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Do transmitters affect survival and body condition of American beavers *Castor canadensis*?

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One key assumption often inferred with using radio-equipped individuals is that the transmitter has no effect on the metric of interest. To evaluate this assumption, we used a known fate model to assess the effect of transmitter type (i.e. tail-mounted or peritoneal implant) on short-term (one year) survival and a joint live–dead recovery model and results from a mark–recapture study to compare long-term (eight years) survival and body condition of ear-tagged only American beavers *Castor canadensis* to those equipped with radio transmitters in Voyageurs National Park, Minnesota, USA. Short-term (1-year) survival was not influenced by transmitter type ($w_i = 0.64$). Over the 8-year study period, annual survival was similar between transmitter-equipped beavers (tail-mounted and implant transmitters combined; 0.76; 95% CI = 0.45–0.91) versus ear-tagged only (0.78; 95% CI = 0.45–0.93). Additionally, we found no difference in weight gain ($t_9 = 0.25$, p = 0.80) or tail area ($t_{11} = 1.25$, p = 0.24) from spring to summer between the two groups. In contrast, winter weight loss ($t_{22} = -2.03$, p = 0.05) and tail area decrease ($t_{30} = -3.04$, p = 0.01) was greater for transmitter-equipped (weight = − 3.09 kg, SE = 0.55; tail area = − 33.71 cm², SE = 4.80) than ear-tagged only (weight = − 1.80 kg, SE = 0.33; tail area = − 12.38 cm², SE = 5.13) beavers. Our results generally support the continued use of transmitters on beavers for estimating demographic parameters, although we recommend additional assessments of transmitter effects under different environmental conditions.

The use of radio or satellite transmitters to locate animals has been of great importance for understanding the population ecology and life-history characteristics of wildlife species. They have enabled researchers to gain greater insight into survival (Heisey and Fuller 1985), resource selection and home range use (Benson et al. 2015), causes and timing of mortality (Smith et al. 2014), as well as other topics such as disease transmission (Cheeseman and Mallinson 1980), predation (Knopff et al. 2010), and physiology (Kreeger et al. 1990). One key assumption often inferred is that the transmitter has no effect on the metric of interest (e.g. survival; White and Garrott 1990). Despite numerous studies attempting to document or quantify the impacts (Godfrey and Bryant 2003, Barron et al. 2010, Walker et al. 2012) this assumption is often ignored in wildlife studies.

Even when following best management practices to minimize negative effects of transmitters on wildlife (e.g. transmitter should weigh < 3% of the instrumented animal, Kenward 2001), certain species may be affected in some cases. For instance, moose *Alces alces* calves equipped with ear-tag transmitters had higher mortality than moose equipped with ear-tags only (Swenson et al. 1999). Migratory caribou *Rangifer tarandus* equipped with heavier satellite collars exhibited lower survival than caribou equipped with lighter very high frequency (VHF) radiocollars (Rasiulis et al. 2014). In aquatic or semiaquatic species, increased drag from external transmitters may affect locomotion (Watson and Granger 1998), energy expenditure and weight gain (Vandenabeele et al. 2015), or reproductive performance (Pietz et al. 1993). While internally placed transmitters may reduce some of these negative effects in aquatic species, these devices can cause tissue damage or infection, and are occasionally rejected by the body (Guynn et al. 1987, Lander et al. 2005).

The effects of equipping an animal with a transmitter will likely depend on the species, individual, region, handling and attachment methods, and type of transmitter deployed. Therefore, assessing these effects is important and should be studied when feasible (White and Garrott 1990, Bank et al. 2000). This study was part of a larger study examining survival of beavers *Castor candensis* in Voyageurs National Park (VNP), Minnesota, USA. Our objectives were to 1) assess the short-term (1-year) effects of transmitter type (i.e. tail-mounted or peritoneal implant) on beaver survival and 2) assess potential long-term (1–8 years) effects on beaver survival and body condition associated with equipping them with radio transmitters.

Material and methods

Study area

Our study was conducted in Voyageurs National Park (VNP), Minnesota, USA (48°30′N, 92°50′W), an 883-km^2 protected area where hunting and trapping are prohibited. The park is typical of the Canadian Shield, with nearly 40% of the area comprised of large lakes (> 3500 ha) and 10% comprised of wetlands and smaller lakes (Kallemeyn et al. 2003). Beaver abundance in VNP ranged from 0.6 to 0.9 active lodges km^{-2} during 2006–2014 (Johnston and Windels 2015, VNP unpubl. data). Gray wolves *Canis lupus* were the most common predator of beavers in the park, and mean mid-winter density during the study period was 50 wolves 1000 km^{-2} (VNP unpubl. data). Black bears *Ursus americanus* were also common in the study area and occasionally prey on beavers (Smith et al. 1994, VNP unpubl. data). Vegetation was dominated by southern boreal forest types in the uplands and submergent and emergent vegetation types in littoral areas of lakes and wetlands (Faber-Langendoen et al. 2007). The climate was typified by cold winters and warm, humid summers; mean annual temperature was 2.4°C and mean annual precipitation was 63 cm (Kallemeyn et al. 2003).

