AGE-MASS RELATIONSHIPS FOR BEAVERS IN MONTANA

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Abstract

Beavers (*Castor* spp.) are receiving increased attention due to their impact on ecosystems and potential for use in stream restoration. Beaver research and relocation projects are especially common in the western United States, and professionals using live-captured animals for projects will benefit from a reliable technique for aging live-caught beavers. The only reliable technique for aging live beavers without sedation is to estimate age based on mass, but estimates of the age-mass relationship for beavers vary regionally and are not adequately quantified in the western United States. We collected beaver carcasses and skulls from trappers throughout southwest Montana to estimate the age-mass relationship using a robust sample collected from a large geographic area. We weighed beaver carcasses and extracted molar teeth from the mandibles to estimate age by counting cementum annuli on cross-sections of the teeth. We collected 193 beaver carcasses and hanging weights from nine major river drainages in Montana. Multiple regression analysis indicated the top prediction equation was mass = $9.4611 + 8.2234 \times \log(age)$ + drainage, indicating drainage-level differences in the average mass of beavers. Beavers from the Ruby, Jefferson, and Yellowstone River drainages were larger than those from the other river drainages in Montana. We could reliably separate beavers into four age classes: kits, yearlings, two-year-olds, and adults (>3 years). Our results are useful for researchers who need to estimate beaver age to understand population dynamics and age-specific life history characteristics, as well as restoration practitioners who need to determine colony compositions and recruitment rates to evaluate the success of restoration projects.

Key words: age-weight curve, beavers, Castor canadensis, Montana

INTRODUCTION

Humans and wildlife depend on riparian areas and wetlands to enhance landscape-scale water storage capacity and bolster the resilience and connectivity of ecosystems. An extensive body of scientific literature recognizes the habitat-modifying activities of beavers (Castor canadensis) as instrumental in the creation, expansion, and maintenance of healthy and productive riparian and wetland areas (Naiman et al. 1988, Collen and Gibson 2001, Wright et al. 2002). As a result, beavers are increasingly used as a tool for habitat restoration, especially in the western United States where water resources are strained by increasing demand and ongoing drought (Baker 2003, Barnett et al. 2008, Hidalgo et al. 2009, Pollock et al. 2017). Projects aimed at recovering beaver populations in areas of their historic range are increasing in popularity and scope, and research directed towards understanding beaver population dynamics, habitat selection, and influence on ecosystems will be important in the future management of this species.

Beavers are territorial mammals that live in well-defended colonies generally composed of a mating pair of adults, kits, and yearlings (Muller-Schwarze 2011). In large colonies located in good habitat, sub-adult beavers between two and four years of age may also be present (McTaggart and Nelson 2003, Muller-Schwarze 2011). The presence of extra adults in the colony means researchers and restoration practitioners relying on live-captured beavers for their work will be capturing a wide range of beaver age classes in a given colony. Researchers may want to estimate the age of captured beavers to evaluate colony size and composition and to study age-specific processes such as dispersal

and breeding. Restoration practitioners looking to translocate beavers may wish to selectively remove beavers from a source colony without disrupting the breeding pair or translocating vulnerable kits. Additionally, restoration practitioners may want to monitor colonies established as part of a restoration effort to evaluate age composition of the colony and recruitment rates.

There are few reliable techniques for aging live beavers, and most require sedation or heavy restraint in order to safely gather measurements (Patric and Webb 1960, Layne 2003). Aging beavers via inspection of cementum annuli on crosssections of teeth is the preferred method to age beavers, but is not possible with live animals (Van Nostrand and Stephenson 1964, Novak 1987). Many authors have proposed using the body mass of captured beavers to differentiate age classes (Bradt 1939, Hammond 1943, Patric and Webb 1960, Payne 1979, Van Deelen 1991, McTaggart 2002, Layne 2003). However, regional variation in growth rates driven by differing food resources and climatic conditions can cause the relationship between the age of beavers and body mass to vary widely across study areas (Table 1).

Calibration of the age-mass relationship for beavers has been especially lacking in the western United States, where the few studies conducted relied on small samples of beavers from one or two drainages (Townsend 1953, Van Deelen 1991). Accurate estimation of the agemass relationship for beavers will improve current and future research projects in southwest Montana and similar habitats within the Greater Yellowstone Ecosystem (GYE). Additionally, beaver reintroduction programs, which are most common in the western United States, will benefit from a reliable technique for aging live-captured beavers to determine colony composition and select appropriate individuals for release at restoration sites.

