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Assessment of transmitter models to monitor beaver Castor canadensis and C. fiber populations

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Dispersal and long-term monitoring of beaver *Castor canadensis* and *C. fiber* populations has been hampered by the inability to retain external transmitters on the animals and the limited range of internal transmitters. We tested several transmitter designs to develop an effective and reliable external transmitter for beavers. A modified ear-tag transmitter fitted with a plastic sleeve and attached to the tail was found efficacious in pen trials. We captured and tagged 31 beavers in Phoenix, Arizona, USA, to further test these modified ear-tag transmitters in the field. Retention of the sleeve transmitter averaged 343.5 days±44.2 (SE), more than triple the time previously reported. The addition of neoprene washers to the underside of the tail increased retention to 89%. Long-term monitoring of beaver populations may now be possible with increased retention of transmitters with the addition of neoprene washers.

Key words: Arizona, beaver, Castor canadensis, tail-mount, radio transmitter, retention

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Although habitat modification and harvest pressure, as well as other causes have restricted North American beaver Castor canadensis populations in many areas, beavers now occupy much of their former North American range (Larson & Gunson 1983, Baker & Hill 2003). As the largest rodent in North America, beavers can successfully alter existing habitats, natural and man-made, to meet their needs (e.g. see review by Rosell et al. 2005). However, in some cases, such as in Maricopa County, Arizona, USA, beaver activity can negatively impact wetland establishment (Nolte et al. 2003). In an effort to understand beaver populations in this desert environment, a system to monitor resident beaver movements as well as to determine the distances that transient beavers are travelling was necessary.

Telemetry is used to document many demographical and ecological factors on species that are otherwise unobservable. Beavers have been radiotagged to study dispersal and movement patterns (Busher 1975, Lancia et al. 1982, Van Deelen & Pletscher 1996, Hartman 1997, Herr & Rosell 2004, McNew & Woolf 2005), population densities (Breck et al. 2001), success of relocations (Nolet & Rosell 1994, McKinstry & Anderson 2002), as well as life history and behavioural traits (Breck et al. 2001, Baker 2006, Sharpe & Rosell 2003, Rosell & Thomsen 2006). A variety of transmitter models have been used, with varying success, to monitor beaver populations. Conventional neck-collar transmitters, or collars, may not be useful and may be potentially hazardous on aquatic mammal species with tapered necks and fusiform bodies (Lancia 1979, Wheatley 1997). Others have found that tail-collared transmitters remained attached for short periods of time and were usually only suited for adult beavers (Busher 1975, Wheatley 1989, Rothmeyer et al. 2002). Due to the problems associated with external transmitters, most beaver telemetry studies have used implants (e.g. Wheatley 1997, Breck et al. 2001, Sharpe & Rosell 2003, Ranheim et al. 2004, Campbell et al. 2005). Surgical implants however, are expensive (cost of implants in addition to the expenses of a veterinarian to perform the surgeries) and may pose additional risks to the animal from immune responses, anaesthesia and surgical recovery (Davis et al. 1984, Wheatley 1997, Rothmeyer et al. 2002). In addition, Rothmeyer et al. (2002) found that implantable transmitters had limited range in which signals were rarely detected > 100 m and never > 300 m away, although others

have found that reception from implants range within 300-600 m (Nolet & Rosell 1994). The decrease in the signals of internal transmitter is likely due to 1) layer of muscle and body fat which causes the signal to attenuate, 2) aquatic habitats of the beaver, and 3) inefficiencies of an internal coiled antennae. Modified ear-tag tail transmitters placed on the adipose tissue-based tail were considered the next 'phase' in beaver transmitter design. Rothmeyer et al. (2002) and Baker (2006) have found some limited success with these modified tail mounts as retention time on the tail was minimal. Several recommendations for future transmitter designs. including using a two-post attachment or a bolt and sleeve mechanism were made by Rothmeyer et al. (2002). A bolt, washer and plastic holder (for withdrawal of the bolt) system was used in a few Eurasian beavers Castor fiber, however, no information on the retention of these transmitters was noted (Sharpe & Rosell 2003, Herr & Rosell 2004, Rosell & Thomsen 2006). The overall objective of our study was to modify or develop a beaver transmitter model that is cost effective, reliable and relatively unobtrusive.