Capturing and monitoring

As part of a long-term research project initiated in 2006, we live-trapped beavers in late fall (2006–2009, 2011–2014) and early spring (2006–2010) in two large lakes in the park (Rainy Lake and Kabetogama/Namakan Lakes). We set Hancock live traps in the water at active lodges and either baited with fresh trembling aspen *Populus tremuloides* and commercially available ground castoreum or set as unbaited blind sets. Traps were checked within 24 h. Standard trapping protocol was for each site to receive 15 attempted trap-nights. We restrained beavers in the trap to check for ear-tags and recorded the tag numbers, if present. If no tags were present, one uniquely numbered, self-piercing no. 3 monel ear-tag (National Band & Tag Company, Newport, KY) was applied to each ear (Windels 2014). We restrained each beaver in a burlap sack to record weight (± 0.1 kg), zygomatic breadth (± 0.1 mm), maximum tail length (± 0.1 cm), and tail width at midpoint (± 0.1 cm). We primarily classified beavers as male or female based on the presence of an externally palpated baculum (Osborn 1955), but we further verified sex by genetic analysis (Williams et al. 2004) or necropsy of recovered dead beavers in some cases. Beavers were released on site, with most handling events taking < 10 min. All beavers were later classified into age categories (0.5, 1.0, 1.5, 2.0, 2.5, 3.0, ≥ 3.5 year) using a discriminant function based on body measurements, dentition (when available from dead animals), and time of year when captured (spring or fall; S. Windels, VNP, unpubl.).

From Fall 2006 to Spring 2007, a subset of beavers ≥ 2.5 year received tail-mounted modified cattle-ear-tag VHF transmitters (model M3500, weight = 35 g, Advanced Telemetry Systems, Isanti, MN). Expected battery life was ~2 years at 40 ppm. The attachment protocol followed that of Arjo et al. (2008) with modifications by Windels and Belant (2016). The entire capture and attachment procedure was generally completed in 15–30 min and beavers were released immediately. Because of issues with poor retention with the tail-mounted transmitters (Windels and Belant 2016), in fall 2007 and fall 2008, a subset of beavers ≥ 2.5 year received internal VHF transmitters (model 1245B, Advanced Telemetry Systems) surgically implanted into the peritoneal cavity. Expected battery life was ~1 year at 40 ppm. Beavers were brought to a heated facility in the Hancock traps and immobilized using a mixture of ketamine (7 mg kg^{-1}) and medetomidine (0.1 mg kg^{-1}). Surgical implantation of transmitters followed Ranheim et al. (2004). Transmitters (42 g; 20 × 102 mm) weighed 0.17–0.25% of beavers (range = 16.5–25.0 kg) in our sample. We monitored beavers for temperature, heart rate and respiration before, during and after the procedure. We released beavers 8–14 h after initial capture at their original capture site, and only after they appeared recovered enough from the anesthesia to be free swimming. We monitored radio signals of radioed individuals opportunistically throughout the year by aircraft, boat, or snowmobile from 2006–2009, with 1–3 locations week^{-1} during the winter and at least monthly checks in summer.

Recaptured beavers equipped with transmitters were weighed and measured (as described above) and examined for external signs of wounds or trauma caused by the transmitter. Carcasses of beavers with implant transmitters found dead or reported by legal fur trappers were examined when possible for internal and external signs of wounds or trauma. Capture, handling and surgical procedures were approved by Institutional Animal Care and Use Committees at the National Park Service or Northern Michigan University (no. 0087), and conformed to American Society of Mammalogists guidelines for care and handling of live mammals (Sikes et al. 2011).

