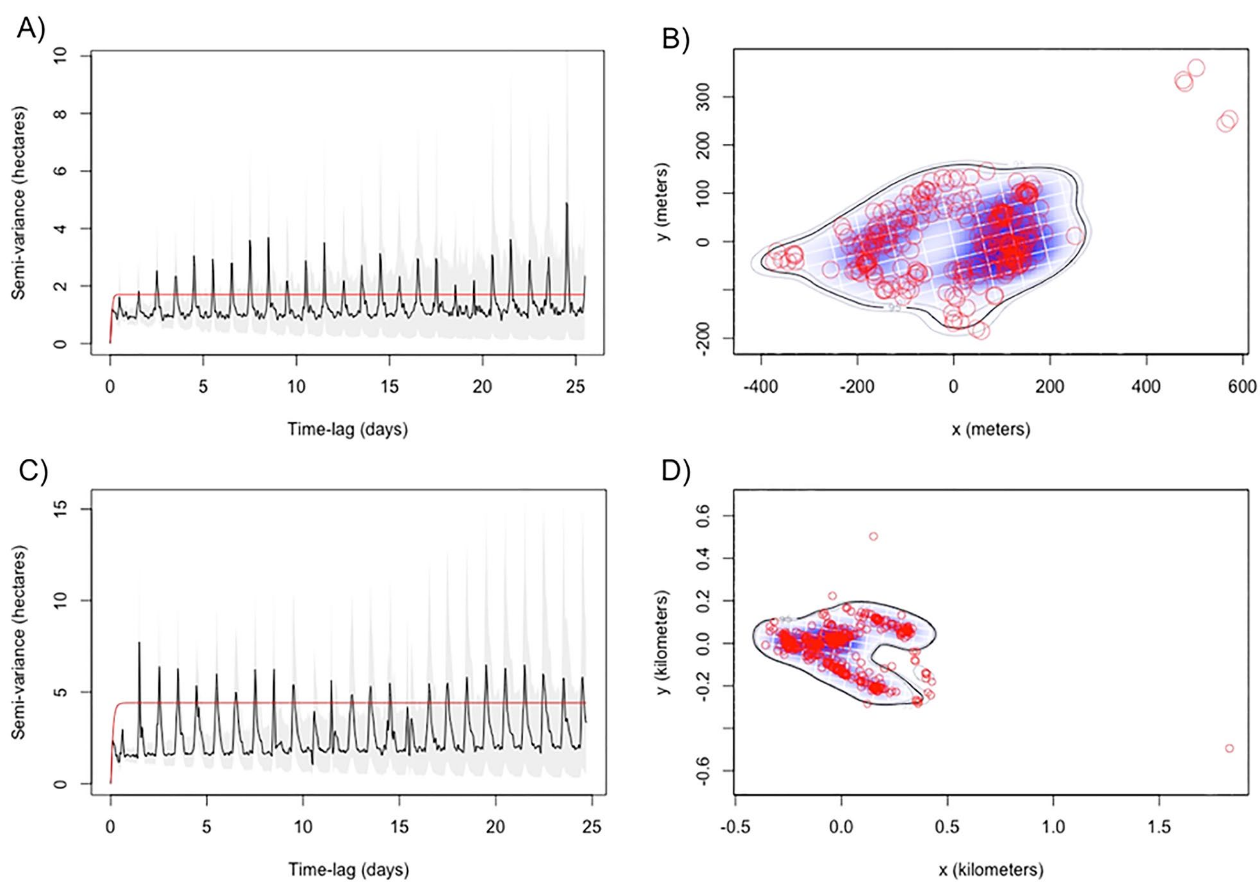

Fig. 2 Examples of ctmm output including variograms and AKDE home range. Examples of ctmm output for two beavers including **A** the variogram ($\tau = 22.89$ min, Asymptote = 36.33 min) and **B** estimated AKDE home range size (14.37 ha) for "Scar", and **C** the variogram ($\tau = 23.34$ min, Asymptote = 37.04 min) and **D** estimated AKDE home range size (24.9 ha) for "Pumbaa". The red line represents the fitted variogram

individual can cross its home range several times. This is also inferred as the length of time required for an individual to begin displaying home-ranging behavior based on the relocation data [7, 43]. Therefore, crossing times were divided by 0.63 to obtain the asymptote for each individual. Using the parameters identified in the fitted variogram, we also determined home range estimates via autocorrelated kernel density estimation (AKDE) (Fig. 2B and D) [14]. Lastly, we estimated travelling distance (or speed) as the distance travelled between two consecutive locations.