Material and methods

Pen trials

The beavers, 20 in all, were housed in individual pens $(5 \times 3.5 \text{ m})$ at the United States Department of Agriculture's National Wildlife Research Center (USDA/APHIS/WS/NWRC) Olympia Field Station, Olympia, Washington, USA. The beavers were captured and removed as nuisance beavers by Wildlife Services and were maintained in captivity for other behavioural studies and not re-released after completion of this project. Each pen contained a PVC plastic den box (53 cm diameter × 53 cm tall) with a hinged roof to allow for cleaning. The bottom of the den box was covered with heat-treated shavings for nesting material. In addition, each pen also contained an artificial pond (approximately 1,125 liters). Beavers accessed the pond through a series of steps made from logs and exited using cement blocks. We provided daily, untreated sticks of native vegetation for chewing as well as water and maintenance diet consisting of apples, dried corn, carrots and laboratory rodent diet.

Initially, four different transmitters were tested on 10 beavers: a tail design and body design per beaver. Transmitter designs included: 1) modified ear-tag

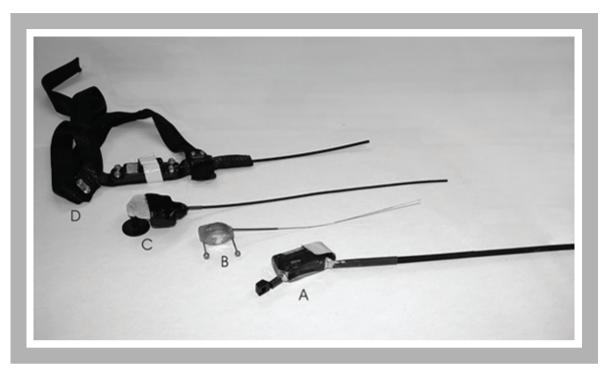


Figure 1. Beaver transmitter designs tested including from the front to the back: A) neck collar, B) double-post tail transmitter, C) eartag tail transmitter and D) backpack harness.

tail attachment, 2) neck radio-collar, 3) tail attachment with two posts, and 4) backpack harness (Fig. 1). Five beavers randomly received the modified ear-tag tail mount and five beavers the two-post tail mount. Procedures for attaching tail mounts were modified from Rothmeyer et al. (2002) and are briefly outlined here. Beavers were restrained with a squeeze chute and anaesthetized intramuscularly with a ketamine/xylazine combination (10 mg/kg and 1 mg/kg). We monitored heart rate, respiration, temperature and blood pressure until the beaver recovered from the anaesthesia, which usually took < 1 hour. Handling time for each beaver was ≥ 15 minutes. Prior to attaching tail-transmitters, tails were cleaned with iodine. Tail mount placement varied due to the necessity of a thickness of 1.3 cm for the ear-tag antiseptic button backing. An attempt was made to place the transmitter as close to the base (not more than half way down the tail) and middle of the tail as possible while avoiding the blood vessels and tail bone on the dorsal side of the tail. Mortality-sensor ear-tag transmitters (Advanced Telemetry Systems, Isanti MN, USA, (ATS) Model M3530, pulse rate 45 ppm, pulse width 20 ms, weight 35 g, battery life 370 days) and antiseptic button, used as backing plates were

loaded into an ALLFLEX (ALLFLEX USA Inc., Dallas, Texas, USA) livestock ear-tag applicator and punched through the tail after cleaning the section of the tail completely with iodine. For the two-post tail mounts (ATS Custom Model 2477, pulse rate 40 ppm, pulse width 20 ms, weight 18 g, battery life 260 days) hollow needles were inserted into the end of the stainless steel labret post and then through the tail after sedating the animal. The needles were then pulled out from the bottom of the tail, and labret round-post balls were attached to the bottom of the studs. All tail transmitters were located on the dorsal side of the tail.

In addition to the tail mounts, five beavers randomly received the backpack harness, and the other five beavers the collar transmitters. Zip ties were used to attach collar transmitters (ATS Model M1930, pulse rate 40 ppm, pulse width 20 ms, weight <30 g, battery life 383 days) to the beaver. Zip ties have been successfully used on mountain beavers *Aplodontia rufa* where neck morphology and climate prevent the use of conventional neoprene collars (Arjo et al. 2007). Backpack harness transmitters (ATS Custom Model 16M, pulse rate 60 ppm, pulse width 25 ms, weight 80 g, battery life 239 days) have been successfully used on badgers

Taxidea taxus (M. Slovada, pers. comm.) with similar fusiform body shapes as beavers. Each backpack harness was custom-fitted to the beaver. After two unsuccessful attempts at maintaining the backpack harnesses on the beaver, we redesigned the backpack using a dog harness and a zip tie for the neck portion of the harness. Durability and acceptability by the beaver of each transmitter model were monitored for one month, after which time all remaining transmitters were removed to examine wear on the beaver.