Data analysis

Known fate

To evaluate the influence of transmitter type on beaver survival, we used a known-fate model in program MARK (White and Burnham 1999) with the logit-link function. Records from radio-tracking surveys were converted to monthly encounter histories (White and Burnham 1999) for each year beavers were monitored. We censored individuals if we were unable to monitor them in a given month and right-censored individuals when transmitters failed to transmit or were separated from the beaver (Windels and Belant 2016). Deaths were assigned to the month when date was known or mean date between the first mortality signal and the date the last active signal was obtained. We compared three a priori models: 1) survival was constant ($S_.$), 2) survival varied as a function of transmitter type (S_{trans}), and 3) survival varied by year (S_{year}). Due to the lack of temporal overlap in deployment of the different transmitter types on beavers, we incorporated our third model (S_{year}) to rule out transmitter effects from yearly effects. We used Akaike's information criterion adjusted for small sample size (AIC_c) to select the best model and considered models differing by ≤ 2 AICc units from the selected model as potential alternatives (Burnham and Anderson 2002). We investigated model robustness by artificially inflating $\hat{c}$ (i.e. a model term representing overdispersion) from 1.0 to 3.0 (i.e. no dispersion to extreme dispersion) to simulate various levels of dispersion reflected in quasi-AIC_c ($QAIC_c$; Devrie et al. 2003, Barber-Meyer et al. 2008, Grovenburg et al. 2011).

Joint live–dead recovery

To evaluate potential long-term effects on survival of equipping beavers with transmitters, we used the Burnham joint live–dead recovery model in Program MARK (White and Burnham 1999) with a logit-link function to estimate annual survival of transmitter-equipped beavers and ear-tagged only beavers based on capture–mark–recapture (CMR) data derived from live-trapping in 2006–2014. This technique allows for estimating survival (*S*), probability of recapture conditional on being alive and in the sampling area (*p*), the probability of being found dead and reported (*r*), and the probability of fidelity to the sampling area (*F*; Burnham 1993). While harvesting of beavers is not permitted within VNP, trapping is permitted in the surrounding area. Consequently, this technique allowed us to account for known mortalities (e.g. mortality signal from transmitter or trappers reporting harvest of marked animals) and adjust capture histories accordingly. We adjusted time intervals in program MARK to correspond to the number of months between trapping intervals (White and Burnham 1999). We did not use telemetry data for CMR survival analysis, as estimates generated from telemetry versus CMR data are not comparable (Alisauskas and Lindberg 2002).

All documented mortalities were considered dead in the interval they were recovered, or the prior interval in cases where the mortality occurred before we initiated that season's trapping session. We constrained our evaluation to a core trapping area where trapping effort was spatially equivalent across all years. As our sample of transmitter-equipped beavers consisted of animals ≥ 2.5 year, we also limited our set of ear-tagged only animals to those ≥ 2.5 year and did not include captures prior to reaching that age (e.g. if an animal was captured at 1.5 year in 2006 and recaptured in 2008 at 3.5 year, the animal was considered available beginning in 2008). We considered all capture events after the first capture event for beavers ≥ 2.5 year for the period 2006–2014, i.e. we assessed annual survival out to a maximum of eight years after initial capture. The likelihood of beavers losing both ear-tags was extremely low over the study period (0.1%, Windels 2014), thus, we did not account for ear-tag loss in our survival estimates for ear-tagged only animals.

We classified beavers into two groups: 1) transmittered, consisting of animals equipped with either tail-mounted or peritoneal implant transmitters based on the assumption there was no difference in survival between the two, and 2) ear-tagged only. Our primary objective was to determine if transmitters influenced survival, consequently we constructed eight a prior models we thought biologically relevant to this process. These models consisted of varying survival (*S*), detection probabilities (*p*), and recovery probabilities (*r*) as a function of group (i.e. whether the beaver was equipped with a radio transmitter or not; Table 1). We did not vary fidelity (*F*) as a function of group as we were primarily targeting adult individuals and assumed equal probability of fidelity to the area between the two groups. We also ran one post hoc model to examine the potential influence of initial capture year (i.e. 2006, 2007 or 2008) on survival using our best approximating model from the eight a priori models.

To assess model fit, we performed a median $\hat{c}$ analysis (White and Burnham 1999) on the most parameterized model we could get to converge ($S_g\ p_g\ r_g\ F_g$). We used 500 replicates with three intermediate points between the lower (1.0) and upper (3.0) bounds (White and Burnham 1999). We accounted for potential overdispersion by adjusting AICc to QAICc and considered models with $\Delta QAIC_c \leq 2.0$ competitive (Burnham and Anderson 2002).

Condition

To assess potential effects of transmitters on beaver condition, we calculated changes in weight (kg) and tail area (cm^2) over summer and winter for transmitter-equipped and ear-tagged only animals. For summer estimates we used a subsample of animals that were captured during the same

Table 1. A priori models constructed in joint live-dead recovery models to determine the influence of equipping American beavers with a radio transmitter on survival in Voyageurs National Park, Minnesota, USA, 2006–2014.