Results

We captured and tagged 32 beavers between March 4, 2021, and November 9, 2021, with 19 individuals captured during the spring and 13 during the fall. We captured an equal number of males and females, 18 of which were adults, seven subadults, and seven juveniles. During the spring, three individuals received tail-mounts while the remaining 16 received the lower back mounts attached using adhesives. Of the 16 lower back mounts, we recorded three mortalities, one predation via bobcat, one unknown predation, and one unknown cause of mortality. In addition, one transmitter malfunctioned during deployment. Due to the mortalities and malfunctions experienced in the spring, coupled with the complications experienced with tail-mounted transmitters (see "Tail-mounted transmitters") 12 individuals from the spring were retained for analysis. During the fall, seven beavers were outfitted with upper back mounts and six with lower back mounts. While no mortalities were recorded during the fall, one lower back transmitter malfunctioned and was excluded from analysis. After exclusions, a total of 24 beavers were retained for analysis including 15 adults, 5 subadults, and 4 juveniles (see Table 1).

Tail-mounted transmitters

We initially intended to deploy eight transmitters using the tail attachment method to provide a one-to-one comparison with the adhesive mount approach. However, after three deployments we observed that FSR was consistently < 1% for each deployed unit, resulting in the abandonment of this method. Of the three individuals that received the tail-mounted transmitter, one was found as an unknown mortality, one transmitter malfunctioned, and the remaining individual was recaptured approximately 1 month from the initial capture and the respective transmitter removed for later use.

Retention time of glued-on transmitters

RT of transmitters ranged from 16 to 56 days, with a mean of 30.3 days across all captured individuals. There was a difference in RT among the treatments ($F_{2,21} = 14.89$, $p < 0.001$, Fig. 3A). LF ($n = 5$) was the most effective treatment (mean = 42.8 days, range = 35–56 days). A Tukey's HSD post hoc test found that the mean RT for LF attachments was different ($p = 0.026$) from the second top performing treatment, UF ($n = 7$, mean = 32 days, range = 19–45 days). Mean RT for UF attachments outperformed ($p = 0.045$) LS ($n = 12$, mean = 24 days, range = 16–33 days). There was a difference in RT of transmitters, between males (mean = 34.4 days) and females (mean = 26.1 days) ($t(22) = -2.281$, $p = 0.032$, see Additional file 1C), but not across age class ($F_{2,21} = 0.491$, $p = 0.619$, see Additional file 1D).

Fix success rate of glued-on transmitters

FSR ranged from 15.46 to 59.95%, with a mean of 38.82% across all tagged individuals. There was a difference in FSR among the three treatments ($F_{2,21} = 13.23$, $p < 0.001$, Fig. 2B). LF ($n = 5$, mean = 51.59%, range = 37.44–59.95%) and UF ($n = 7$, mean = 45.93%. range = 35.7–56.03%) were the top performing treatments. A Tukey's HSD post hoc test indicated no difference in mean FSR between LF and UF ($p = 0.563$). LS was the least effective treatment (mean = 29.39%, range = 15.46–47.54%). A Tukey's HSD post hoc test indicated that the mean FSR was different between LF and LS ($p < 0.001$), and between UF and LS ($p = 0.002$). There was no difference in FSR between males (39.33%) and females ($M = 38.31\%$, $t(22) = -0.186$, $p = 0.854$, see Additional file 2C) or age class (F

Table 1 Summary of sample size in relation to age, sex, and attachment method

	Male			Female		
	Adult	Subadult	Juvenile	Adult	Subadult	Juvenile
LS	1	2	2	6	0	1
LF	4	0	1	0	0	0
UF	2	0	0	2	3	0