To address the shortcomings in fieldbased age estimation for beavers, we initiated a study to estimate the age-mass relationship for beavers in southwest Montana. Specifically, our objectives were to: 1) provide a region-specific calibration of the age-mass relationship for beavers inhabiting willow- and cottonwood-dominated streams and rivers, and 2) evaluate drainage-level variation in age-mass relationships for beavers in southwestern Montana. Our goal was to provide researchers and managers with an accurate and efficient tool for estimating the age of live-captured beavers in the field.

METHODS

We collected beaver carcasses or skulls from recreational trappers throughout southwest Montana during Fall 2015–Spring

Authors	Location	Kits (0-1 yr)	Yearlings (1-2 yr)	Two-year-olds (2-3 yr)	Adults (> 3 yr)
Ritter and McNew, this study	Southwest Montana	< 7.8	7.8–14.3	14.3–17.8	> 17.8
Hammond (1943)	North Dakota	—	4.1–11.3	11.8–20.8	15.9–27.2
Townsend (1953)	Montana	3.6-5.4	9.1–11.8	> 13.6	—
Beer (1955)	Minnesota	< 4.5	5.4-11.8	> 13.6	> 13.6
Patric and Webb (1960)	New York	< 6.8	6.8-10.8	10.9-16.0	> 16
Brooks et al. (1980)	Massachusetts	< 6	6-11	11-15	> 15
Van Deelen (1991)	Western Montana	< 6.5	6.5-10.5	10.5-14.5	> 14.5
McTaggart (2002)	Central Illinois	3.2-11.4	10-19.1	15-23.6	> 15.5

Table 1. Estimated age-mass (kg) relationships for beavers from various projects in North America, 1943–2018.

2017. To make age-mass calibrations regional, we limited the sample to within 500 km of Montana State University (Bozeman, MT). We contacted trappers with the assistance of biologists with the Montana Department of Fish, Wildlife and Parks (MFWP), local game damage specialists, the Montana Trapper's Association newsletter and e- mail list, and e-mail lists for conservation and outdoor recreation groups in the area. We asked trappers to submit whole beaver carcasses, skulls, or mandibles and record the mass of each beaver they caught with the pelt on. Many trappers also provided the sex of each beaver. We obtained the general location of harvested beavers and grouped them by major river drainage (Fig. 1).

We processed all samples at the MFWP Wildlife Disease Lab in Bozeman, MT. We separated the lower mandible from

the skull of each beaver and extracted a molar tooth for use in age determination by cementum annuli. To extract the teeth, we soaked mandibles in water kept just below boiling for approximately three minutes. We then wrapped the mandibles in cloth and struck them with a hammer, targeting the thickest part of the mandible where the ridges coming off the condylar process and angular process meet. We then extracted teeth from the broken mandible parts. We soaked teeth in a 70% ethanol solution and then in Nolvasan Solution (Zoetis. Inc.; 0.8% concentration) for 30 seconds before drying the teeth on a paper towel and depositing them in uniquely marked coin envelopes. We submitted teeth to Matson's Laboratory (Manhattan, MT USA) for aging via inspection of cementum annuli. The lab returned a best estimate of age in years for each beaver tooth sample assuming a common birth date of 1 June each year.



Figure 1. Major river drainages in southwest Montana, USA, where we obtained carcasses and skulls from trappers during 2015–2017 to estimate the age-mass relationship for beavers. The number of beavers submitted from each drainage are denoted in parentheses. No beavers were captured from within Yellowstone National Park (YNP).

We used multiple linear regression to evaluate the relationship between age determined from cementum annuli and hanging mass of carcasses. We constructed and analyzed models using R Statistical Computing Software (R Version 3.3.2, www.r-project.org, accessed 11 Feb 2018). The residuals of the independent variable for age were not normally distributed so we log- transformed the variable and examined residual plots to determine if the assumption of homoscedasticity was reasonably met with transformation. We fit and evaluated four linear models using mass as the response and tested a main effect of age in years, an additive effect of drainage, an interaction between age and drainage, and an intercept-only null model. We ranked models using Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002). We considered all models $\leq 2 \text{ AIC}_{c}$ from the top model to be parsimonious. Goodness of fit was evaluated for each competing model using adjusted R-squared. We used the coefficients from the top model to predict the age of beavers based on the entire range of beaver masses observed in the study area, and examined the means, standard deviations, and ranges of beaver masses representing each year of age to evaluate support for separation of ages based on the predictions from the top-ranked model. We used a Student's t-test to evaluate differences in mean mass between subsequent ages.