After evaluating the duration of each type of transmitter and the condition of the beaver when the transmitter was removed, the modified ear-tag design seemed the most promising design. However, large holes were often produced from the movement of the transmitter which may facilitate loss of the transmitter if left on the beaver longer than the 30day monitoring period. Adjustments were made to limit the movement of the transmitter in the tail using a nylon sleeve (5 mm in diameter), stainless steel bolt (various sizes), and washer (2.54 cm). After cleaning the surface of the tail with iodine, a 5mm hole was drilled in the tail using a cordless drill. The hole was then rinsed with iodine and filled with hydrophilic antiseptic ointment. A nylon sleeve cleaned with alcohol was inserted into the predrilled hole flush with the underside of the tail. The top of sleeve was then cut flush with the top of the tail. Bolt lengths were then chosen to protrude enough past the tail to fit the radio tag, two stainless

steel washers, and a nut. The stainless steel bolt was then inserted through a washer and then through the radio taginto the plastic tubing in the beaver's tail. A stainless steel washer (2.54 cm) followed by another smaller stainless steel washer and the locknut was then placed on the underside of the tail. We tested this new design on five different beavers for one month. Although this design limited the movement of the transmitter in the tail hole, the stainless steel washers were excessively rubbing on the underside of the tail. We modified the tail mount again (third generation ear-tag model), replacing the stainless steel washers against the underside of the tail with neoprene washers (2.54 cm) obtained from the local hardware store followed by a smaller stainless steel washer (<2.54 cm; Fig. 2) to prevent any rubbing and again tested the design on five different beavers for one month. We compared the six designs for retention time using a Kruskal-Wallis non-parametric ANOVA (SAS® Version 8.0, SAS institute Inc., Cary, North Carolina, USA). In addition, the three modified ear-tag designs were tested for difference between sizes (area) of the hole developed using a Kruskal-Wallis test (SAS® Version 8.0, SAS Institute Inc., Cary, North Carolina, USA). Capture and handling protocols were approved by Institutional and Animal Care Use Committee at the National Wildlife Research Center, Mention of companies or commercial products does not imply recommendation or endorsement by the U.S. Department of Agriculture (USDA) over others not



Figure 2. Modified ear-tag transmitter with plastic sleeve and neoprene washer design.

mentioned. The United States Department of Agriculture neither guarantees nor warrants the standard of any product mentioned. Product names are mentioned solely to report factually on available data and to provide specific information.

Field trial

Modified ear-tag transmitters with plastic sleeves were field tested at the Tres Rios project located in Maricopa County, Arizona, USA. The project area encompasses approximately 2,300 ha, within the vicinity of three river systems: the Salt River, the Gila River and the Aqua Fria River. Beaver populations and colony composition were unknown in the area, so an effort to trap the entire study area (approximately 10 km surrounding the river systems) was employed. Beavers were captured in Hancock livetraps from May 2004 through June 2006 along the main river channel of the Salt River. Traps were placed near active travel routes, scent mounds and near and on the few dams along the river system with a small amount of castor applied to a mound in the trap as an attractant. After an extensive anaesthesia study conducted under the guidance of the Wildlife Services National Veterinarian, we altered our anaesthesia procedure for the field. We determined that a combination of ketamine/medetomidine was a more predictable anaesthesia for beaver (S. DeLiberto, unpubl. data). Beavers were anaesthetized using a combination of ketamine (7 mg/kg) and medetomidine (0.1 mg/ kg) administered intramuscularly. Although others (Rothmeyer et al. 2002, Baker 2006) have used physical restraint when tagging beavers with a large field crew, during our study only one person was usually present for handling. Transmitters were attached to adult (≥16 kg; Breck et al. 2001) and subadult beavers following procedures for modified ear-tag sleeve transmitters (washers and nylon sleeve) described previously in pen trials. We used bolts ranging within approximately 2.5-5.0 cm (1-2) inches) in the transmitters based on the thickness of the tail to ensure the transmitter was no more than half way down the tail and approximately 2 cm from the tail bone. We monitored anaesthetized beaver temperatures, heart rate and respiration, every 10 minutes after lateral recumbency occurred. After transmitters were attached, the beavers were placed in recovery cages lined with a piece of carpet or a towel to insulate the beaver from the ground, and antisedan at 5 mg to 1 mg of medetomidine was administered. We continued to monitor temperature until the beaver had fully recovered. Beavers were released at the points of capture. We monitored transmittered beavers using remote dataloggers (ATS model R4500) placed along the main channel system and the project area for activity. In addition, beavers were radio-tracked using a handheld Yagi antenna ≥1 time a week to determine survivorship and transmitter fates. We attempted to recover all mortalities.