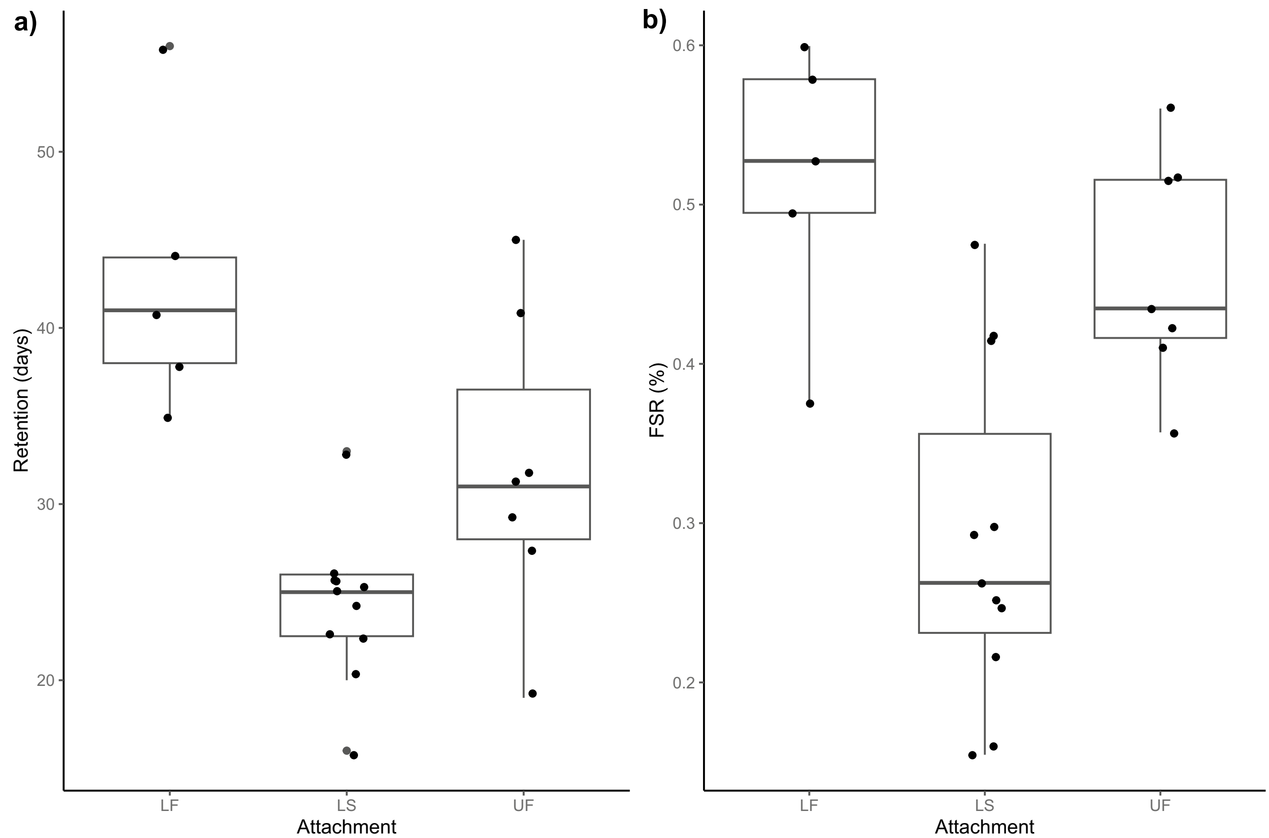

Fig. 3 Retention time results of transmitters for attachment, season, sex, and age. Boxplots representing how **a** retention time (number of days the transmitter remained attached to the beaver) and **b** FSR (fix success rate) varied across individuals with respect to attachment treatment (*LF* lower back/fall, *LS* lower back/spring, *UF* upper back/fall)

2,21 = 0.404, p = 0.619, see Additional file 2D). Most fixes were at night, but 13.65% of our locations were acquired between 700–1900 h. Fix success rates were also lower during the day (see Additional file 3).

Home range parameters and size

We collected sufficient data to capture home-ranging behavior for 21 of the 23 individuals included in home-ranging analysis. During the spring, one juvenile male had an estimated home range of 15.41 km^2 and an associated time lag of 1588.05 min to reach the asymptote of the variogram. Given the large difference with other individuals, we considered this individual as an outlier and did not include it in population summary statistics. For variograms of all other individuals to reach their asymptote, the time lag observed ranged from 20.48 min to 544.14 min, with a mean of 100.33 min (see Additional file 4A). For all individuals, home range sizes ranged from 0.03 km^2 to 1.08 km^2, with an average home range size of 0.29 km^2 (see Additional file 4B). Hourly travelled distance ranged from 3 to 1572 m/h with an average of 202 m/h.

Discussion

We tested two different methods of GPS transmitter attachment over two seasons for beavers to identify which provided the greatest FSR and RT and investigated how season, sex, and age class affected these results. We then evaluated whether the data collected were sufficient for identifying home-ranging behavior in beavers. We found that transmitters attached to the lower back during the fall using adhesives proved to be the top performing treatment. Of the 23 beavers included in the home-ranging behavior analysis, the data collected during transmitter deployment were sufficient for identifying home-ranging behavior for all but two individuals. While previous attempts have been made with tracking beavers using GPS telemetry [16, 17, 20, 45] our work explicitly shows what can be expected out of glued-on GPS transmitters and that they are an effective way of obtaining fine-scale relocation data for semi-aquatic mammals.