Model[a]	*K*[b]	Description
S(.)p(.)r(.)F(.)	4	all parameters constant
S(g)p(.)r(.)F(.)	5	survival varied by group
S(.)p(g)r(.)F(.)	5	detection probabilities varied as function of group
S(g)p(g)r(.)F(.)	6	survival and detection probabilities varied as function of group
S(.)p(.)r(g)F(.)	5	recovery varied as a function of group
S(g)p(.)r(g)F(.)	6	survival and recovery varied as a function of group
S(.)p(g)r(g)F(.)	6	detection probabilities and recovery varied by group
S(g)p(g)r(g)F(.)	7	survival, detection probabilities and recovery varied by group
S(capt year) p(.) r(.) F(.)	6	survival varied as a function of capture year

[a]S = survival, p = recapture probability, r = recovery probability, F = fidelity to area, (.) = parameter was constant, (g) = parameter varied as a function of group (i.e. transmitter-equipped or ear-tagged animal), and (capture year) = survival allowed to vary as a function of initial capture year.
[b]No. of parameters.

year's spring and fall trapping sessions from 2007 to 2009, and for winter we used animals that were captured in the fall and again in spring the following year (2006–2010). We used a t-test assuming unequal variances in program R (<www.r-project.org>) to evaluate the effects of transmitters on beaver condition.

Results

Known fate

From September 2006 – October 2008 we captured and equipped 71 (males = 25, females = 46) beavers with implant (n = 28) or tail-mounted (n = 35) transmitters for inclusion in known fate analysis. Eight beavers received both transmitters types, i.e. they were equipped with implants after loss of a tail-mounted transmitter. From model results on known fate analysis, we considered model {*S*.} as the best approximating model (w_i = 0.64; Table 2). One model, {$S_{\text{trans type}}$}, was within ≤ 2.0 ΔAIC_c units, however, as deviance was essentially unchanged and beta estimates incorporated 0 (0.13, 95% CI = − 1.58–1.83), we considered transmitter type an uninformative variable (Arnold 2010) and excluded this model from consideration. Furthermore, model {*S*.} had the lowest $QAIC_c$ when $\hat{c}$ = 2.0 (moderate dispersion; w_i = 0.65) and through $\hat{c}$ = 3.0 (extreme dispersion; w_i = 0.66). Monthly survival estimate was 0.99 (95% CI = 0.97–0.99); overall probability of surviving 12 months was 0.86 (95% CI = 0.71–0.94).

Joint live–dead recovery

From September 2006 – October 2014 we captured 129 (males = 46, females = 83) beavers (≥ 2.5 year) in the core trapping area for inclusion in joint live–dead encounter modelling. We incorporated 72 (males = 27, females = 45) beavers equipped with radio transmitters (tail-mounted = 38, implants = 27, both = 7) while 57 (males = 20, females = 37) received ear-tags only. We documented 12 (ear-tag only = 5, radioed = 7) mortality events with legal harvest outside VNP accounting for 42% (n = 5) of recovered animals. Additionally, we right censored 3 individuals (ear-tag only = 1, radioed = 2) due to possible capture-related mortality. The maximum time we documented between first capture of beavers ≥ 2.5 year and last contact (i.e. by recapture or confirmed death) was 2689 days (7.4 years) for tail-transmitters, 2194 days (6 years) for implants, and 2190 days (6 years) for ear-tagged only.

Goodness-of-fit test suggested the presence of slight extra-binomial variation ($\hat{c}$ = 1.08), so we adjusted AIC_c to $QAIC_c$. Overall we had three models ≤ 2 $\Delta QAIC_c$ units from each other; our top two models indicated no difference in survival by group while the third indicated otherwise (Table 3). Given these discrepancies, we model averaged across all models and found no difference in survival between transmitter-equipped beavers (annual survival = 0.76, 95% CI = 0.45–0.91) and those with ear-tags only (annual survival = 0.78, 95%CI = 0.45–0.93). Additionally, our post hoc test indicated little support for survival varying as a function of initial capture year ($\Delta QAIC_c$ = 3.62; Table 3).

Condition

We captured 28 beavers (ear-tagged only = 20, radioed = 8) in both the spring and fall and 35 (ear-tag only = 21, transmitter-equipped = 14) animals in the fall and subsequent spring to assess seasonal changes in weight and tail area (Table 4). We found no difference in weight (t_9 = 0.254, p = 0.801) or tail area (t_{11} = 1.251, p = 0.236) change between the two groups over summer. In contrast we did find weight loss (t_{22} = − 2.033, p = 0.054) and tail area decrease (t_{31} = − 3.037, p = 0.005) were different over winter, with transmitter-equipped beavers losing more mass than their ear-tagged only counterparts (Table 4).