Results

Pen trials

We found a difference in retention time between the six transmitter models tested in the pens (Kruskal-Wallis = 24.55, df = 5, P = 0.0002). Retention time for the backpack harness and two-post transmitters was shorter than the other four models which all had similar retention times. Backpack transmitters, even modified with dog harnesses, were difficult to keep on the beaver. Even though we feel that each chest strap was fitted snuggly around the beaver, the slick fur and small front legs, as well as the stretching of the material, made it very easy for the beaver to get out of the chest strap, while the collar portion remained on the beaver. Retention time ranged within 2-23 days (10.8 ± 3.9 SE). Retention time of the collar transmitters was high (range: 22-30 days, 28.4 ± 1.6 SE); however, 80% of beavers developed abrasions underneath the chin from wear of the collar. The modified ear-tag (single plastic post) lasted the entire month on all the beavers; however, large holes were produced in the tail. Holes averaged 12.91 mm \pm 2.34 (SE) in length and 6.45 mm \pm 0.84 (SE) in width. In addition, these large holes did not completely close once the transmitters were removed and would have eventually allowed the transmitters to pull free from the tail. We hoped that the smaller posts used for the double tail mounts would not create large holes and would prevent transmitter loss. Double tail mounts had very low retention time (range: 1-8 days ± 1.6 SE). The size of the labret balls limited the number of threads, and hence the ability to grip the post under the constant dragging motion by the beaver. However, using the smaller holes did prevent the enlarging of the post holes and the tails healed completely after the transmitters were removed.

The modified ear-tag (single post) with the stainless steel washers and nylon sleeve remained on four of the five beavers for the duration of the

study. The plastic nylon sleeve prevented the predrilled holes from enlarging; however, the stainless steel washer cut into three of the five beavers' tails and in one case, the transmitter completely pulled through and fell off (retention $27.8 \text{ days} \pm 2.2 \text{ SE}$). The replacement of the stainless steel washers with neoprene washers, while maintaining the plastic sleeve, produced a tail mount design that remained on all the beavers for the full 30 days and resulted in very little damage to the beaver's tail. Although neoprene washers produced smaller area holes, we found no difference between area of the hole produced by the three different single post attachments for the modified ear-tag transmitter (Kruskal-Wallis = 1.82, df = 2, P = 0.40).

Field trial

We captured and tagged 31 beavers (N=24 adults and N=7 subadults) from May 2004 through

February 2006. Of the tagged beavers, nine were males and 22 were females. Attachments for the transmitters in the field were modified as information from the pens was available. Two animals died < 1 week after capture and death was attributed to capture myopathy; these animals were not included in the analyses. Three other animals died during the study but were recovered. We originally tagged beavers using the modified ear-tag transmitter with the sleeve and 1.3 cm (1/2 inch) stainless steel washers. Of the 11 beavers fitted with these transmitters, four dropped the transmitter (36%). When larger washers 2.5 cm (1 inch) were used, transmitters loss decreased to 7% (N=1 of 14). One animal with the larger washer dropped the transmitter after 326 days; however, this transmitter was lost due to a rusted bolt discovered broken in the transmitter. Overall, retention of the sleeve transmitters with stainless steel washers was 80% (N=25).

Table 1. Fate of individually identified beavers and the modified sleeve ear-tag transmitters in Phoenix, Arizona during May 2004 - June 2006. Stainless steel washers were used on beaver 1-27 (B1-11 used 1.3 cm washer and B12-27 used 2.5 cm washer). All replaced tags used the neoprene washer (2.54 cm) combination. For animals no longer detected, retention time was calculated as a conservative effort until the first of the month in which the signal was lost. Retention times for the second transmitter on animals with replaced tags are listed in the status column.