Glued-on transmitter performance

Using glued-on transmitters, we successfully tracked individuals for roughly one month while some transmitters approached two months before falling off. Our method produced higher average RT to previous attempts such as in [16, 17] (average RT of 11 days, ranging from 5 to 22 days) and [45] (average RT of 13.5 days, ranging from 8 to 25 days) though these projects purposefully attempted to recapture tagged individuals and remove transmitters. Other projects that have also attempted to use adhesives for long-term GPS transmitter attachment abandoned the method due to complications and therefore lack extensive data for comparison [9, 18]. While the extended retention time observed in our studies might help answer novel questions, considerations should also be given regarding animal welfare. Several studies have documented tagging effects on beavers [30, 44]. As such, glued-on tags might provide a good intermediate duration for tracking beavers without risking beavers being impacted by those devices over a long duration, especially if animals only need to be handled once [37].

We are only aware of one other study investigating FSR for GPS tagged beavers, which reported a much higher average FSR of 86.2% [20] in comparison to our findings which resulted in an average FSR of 38.82%. This discrepancy can partly be explained because of differences in GPS programming. Justicia et al. [20] programmed GPS transmitters to acquire fixes from 1900 to 700 h when beavers are considered most active, as opposed to our GPS schedule which collected fixes throughout the entire 24-h period, resulting in a higher proportion of fixes attempted when beavers were in their lodge. In comparison, our FSR rates between 1900 and 700 was around 50%. Though scheduling GPS fixes through the day stands to reduce overall FSR when attempting to track movement of beaver, movements outside of their regular activity could be overlooked which may yield interesting insight into their biology.

While these results might be partly confounded by other factors, one interesting result is the difference in both FSR and RT performance between seasons. Fall transmitter deployments (upper and lower back) consistently outperformed the spring lower back attachment. This potentially resulted from variation in behavior exhibited between seasons. Beavers primarily establish obligate monogamous pairs (but see Crawford et al. [10]) where both male and female care is needed for offspring survival [6, 42]. During the spring, when kits are present, the requirement for parental care may have led to increased time spent inside the lodge for both males and females, reducing FSR [45]. In contrast, during the fall less time is required for parental care and the time spent outside the lodge is increased to collect building materials for lodge repair and food in preparation for the winter [2, 16, 17, 19]. This would presumably allow more opportunities for successful GPS fixes to be acquired during the fall resulting in a greater FSR as opposed to the spring.

Differences in behavior and biology between seasons may have also contributed to the reduced average RT observed in the spring. Like many other semi-aquatic species, beavers will engage in both self and social grooming to keep their fur dry, waterproof, and insulated through nibbling and shaking [13, 33]. It is possible that the increased time spent in or near the lodge during spring due to kit presence, coupled with shorter activity periods led to a relative increase in social grooming behavior. This may have resulted in more time aggravating transmitter attachments via social grooming, thereby compromising the integrity of the attachment and contributing to the reduced average RT recorded in the spring. In addition, similar to other mammals, beavers experience annual shedding which begins in late spring and continues into the summer. Our spring transmitter deployments overlapped with this time period, further degrading the integrity of the attachment. Though anecdotal, while recovering all units, seven transmitters were found inside a lodge/den with an additional 11 transmitters located within 10 m of a lodge/den. In addition, all recovered transmitters exhibited scarring presumably left from individuals chewing on the transmitter (see Additional file 5). The proximity to a lodge/den of dropped transmitters coupled with the obvious scarring that was observed on all recovered units further suggests that social grooming behavior plays a significant role in reducing RT of attachments. Compared to other semi-aquatic mammals, beavers are unique in that they are generally considered an obligate monogamous species (but see Crawford et al. [10]) with both males and females providing parental care, it is assumed that males still have a higher propensity for engaging in territorial defense while females are more constrained by parental care due to the energetic costs associated with producing and nursing offspring [39]. Assuming that increased time inside the lodge is associated with an increase in exposure to social grooming, this would help explain the greater RT results observed for males as opposed to females.