Discussion

We found no difference in monthly or annual survival between beavers equipped with tail-mounted or peritoneal-implanted transmitters monitored for up to one year. Both techniques have been used successfully to monitor beaver survival, demography and dispersal (Davis et al. 1984, Smith and Peterson 1991, McNew and Woolf 2005, Rosell and

Table 2. Known fate model selection results, based on Akaike's information criterion corrected for small sample sizes (AIC_c), for analyses examining American beaver survival (S) in Voyageurs National Park, MN, USA, 2006–2009 when $\hat{c}$ (model term representing overdispersion) was 1.0 (i.e. assumed no dispersion).

Model[a]	AICc	ΔAIC_c[b]	w_i[c]	K[d]	Deviance
S(.)	66.34	0	0.64	1	64.33
S(trans type)	68.34	2.00	0.24	2	64.31
S(year)	69.63	3.29	0.12	3	63.57

[a]S(.) = survival was constant, S(trans type) = survival varied as a function of transmitter type (tail or implant), and S(year) = survival varied across years.
[b]Difference in AIC_c relative to min. AIC_c.
[c]Akaike wt (Burnham and Anderson 2002).
[d]No. of parameters.

Table 3. Joint live-dead encounter model selection results, based on quasi-likelihood Akaike's information criterion corrected for small sample sizes ($QAIC_c$), for analysis examining beaver survival (S) in Voyageurs National Park, MN, USA, 2006–2014 when $\hat{c}$ (model term representing overdispersion) was 1.08.

Model[a]	QAICc	$\Delta QAIC_c$[b]	w_i[c]	K[d]	Deviance
S(.)p(.)r(.)F(.)	643.58	0.00	0.28	4	635.40
S(.)p(g)r(.)F(.)	644.11	0.53	0.21	5	633.84
S(g)p(.)r(.)F(.)	644.96	1.38	0.14	5	634.69
S(.)p(.)r(g)F(.)	645.65	2.08	0.10	5	635.39
S(g)p(g)r(.)F(.)	646.09	2.52	0.08	6	633.71
S(.)p(g)r(g)F(.)	646.21	2.63	0.07	6	633.83
S(g)p(.)r(g)F(.)	646.97	3.40	0.05	6	634.60
S(capture year)p(.)r(.)F(.)	647.19	3.62	0.05	6	634.81
S(g)p(g)r(g)F(.)	648.19	4.61	0.03	7	633.68

[a]S = survival, p = recapture probability, r = recovery probability, F = fidelity to area, (.) = parameter was constant, (g) = parameter varied as a function of group (i.e. transmitter-equipped or ear-tagged animal), and (capture year) = survival allowed to vary as a function of initial capture year.
[b]Difference in $QAIC_c$ relative to min. $QAIC_c$.
[c]$QAIC_c$ wt (Burnham and Anderson 2002).
[d]No. of parameters.

Table 4. Winter and summer change in mass and tail area for beavers *Castor canadensis* equipped with ear-tags only and radio transmitters in Voyageurs National Park, Minnesota, USA, 2006–2010.

	Winter			Summer		
Mass	n	Mean Δ (kg)	SE (kg)	n	Mean Δ (kg)	SE (kg)
Ear-tag only	21	− 1.8*	0.3	20	3.9	0.2
Transmitter[a]	14	− 3.1*	0.5	8	3.7	0.9
Tail[a]	5	− 4.8	0.5	4	4.0	1.7
Implant[a]	10	− 2.3	0.6	5	2.9	0.7
	Winter			Summer		
Tail area	n	Mean Δ (cm²)	SE (cm²)	n	Mean Δ (cm²)	SE (cm²)
Ear-tag only	21	− 12.4*	5.1	20	29.9	4.3
Transmitter[a]	13	− 33.7*	4.8	8	18.7	7.8
Tail[a]	5	− 42.8	6.1	4	4.5	1.4
Implant[a]	9	− 28.4	5.5	5	27.9	7.8

[a]Includes one animal that was equipped with both transmitter types.
*Indicates significant difference ($p \leq 0.05$).

Thomsen 2006, Bloomquist and Nielsen 2010), however, both have strengths and weaknesses. Internal transmitters require the use of anesthesia and a relatively sterile environment to perform surgeries, and require post-surgical monitoring which can limit the number of animals that can be marked in a given amount of time (Davis et al. 1984, Ranheim et al. 2004). Furthermore, this invasive procedure can be difficult to perform in remote settings or in inclement weather, exacerbating potential negative immune responses and other complications by the animal. Signal strength from VHF internal transmitters is weaker than external systems because of the coiled antenna and signal attenuation from the body. Conversely, internal transmitters provide less risk of entanglement, are not likely to become expelled from the animal, and are less likely to influence locomotion (Davis et al. 1984).