				Weight	Retention	
Animal ID	Gender	Age	Date tagged	(kg)	time (days)	Status
B1	φ	Adult	14-05-04	23	757	Tag replaced in June 2006, original tag on animal
B2	φ	Adult	03-06-04	24	607	Last detected in February 2006
B3	\$	Adult	22-06-04	21	588	Last detected in February 2006
B4	3	Subadult	23-06-04	12.5	587	Last detected in March 2006
B5	φ	Adult	01-07-04	22	48	Tag dropped on 18-08-04, not retrapped
B6	\$	Adult	08-07-04	22	36	Tag dropped on 13-06-05, not retrapped
B 7	φ	Adult	08-07-04	22	661	Last detected in May 2006
B 8	3	Adult	20-07-04	24.5	86	Tag dropped on 14-10-04, not retrapped
B9	\$	Adult	22-07-04	24	672	Tag replaced on 14-06-05, mortality 01-06-06 (296 days)
B10	\$	Subadult	24-08-04	15	359	Tag replaced on 18-08-05, last detected in April 2006 (225 days)
B11	φ	Adult	25-08-04	21	16	Tag dropped on 10-09-04, not retrapped
B14	3	Adult	21-09-04	20	627	Still active
B15	3	Adult	21-09-04	17	282	Last detected in July 2005
B16	3	Adult	22-09-04	25	554	Last detected in April 2006
B17	3	Adult	19-10-04	25	260	Tag replaced on 06-07-05 (339 days)
B18	3	Subadult	20-10-04	15	303	Tag replaced on 19-08-05 (295 days)
B19	φ	Adult	21-10-04	23	305	Tag replaced on 16-08-05 (298 days)
B20	φ	Adult	22-10-04	22	292	Mortality, tag recovered on 10-08-05
B21	\$	Adult	22-10-04	24	596	Still active
B22	φ	Adult	28-10-04	25	91	Animal not been detected since 27-01-05
B23	φ	Adult	29-10-04	24	487	Last detected in March 2006
B24	φ	Adult	29-10-04	20	289	Still active
B25	φ	Adult	08-02-05	23	326	Tag dropped in January 2006 - bolt rusted, not retrapped
B26	φ	Subadult	14-06-05	13	47	Tag dropped on 01-08-05, not retrapped
B27	φ	Subadult	14-06-05	12	361	Still active
B28	₫	Adult	13-12-05	20	59	Mortality, tag recovered 10-02-06
B29	φ	Subadult	08-02-06	11	122	Still active
B30	φ	Subadult	08-02-06	11	122	Still active
B31	φ	Adult	08-02-06	28	122	Still active

Neoprene washers were used from June 2005 through February 2006 to reduce wear of washers on the underside of the tail. Nine beavers were fitted with the transmitters with neoprene washers under the tail including five recaptures. All recaptured beavers had tails that were completely healed around the sleeve attachment and transmitters were replaced using the same sleeved hole. One transmitter with the neoprene design was fluctuating between active and mortality signal within a den. We were unable to retrieve this transmitter without disturbing the den and the fate of the animal is therefore, unknown. This mortality signal may be due to a dropped transmitter, however, and retention time of neoprene transmitters was calculated as such (89%; N=8 of 9). An additional four beavers were captured in June 2006 including the first beaver (B1) tagged in May 2004 whose transmitter ceased transmitting in October 2005. The three new beavers were tagged using the neoprene combination and the tag on B1 was removed and replaced with a new transmitter.

A total of 36 transmitters were deployed from May 2004 through June 2006 including five recaptures. Retention time varied between beavers $(\bar{x} = 343.45 \text{ days} \pm 44.24 \text{ SE})$, but usually exceeded the warranted battery life of the transmitter (Table 1). Of the 36 transmitters, seven had a retention time of < 100 days. Even after extensive searches of the area, we could not locate signals that were lost on a few transmitters (N=8). Average weight of these missing beavers was $21.3 \text{ kg} \pm 1.6 \text{ SE}$, and one beaver was classified as a subadult when captured. Dispersal out of the study area may have been the cause; however, the warranty battery life for the beaver transmitters at 40 ppm (pulses per minute) is 421 days and these transmitters have exceeded the battery life. Missing antenna were actually the biggest problem encountered with the beaver transmitters recovered in Arizona (N=8). The combination of missing antenna as well as transmitters that exceeded battery life is likely the cause for missing signals in the eight beavers.