Tail-mounted transmitter complications

We initially intended to deploy eight tail-mounted transmitters for a direct comparison with the adhesive mounted units. Early deployments showed extremely poor FSR performance (< 1%) and this method was discontinued. The poor FSR performance was likely due to the location of the transmitter. Since the tail is generally submerged while swimming this resulted in attempted GPS fixes failing due to water interference [20, 34]. While we predicted that the tail-mounted transmitters would have the lowest FSR due to the attachment location, we did not anticipate such a low FSR. We assumed that GPS fixes would be taken during trips on land, but it appears that even during these trips, the GPS devices struggled to acquire locations. Overall, our results showed that tailed-mounted GPS transmitter are unlikely a replacement to VHF telemetry if long-term tracking is needed given our FSR was lower than many VHF telemetry studies where beavers are often relocated daily [4, 48, 50].

Home-ranging behavior

We were able to detect home-ranging behavior for all but two individuals. Our results indicated that on average, variograms produced for each individual reached the asymptote after a time lag of 100.39 min. This is considered a rough estimate of the time required for an individual to cross its home range several times, signaling restricted space use and range residency [7, 43]. In addition, the data collected were sufficient for not only identifying home-ranging behavior but also daily activity patterns. The oscillation produced in the variograms post-asymptote, seemed to capture the periods during which a beaver was active outside of the lodge or den and when it returned to rest through the day.

The short time required for beavers to begin displaying home-ranging behavior could be driven by various factors related to both behavior and the environmental features characterizing our study site. Beavers are highly territorial once a colony has been established [8], and will frequently patrol their territory deploying or refreshing territorial markers (scent mounds) to deter conspecifics [16, 17, 38]. A study involving Eurasian beavers investigated scent marking behavior of six reproducing pairs and reported that beavers were capable of deploying or refreshing up to 22 scent mounds per day [39]. This suggests beavers have both the ability and biological drive to engage in intensive scent marking as a territorial defense mechanism. As semi-aquatic mammals, beavers move efficiently through water, with one study reporting an average distance traveled of 682 ± 204 m/h while swimming [16, 17]. During the course of our study, we recorded a maximum mean distance traveled of 794 m/hr. Small home ranges, coupled with a high degree of territoriality and the ability to move quickly through water could result in the relatively short time lags observed for home-ranging behavior to occur.

Conclusions

Our results highlight that glued-on transmitters can be a viable method for tracking semi-aquatic mammals. Given some of the unique behaviors associated with beaver, we suspect retention time may be higher in other semi-aquatic mammals engaging in less social grooming behavior. Even with the increase in RT with our approach relative to previous attempts, RT remained relatively short compared to the transmitter battery life. We recommend that tags should be programmed to maximize data collection during the expected longevity of deployment. Given current battery and GPS tags performance, this means that most devices could be able to obtain locations at < 15 min intervals. If such temporal resolution is not needed, we suggest that researchers consider programming their tags to take locations throughout the day. While beavers are assumed to be nocturnal, a significant portion (> 13%) of our locations were acquired during the day. Since GPS fix acquisitions are rare when a beaver is inside a lodge or den, this would indicate that there are periods of activity outside of the lodge during the day. While this is a smaller proportion of locations when compared to those collected during crepuscular and nocturnal hours, these understudied movements can provide additional insights into beaver behavior [24, 34, 53]. We expect similar patterns to hold for other semi-aquatic species, as many exhibit similar periods of activity, while commonly using dens or burrows during periods of rest.

Abbreviations

GPS	Global Positioning System
RT	Retention time
FSR	Fix success rate
VHF	Very high frequency
UCCA	Union County Conservation Area
UF	Upper back/fall
LF	Lower back/fall
LS	Lower back/spring
AKDE	Auto-Correlated Kernel Density Estimation

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40317-023-00335-0.

Additional file 1. Boxplots displaying how retention time (number of days the transmitter remained attached to the beaver) varied across individuals.

Additional file 2. Boxplots displaying individual variation in GPS fix success rate (% of successful fixes vs. total attempted fixes).

Additional file 3. Variation in fix success rate through the diel period.

Additional file 4. Variation in A) home range crossing times and B) home range sizes across individuals.

Additional file 5. Pictures displaying damage to recovered GPS transmitters, presumably caused from chewing on the attachment.

Acknowledgements

We thank the IDNR for allowing our research to be conducted on the Union County Conservation Area, and respective biologists, Kenneth Delahunt and Drew Fehrenbacher for assisting with research efforts. The Forest Service for providing housing for technicians near the study site. Special thanks to Clay Nielsen and Craig Bloomquist for providing valuable information for trapping and working with beavers. Additionally, we thank Matt Bowers for guidance on the use of adhesives for transmitter attachment. We thank Storm Crews and Nicole Gorman for assistance with analyses. Lastly, we thank Kristin Botzet and Blake Abt for assistance in the captures.