In contrast, tail-mounted transmitters are relatively easy to attach and the external antenna may increase monitoring range (Arjo et al. 2008, Baker 2006). The two biggest drawbacks of this technique that we observed in our study area were: 1) poor retention rates (7% retained > 1 year), and 2) loss of the antenna, either through breaking off or the animal chewing it off (Windels and Belant 2016). Tail-mounted transmitters are most frequently lost when transmitter attachments pull through the attachment hole or tear through the side of the tail (Windels and Belant 2016). In both cases, the tail is permanently scarred or disfigured. Based on examination of recaptured live and dead individuals from two months to two years after transmitter loss, Windels and Belant (2016) noted that wounds appeared to scar over and heal within as little as two months after loss. Nevertheless, similar natural tail wounds are common on subadult and adult beavers of both sexes, caused by intraspecific territorial battles and predators such as wolves and black bears (Müller-Schwarze and Schulte 1999). Müller-Schwarze and Schulte (1999) documented ≥ 50% of adults in their study area had ≥ 1 tail injury. Increased drag from external transmitters could interfere with an aquatic animal's ability to forage or escape predators, however, that we observed no short-term difference in survival between beavers equipped with external versus internal transmitters suggests this was not the case. Rather, our results support both methods as suitable for estimating survival rates in beaver populations. Recent studies using similar tail-mounted transmitters experienced fewer lost transmitters in more temperate systems than our study area (e.g. 4.8% lost in Bloomquist and Nielsen 2010), likely because seasonal changes in tail area are less dynamic (Windels and Belant 2016). If similarly high retention rates can be acquired, tail-mounted transmitters would be a more cost-effective and less intrusive technique for estimating demographic parameters in beaver populations. We used a topical analgesic and no anesthetic when we attached tail-mounted transmitters in 2006–2007. We recommend using additional measures to control pain and distress, such as injectable Lidocaine or anesthesia, if tail-mounted transmitters are used in future studies.

We failed to detect a difference in survival between ear-tagged only versus transmitter-equipped beavers. Other studies have suggested that tail-mounted transmitters (Arjo et al. 2008) or peritoneal implant transmitters (Guynn et al. 1987, Ranheim et al. 2004) do not negatively affect survival in American and European beavers, though none specifically tested as we did. Williams and Siniff (1983) recommended radio transmitters be placed in the intraperitoneal cavity of sea otters *Enhydra lutis* to reduce the risk of subcutaneous hemorrhaging, and speculated that this placement would likely not hinder the otter physically or behaviorally. The peritoneal transmitter in a female beaver in our study killed by a fur trapper 1.5 year after implantation was completely encapsulated by mesenteric tissue that was connected to the peritoneal wall. Although we did not compare other placements of internal transmitters (e.g. subcutaneous), that we found similar survival between transmittered and ear-tagged only animals appears to support their hypothesis. We did not differentiate between times when tail transmitters were attached to beavers and when they were not attached in our survival models. We assumed that, in addition to possible physiological stresses incurred from wearing tail-mounted transmitters, survival could be influenced as a result of trauma associated with attachment, increased risk of infection, or possible long-term tail damage even if the transmitter was removed. Our estimates of survival could be biased somewhat by low retention rates of tail-mounted transmitters in our study; however, we believe our results are valid given the other risks associated with transmitter attachment that would have been present for all beavers regardless of duration the transmitter was attached.

Beaver body condition was relatively similar between transmitter-equipped and ear-tagged only beavers, though transmitter-equipped animals lost more weight and tail area over winter than ear-tagged only animals. Although we were unable to test for differences in body condition based on transmitter type due to small sample sizes, beavers equipped with tail-mounted transmitters on average lost more mass and tail area over winter than implant-equipped animals (Table 4). Beaver tails are primarily comprised of fatty tissue, with minute blood vessels throughout that act as a heat-exchange system (Aleksiuk 1970). It is possible that damage to the tail that occurred from the attachment of the transmitter itself (i.e. creating the 6 mm hole) or when the tail was further damaged when a transmitter tore out of the tail might cause enough trauma that fat storage and mobilization were affected over-winter. Furthermore, summer weight gain more than compensated for over-winter weight loss for both groups. It is possible our estimates of body condition were influenced by relatively small sample sizes and differences could be exacerbated by yearly environmental stochasticity. Smith and Jenkins (1997) found a significant correlation in beaver weight loss and severity of winter. Sample size limitations precluded us from testing for similar effects on body condition across years based on group status. Additional research on the effects of transmitter attachment to pregnancy rates, birth rates, body size of kits or post-natal care would be useful.