Discussion

Several transmitter models (e.g. implants, collars and tail-mounts) have been used to monitor beaver populations; however, retention time, animal safety and signal strength are often compromised. Although collars have been successfully used on

semi-fossorial mountain beaver (Arjo et al. 2007), we have noticed little wear along the neck compared to the problems we observed with the North American beaver. Backpack harness transmitters too are more successful on badgers, even with similar body form to the beaver, than we observed in this study. We believe both problems associated with this lack of success were due largely to the aquatic habits of the beaver. Continual soaking and drying of the plastic and nylon materials associated with the two transmitters may cause expansion and contraction of the material. As the material expands on the backpack harness transmitters, the beavers were able to pull their front feet through the chest strap even though these straps were initially tightened.

Tail tagging has been used to identify individual beavers (Day 1976), but has only recently been used in association with transmitters (Rothmeyer et al. 2002, Sharpe & Rosell 2003, Herr & Rosell 2004, Baker 2006). Modified ear-tag transmitters allow for easy attachment and convenience of location as well the ability to handle animals without the complications of surgical implants (Rothmeyer et al. 2002, Baker 2006). Retention time of these modified ear-tag transmitters, however, is not high. Rothmeyer et al. (2002) documented that retention time of 44 beaver transmitters averaged only 104 days, and that low retention time was probably due to high mortality of translocated beavers (36%). Similar results of low retention time were documented by Baker (2006) who reported that 21 of 41 transmitters were confirmed to have detached (49% retention). Using the fixed-length ALLFLEX backing with the modified ear-tag transmitter resulted in attachments that were either loose in thin tails or close to the edge of the tail (Baker 2006), and average retention time for the detached transmitters was 96 days. In a few cases where previously transmittered beaver tails could be observed, transmitters likely pulled free from the tail due to enlargement of the transmitter hole (Baker 2006).

Although we did not use pre-drilled holes to attach the ALLFLEX backing on the modified eartag transmitter, we did document that the movement of the transmitter and post in itself caused the hole to enlarge and not heal on the beaver tail most likely due to large size. Using a bolt and washer combination would allow for a more flexible placement and tighter fit of the transmitters on the highly variable beaver tails, and possibly reduce the chance of tags being pulled free from the side of the tail. Herr

& Rosell (2004) have also used a similar design with the plastic sleeve to monitor Eurasian beaver movements, and a similar design manufactured by Telonics, Inc. (model ET-7; Mesa, AZ, USA) was used in an Illinois study (McNew & Woolf 2005). With the addition of the nylon sleeve and stainless steel bolt, we lost very few transmitters (76% retention) especially with the use of larger washers. We found however, that the stainless steel washers, especially the smaller ones, cut into the soft adipose tissue of the tail surrounding the bolt and in some cases, pulled free. Transmitter retention increased from previous models with the addition of a plastic sleeve and neoprene washer. The addition of these two components greatly reduced the movement of the transmitter on the tail and hence the enlargement of the transmitter hole. Average retention time was almost triple of that previously reported (343 days). We found that broken antennas, which reduce signal detection, was a problem on a few transmitters. Beavers in the pens were observed regularly sitting with their tails tucked under their bodies causing the wire antenna to bend. This constant bending eventually allowed the $1 \times 7 \times 0.062$ mm bare stainless steel wire to break off from the transmitter. Consideration must therefore be given to strengthening the antenna with thicker wire, or as Baker (2006) suggests, wire encased in a tube. We found that even with a few transmitters missing antennas the efficacy of the new sleeve mounted ear-tag transmitters was greater than any previous tail models.

Conclusions

Beavers pose a challenge to transmitting with conventional collars due to body type; however, the large, flat, adipose tissue-based tail offers another means for attaching transmitters. Modified ear-tag transmitters are easy to place on beavers and can be attached without anaesthetizing the animals (Rothmeyer et al. 2002, Baker 2006). Although the cost of each type of transmitter tested was approximately 190.00 US\$, tail-mounted transmitters were more cost effective than surgical implants where the additional cost of a licensed veterinarian to perform the surgeries is necessary. One of the main limitations of implants is the signal strength and reduced detection distance; however, little quantitative information on either aspect is available. In addition, tail-mounted transmitters can be replaced in the same hole without removing the nylon sleeve that can further reduce future handling time. We feel that the modified sleeve ear-tag transmitters have successfully demonstrated the ability to conduct long-term monitoring with telemetry on beaver populations. Research on beaver dispersal and movements has been hampered due to the inability to retain external transmitters and the reliance on implants for data. With the new tailmount transmitter design, 68% of the beavers retained transmitters for ≥ 300 days.

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