Author contributions
JBP and GBR conceived the idea for the project and developed the research questions. JBP developed protocol and lead deployment of GPS transmitters. JBP carried out analysis and wrote the manuscript. GBR provided edits for the manuscript. Both authors read and approved the final manuscript.

Funding
Southern Illinois University startup fund.

Availability of data and materials
Data will be made available via movebank upon acceptance.

Declarations

Ethics approval and consent to participate
All research was approved by the Southern Illinois University Institutional Animal Care and Use Committee (No. 21-002).

Consent for publication
Not applicable.

Competing interests
The authors declare they have no competing interests.

Received: 1 November 2022 Accepted: 21 May 2023
Published online: 16 June 2023

References

1. Arjo WM, Joos RE, Kochanny CO, Harper JL, Nolte DL, Bergman DL. Assessment of transmitter models to monitor beaver Castor canadensis and C fiber populations. Wildlife Biol. 2008;14(3):309–17. https://doi.org/10.2981/0909-6396(2008)14[309:AOTMTM]2.0.CO;2.
2. Baker BW, Hill EP. Beaver (Castor canadensis) (pp. 288–310). 2003. https://pubs.er.usgs.gov/publication/87287.
3. Bastille-Rousseau G, Fortin D, Dussault C, Courtois R, Ouellet J-P. Foraging strategies by omnivores: are black bears actively searching for ungulate neonates or are they simply opportunistic predators? Ecography. 2011;34(4):588–96. https://doi.org/10.1111/j.1600-0587.2010.06517.x.
4. Bloomquist CK, Nielsen CK. Demography of unexploited beavers in Southern Illinois. J Wildl Manag. 2010;74(2):228–35. https://doi.org/10.2193/2008-456.
5. Bloomquist CK, Nielsen CK, Shew JJ. Spatial Organization of Unexploited Beavers (Castor canadensis) in Southern Illinois. Am Midl Nat. 2012;167(1):188–97. https://doi.org/10.1674/0003-0031-167.1.188.
6. Brotherton PNM, Manser MB. Female dispersion and the evolution of monogamy in the dik-dik. Anim Behav. 1997;54(6):1413–24. https://doi.org/10.1006/anbe.1997.0551.
7. Calabrese JM, Fleming CH, Gurarie E. ctmm: an r package for analyzing animal relocation data as a continuous-time stochastic process. Methods Ecol Evol. 2016;7(9):1124–32. https://doi.org/10.1111/2041-210X.12559.
8. Campbell RD, Rosell F, Nolet BA, Dijkstra VAA. Territory and group sizes in Eurasian beavers (Castor fiber): echoes of settlement and reproduction? Behav Ecol Sociobiol. 2005;58(6):597–607. https://doi.org/10.1007/s00265-005-0942-6.
9. Campbell-Palmer R, Jones S. The Scottish beaver trial: the story of Britain's first licensed release into the wild, Final Report. 2014.
10. Crawford JC, Liu Z, Nelson TA, Nielsen CK, Bloomquist CK. Microsatellite Analysis of Mating and Kinship in Beavers (Castor canadensis). J Mammol. 2008;89(3):575–81. https://doi.org/10.1644/07-MAMM-A-251R1.1.
11. Dittbrenner BJ, Pollock MM, Schilling JW, Olden JD, Lawler JJ, Torgersen CE. Modeling intrinsic potential for beaver (Castor canadensis) habitat to inform restoration and climate change adaptation. PLoS ONE. 2018;13(2):e0192538. https://doi.org/10.1371/journal.pone.0192538.
12. Fairfax E, Whittle A. Smokey the Beaver: Beaver-dammed riparian corridors stay green during wildfire throughout the western United States. Ecol Appl. 2020;30(8):e02225. https://doi.org/10.1002/eap.2225.
13. Fish FE, Smelstoys J, Baudinette RV, Reynolds PS. Fur does not fly, it floats: Buoyancy of pelage in semi-aquatic mammals. Aquat Mamm. 2002;28(2):103–12.
14. Fleming CH, Fagan WF, Mueller T, Olson KA, Leimgruber P, Calabrese JM. Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. Ecology. 2015;96(5):1182–8. https://doi.org/10.1890/14-2010.1.
15. Gallant D, Bérubé CH, Tremblay E, Vasseur L. An extensive study of the foraging ecology of beavers (Castor canadensis) in relation to habitat quality. Can J Zool. 2004;82(6):922–33. https://doi.org/10.1139/z04-067.