Several factors should be considered when assessing the impacts of radio telemetry on animals. That we were unable to detect differences in many of the metrics we analyzed should not be misconstrued as proving transmitters have no effect on beaver population-level metrics. As noted by Godfrey and Bryant (2003), "acceptance of a null hypothesis does not equate to a demonstration that the converse hypothesis is false". Despite finding no differences in survival based on transmitter attachment or type, or changes in body condition during summer, we did observe some overarching trends between these two groups. Beavers equipped with transmitters had, on average, greater weight loss and tail area decrease over winter than their non-transmittered counterparts. Additionally, our results were restricted to beaver ≥ 2.5 year and there could be other consequences of equipping transmitters to younger age classes. Nevertheless, our results tend to support the continued use of transmitters on beavers for estimating demographic parameters, although we encourage other researchers to assess the potential impacts this may incur, and, when possible, consider evaluating similar effects under different environmental conditions and on different age classes.

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References

Aleksiuk, M. 1970. The function of the tail as a fat storage depot in the beaver (*Castor canadensis*). – J. Mammal. 51: 145–148.

Alisauskas, R. T. and Lindberg, M.S. 2002. Effects of neckbands on survival and fidelity of white-fronted and Canada geese captured as nonbreeding adults. – J. Appl. Stat. 29: 521–537.

Arjo, W. M. et al. 2008. Assessment of transmitter models to monitor beaver *Castor canadensis* and *Castor fiber* populations. – Wildl. Biol. 14: 309–317.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. – J. Wildl. Manage. 74: 1175–1178.

Baker, B. W. 2006. Efficacy of tail-mounted transmitters for beaver. – Wildl. Soc. Bull. 34: 218–222.

Bank, M. S. et al. 2000. Assessing the effect of radiocollars on juvenile guanaco survival. – Oecologia 124: 232–234.

Barber-Meyer, S. M. et al. 2008. Elk calf survival and mortality following wolf restoration to Yellowstone National Park. – Wildl. Monogr. 169: 1–30.

Barron, D. G. et al. 2010. Meta-analysis of transmitter effects on avian behavior and ecology. – Meth. Ecol. Evol. 1: 180–187.

Benson, J. F. et al. 2015. Resource selection by wolves at dens and rendezvous sites in Algonquin Park, Canada. – Biol. Conserv. 182: 223–232.

Bloomquist, C. K. and Nielsen, C. K. 2010. Demography of unexploited beavers in southern Illinois. – J. Wildl. Manage. 74: 228–235.

Burnham, K. P. 1993. A theory for combined analysis of ring recovery and recapture data. – In: Lebreton, J. D. and North. P. M. (eds), Marked individuals in the study of bird population. Birkhauser-Verlag, pp. 199–213.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. – Springer.

Cheeseman, C. L. and Mallinson, P. J. 1980. Radio tracking in the study of bovine tuberculosis in badgers. – In: Amlaner, C. J. Jr. and MacDonald, D. W. (eds), A handbook on biotelemetry and radio tracking. Pergamon Press, pp. 649–656.

Davis, J. R. et al. 1984. Implantable telemetry in beaver. – Wildl. Soc. Bull. 12: 322–324.

Devrie, J. H. et al. 2003. Breeding-season survival of mallard females in the prairie pothole region of Canada. – J. Wildl. Manage. 67: 551–563.

Faber-Langendoen, D. N. et al. 2007. Vegetation classification, mapping and monitoring at Voyageurs National Park, Minnesota: an application of the U.S. National Vegetation Classification. – Appl. Veg. Sci. 10: 361–374.

Godfrey, J. D. and Bryant, D. M. 2003. Effects of radio transmitters: review of recent radio-tracking studies. – In: Williams, M. (ed.), Conservation applications of measuring energy expenditure of New Zealand birds: assessing habitat quality and costs of carrying radio transmitters. Science for Conservation, pp. 83–95.

Grovenburg, T. W. et al. 2011. Survival of white-tailed deer neonates in Minnesota and South Dakota. – J. Wildl. Manage. 75: 213–220.

Guynn, D. C., Jr. et al. 1987. Pathological potential of intraperitoneal transmitter implants in beavers. – J. Wildl. Manage. 51: 605–606.

Heisey, D. M. and Fuller, T. K. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. – J. Wildl. Manage. 49: 668–674.