16. Graf PM, Hochreiter J, Hackländer K, Wilson RP, Rosell F. Short-term effects of tagging on activity and movement patterns of Eurasian beavers (Castor fiber). Eur J Wildl Res. 2016;62(6):725–36. https://doi.org/10.1007/s10344-016-1051-8.
17. Graf P, Mayer M, Zedrosser A, Hackländer K, Rosell F. Territory size and age explain movement patterns in the Eurasian beaver. Mammal Biol Zeitschrift Für Säugetierkunde. 2016. https://doi.org/10.1016/j.mambio.2016.07.046.
18. Gribb W, Harlow H. Central place foraging characteristics of beavers (Castor Canadensis) and habitat modeling in grand teton national park. UW Natl Parks Serv Res Station Anl Rep. 2013;36:18–27. https://doi.org/10.13001/uwnpsrc.2013.3975.
19. Hartman G, Axelsson A. Effect of watercourse characteristics on food-caching behaviour by European beaver. Castor fiber Anim Behav. 2004;67(4):643–6. https://doi.org/10.1016/j.anbehav.2003.07.008.
20. Justicia LS, Rosell F, Mayer M. Performance of GPS units for deployment on semiaquatic animals. PLoS ONE. 2018;13(12):e0207938. https://doi.org/10.1371/journal.pone.0207938.
21. Kays R, Crofoot MC, Jetz W, Wikelski M. Terrestrial animal tracking as an eye on life and planet. Science. 2015;348(6240):aaa2478. https://doi.org/10.1126/science.aaa24.
22. Koen EL, Tosa MI, Nielsen CK, Schauber EM. Does landscape connectivity shape local and global social network structure in white-tailed deer? PLoS ONE. 2017;12(3):e0173570. https://doi.org/10.1371/journal.pone.0173570.
23. Lodberg-Holm HK, Garvik ES, Fountain MS, Reinhardt S, Rosell F. Crop circles revealed spatio-temporal patterns of beaver foraging on cereal fields. Agric Ecosyst Environ. 2022;337:108066. https://doi.org/10.1016/j.agee.2022.10806.
24. MacArthur RA. Daily and seasonal activity patterns of the muskrat Ondatra zibethicus as revealed by radiotelemetry. Ecography. 1980;3(1):1–9. https://doi.org/10.1111/j.1600-0587.1980.tb00702.x.
25. Mayer M, Lian M, Fuchs B, Robstad CA, Evans AL, Perrin KL, Greunz EM, Laske TG, Arnemo JM, Rosell F. Retention and loss of PIT tags and surgically implanted devices in the Eurasian beaver. BMC Vet Res. 2022;18(1):219. https://doi.org/10.1186/s12917-022-03333-1.
26. McNew LB Jr, Woolf A. Dispersal and Survival of Juvenile Beavers (Castor canadensis) in Southern Illinois. Am Midl Nat. 2005;154(1):217–28. https://doi.org/10.1674/0003-0031(2005)154[0217:DASOJB]2.0.CO;2.
27. McNew L, Nielsen CK, Bloomquist C. Use of snares to live-capture beavers. Hum-Wildlife Interact. 2007. https://doi.org/10.26077/xzg1-n340.
28. McTaggart, S. Colony Composition and Demographics of Beavers in Illinois. Masters Theses. 2002. https://thekeep.eiu.edu/theses/1394
29. Mortensen RM, Reinhardt S, Hjønnevåg ME, Wilson RP, Rosell F. Aquatic habitat use in a semi-aquatic mammal: the Eurasian beaver. Anim Biotelem. 2021;9(1):35. https://doi.org/10.1186/s40317-021-00259-7.
30. Mortensen RM, Rosell F. Long-term capture and handling effects on body condition, reproduction and survival in a semi-aquatic mammal. Sci Rep. 2020. https://doi.org/10.1038/s41598-020-74933-w.
31. Niemi E, Fouty S, Trask S. Economic Benefits of Beaver-created and maintained habitat and resulting ecosystem services. 2020; 52.
32. Ossi F, Focardi S, Picco GP, Murphy A, Molteni D, Tolhurst B, Giannini N, Gaillard J-M, Cagnacci F. Understanding and geo-referencing animal contacts: proximity sensor networks integrated with GPS-based telemetry. Anim Biotelem. 2016;4(1):21. https://doi.org/10.1186/s40317-016-0111-x.
33. Patenaude F, Bovet J. Self-grooming and social grooming in the North American beaver Castor canadensis. Can J Zool. 1984;62(9):1872–8. https://doi.org/10.1139/z84-273.