Johnston, C. A. and Windels, S. K. 2015. Using beaver works to estimate colony activity in boreal landscapes. – J. Wildl. Manage. 79: 1072–1080.

Kallemeyn, L. W. et al. 2003. Aquatic synthesis for Voyageurs National Park. – USGS/BRD/ITR-2003-0001.

Kenward, R. E. 2001. A manual for wildlife radio tagging. – Academic Press.

Knopff, K. H. et al. 2010. Cougar kill rate and prey composition in a multiprey system. – J. Wildl. Manage. 74: 1435–1447.

Kreeger, T. J. et al. 1990. Physiological monitoring of gray wolves (*Canis lupus*) by radio telemetry. – J. Mammal. 71: 259–261.

Lander, M. E. et al. 2005. Implantation of subcutaneous radio transmitters in harbor seal (*Phoca vitulina*). – Mar. Mamm. Sci. 21: 154–161.

McNew, L. B. and Woolf, A. 2005. Dispersal and survival of juvenile beavers (*Castor canadensis*) in southern Illinois. – Am. Midl. Nat. 154: 217–228.

Müller-Schwarze, D. and Schulte, B. A. 1999. Behavioral and ecological characteristics of a "climax" population of beaver (*Castor canadensis*). – In: Busher, P. E. and Dzięciołowksi, R. M. (eds), Beaver protection, management, and utilization in Europe and North America. Springer, pp. 161–177.

Osborn, D. J. 1955. Techniques of sexing beaver, *Castor canadensis*. – J. Mammal. 36: 141–142.

Pietz, P. J. et al. 1993. Effects of harness transmitters on behavior and reproduction of wild mallards. – J. Wildl. Manage. 57: 696–703.

Ranheim, B. et al. 2004. Field anaesthetic and surgical techniques for implantation of intraperitoneal radio transmitters in Eurasian beavers *Castor fiber*. – Wildl. Biol. 10: 11–15.

Rasiulis, A. L. et al. 2014. The effect of radio-collar weight on survival of migratory caribou. – J. Wildl. Manage. 78: 953–956.

Rosell, F. and Thomsen, L. R. 2006. Sexual dimorphism in territorial scent marking by adult Eurasian beavers (*Castor fiber*). – J. Chem. Ecol. 32: 1301–1315.

Sikes R. S. et al. 2011. Guidelines of the American Society of Mammalogists for the use of wild animals in research. – J. Mammal. 92: 235–253.

Smith, D. W. and Jenkins, S. H. 1997. Seasonal change in body mass and size of tail of northern beavers. – J. Mammal. 78: 869–876.

Smith, D. W. and Peterson, R. O. 1991. Behavior of beaver in lakes with varying water levels in northern Minnesota. – Environ. Manage. 15: 395–401.

Smith, D. W. et al. 1994. Black bear predation on beavers on an island in Lake Superior. – Am. Midl. Nat. 132: 248–255.

Smith, J. B. et al. 2014. Disease and predation: sorting out causes of a bighorn sheep (*Ovis canadensis*) decline. – PLoS ONE 9: e88271.

Swenson, J. E. et al. 1999. Effects of ear-tagging with radiotransmitters on survival of moose calves. – J. Wildl. Manage. 63: 354–358.

Vandenabeele, S. P. et al. 2015. Are bio-telemetric devices a drag? Effects of external tags on the diving behavior of great cormorants. – Mar. Ecol. 519: 239–249.

Walker, K. A. et al. 2012. A review of the effects of different marking and tagging techniques on marine mammals. – Wildl. Res. 39: 15–30.

Watson, K. P. and Granger, R. A. 1998. Hydrodynamic effects of a satellite transmitter on a juvenile green turtle (*Chelonia mydas*). – J. Exp. Biol. 201: 2497–2505.

White, G. C. and Burnham, K. P. 1999. Program MARK: survival estimation from populations of marked animals. – Bird Study 46: 120–139.

White, G. C. and Garrott, R. A. 1990. Analysis of wildlife radio-tracking data. – Academic Press.

Williams, C. L. et al. 2004. Genetic methods improve accuracy of gender determination in beavers. – J. Mammal. 85: 1145–1148.

Williams, T. and Siniff, D. 1983. Surgical implantation of radiotelemetry devices in the sea otter. – J. Am. Vet. Med. Ass. 183: 1290–1291.

Windels, S. K. 2014. Ear-tag loss rates in American beavers. – Wildl. Soc. Bull. 38: 122–126.

Windels, S. K. and Belant, J. L. 2016. Performance of tail-mounted transmitters on American beavers *Castor canadensis* in a northern climate. – Wildl. Biol. 22: 124–129.