34. Quaglietta L, Martins BH, de Jongh A, Mira A, Boitani L. A low-cost GPS GSM/GPRS telemetry system: performance in stationary field tests and preliminary data on wild otters (Lutra lutra). PLoS ONE. 2012;7(1):e29235. https://doi.org/10.1371/journal.pone.0029235.
35. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2021. URL https://www.R-project.org/.
36. Recio MR, Mathieu R, Denys P, Sirguey P, Seddon PJ. Lightweight GPS-tags, one giant leap for wildlife tracking? An assessment approach. PLoS ONE. 2011;6(12):e28225. https://doi.org/10.1371/journal.pone.0028225.
37. Robstad CA, Lodberg-Holm HK, Mayer M, Rosell F. The impact of bio-logging on body weight change of the Eurasian beaver. PLoS ONE. 2021;16(12):e0261453. https://doi.org/10.1371/journal.pone.0261453.
38. Rosell F, Bergan F, Parker H. Scent-marking in the Eurasian beaver (castor fiber) as a means of territory defense. J Chem Ecol. 1998;24(2):207–19. https://doi.org/10.1023/A:1022524223435.
39. Rosell F, Thomsen LR. Sexual dimorphism in territorial scent marking by adult Eurasian beavers (Castor fiber). J Chem Ecol. 2006;32(6):1301–15. https://doi.org/10.1007/s10886-006-9087-y.
40. Rothmeyer SW, McKinstry MC, Anderson SH. Tail attachment of modified ear-tag radio transmitters on beavers. Wildlife Soc Bull. 2002;30(2):425–9.
41. Serra-Medeiros S, Ortega Z, Antunes PC, Miraglia Herrera H, Oliveira-Santos LGR. Space use and activity of capybaras in an urban area. J Mammal. 2021;102(3):814–25. https://doi.org/10.1093/jmammal/gyab005.
42. Sharpe F, Rosell F. Time budgets and sex differences in the Eurasian beaver. Anim Behav. 2003;66(6):1059–67. https://doi.org/10.1006/anbe.2003.2274.
43. Silva I, Fleming CH, Noonan MJ, Alston J, Folta C, Fagan WF, Calabrese JM. Autocorrelation-informed home range estimation: a review and practical guide. Methods Ecol Evol. 2022;13(3):534–44. https://doi.org/10.1111/2041-210X.13786.
44. Smith JB, Windels SK, Wolf T, Klaver RW, Belant JL. Do transmitters affect survival and body condition of American beavers Castor canadensis? Wildlife Biol. 2016;22(3):wlb.00855. https://doi.org/10.2981/wlb.00160.
45. Steyaert SMJG, Zedrosser A, Rosell F. Socio-ecological features other than sex affect habitat selection in the socially obligate monogamous Eurasian beaver. Oecologia. 2015;179(4):1023–32. https://doi.org/10.1007/s00442-015-3388-1.
47. TWC Product and Technology LLC. Scott City, Mo Weather historystar_ratehome. Weather Underground. 2021. https://www.wunderground.com/history/daily/us/mo/scott-city/KCGI/date/2021-1-1.
48. Wang G, McClintic LF, Taylor JD. Habitat selection by American beaver at multiple spatial scales. Anim Biotelem. 2019;7(1):10. https://doi.org/10.1186/s40317-019-0172-8.
49. Wilmers CC, Nickel B, Bryce CM, Smith JA, Wheat RE, Yovovich V. The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. Ecology. 2015;96(7):1741–53. https://doi.org/10.1890/14-1401.1.
50. Windels SK, Belant JL. Performance of tail-mounted transmitters on American beavers Castor canadensis in a northern climate. Wildl Biol. 2016;22(3):124–9. https://doi.org/10.2981/wlb.00159.
51. Wittemyer G, Northrup JM, Bastille-Rousseau G. Behavioural valuation of landscapes using movement data. Philos Trans Royal Soc B Biol Sci. 2019;374(1781):20180046. https://doi.org/10.1098/rstb.2018.0046.
52. Zar JH. Biostatistical Analysis, 5th Edition. 2010. https://www.pearson.com/content/one-dot-com/one-dot-com/us/en/higher-education/program.html.
53. Zschille J, Stier N, Roth M. Gender differences in activity patterns of American mink Neovison vison in Germany. Eur J Wildl Res. 2010;56(2):187–94. https://doi.org/10.1007/s10344-009-0303-2.

Publisher's Note