RESULTS

We obtained teeth and hanging weights from 174 beavers collected by 13 different trappers in southwest Montana during Fall 2015–Spring 2017. Beavers were taken from nine major river drainages (Figure 1). Not all trappers reported locations of trapped beavers to individual stream, but the sample of beavers were harvested from a minimum of 27 different streams. Due to low pelt prices, few trappers were targeting beavers over the two years of the study. Although we directly contacted > 25 trappers, the majority of the samples came from eight individuals. We acquired an additional 19 beavers opportunistically during beaver activity surveys and live-capture trapping efforts for a related study on settlement site habitat selection (Ritter 2018), bringing the total sample size to 193 beavers. Trappers recorded sex for 101 beavers (45 males, 56 females); masses were similar between the sexes (males = 16.6 ± 0.83 SE kg, females = 16.2 ± 0.83 kg) so we did not include sex as a covariate in age-mass models.

An initial screening of the mass distributions by age-class suggested an asymptotic relationship between age and mass, with beavers experiencing rapid growth early in life and slower growth as they age (Fig. 2). Beavers typically ranged from 1–8 years old and weighed 2.3–31.3 kg, although one captured beaver was estimated via cementum annuli to be 11 years old. The distribution of ages was strongly skewed towards younger beavers between one and three years of age. Twoyear-old beavers were the most common age making up 34% of the sample (Table 2).

The top prediction equation using data pooled over all drainages was mass = $9.5911 + 7.9375 \times \log(age)$ (adjusted R² = 0.63, SE = 3.74, N = 193). There was little model uncertainty among the candidate set of models (Table 3). The top-ranked model contained an additive effect of river drainage and accounted for 69% of the candidate set support. The 2nd-ranked model was not considered parsimonious but accounted for 31% of the model support and contained an interaction effect between drainage and age. Confidence intervals on the coefficient estimates for the top model indicated drainage-level differences in the mass of beavers across all ages (Table 4). Beavers in the Yellowstone, Ruby, and Jefferson River drainages were larger overall than those in other drainages (Fig. 3). Beavers from the Big Hole, Boulder, Sun, Madison, and Gallatin River drainages were all similar in size.

Although beaver masses varied within age-classes, we were able to reliably separate one- and two-year-old beavers by mass, with reduced confidence in the separation of two- and three- year-old



Figure 2. Relationship between age and mass for 193 beaver carcasses obtained during fall 2015–spring 2017 in southwest Montana, USA. Ages were determined through inspection of cementum annuli on molars extracted from the lower mandibles.

Age (years)	Number of samples	Mean mass (95% CI)	Range	P ^a
1	46	8.4 (7.5–9.3)	2.3–18.6	_
2	66	15.9 (15.0–16.9)	6.6-24.0	< 0.001
3	33	18.9 (17.6-20.1)	9.8-24.6	< 0.001
4	18	21.8 (20.1-23.6)	16.1-29.5	0.0092
5	11	23.7 (21.0-26.4)	16.8-31.3	0.26
6	6	22.4 (20.9-23.9)	20.0-25.4	0.41
7	10	21.8 (19.5-24.1)	16.8-26.7	0.68
8	2	_	20.9 and 22.2	_
9	0	_	_	_
10	0	_	_	_
11	1	_	22.2	

Table 2. Distribution of ages and masses (kg) from 193 beaver carcasses collected throughout southwest Montana, USA, during fall 2015–spring 2017.

^a *P*-value result of Welch's t-test comparing mean beaver mass between each age-class and the mean mass of the previous age-class.

beavers as well as three- and four-year-old beavers (Table 2). Identification of beaver ages beyond four years was not possible using mass. The model with just the effect of mass had an adjusted R^2 value of 0.63 and was used to offer overall recommended mass ranges for beavers in southwest Montana (Table 1). However, this model was poorly

Table 3. Model selection results testing the influence of age (years) on mass for beavers in southwest Montana, USA, 2015–2017.

Model	K	AIC _c	ΔAIC_{c}	W _i	Cum w _i
age + drainage	10	1033.10	0.00	0.69	0.69
age × drainage	17	1034.68	1.57	0.31	1.00
age	3	1051.24	18.14	0.00	1.00
~ 1 (null model)	2	1237.79	204.69	0.00	1.00

Table 4. Recommended mass ranges (kg) for beavers in eight major river drainages in southwest Montana, USA.

Drainage	Kits	Yearlings	Two-year-olds	Adults
Madison	< 5	5-11.5	11.5-15.5	> 15.5
Sun	< 5.5	5.5-12	12-16	> 16
Boulder	< 6.5	6.5-13	13-16.5	> 16.5
Gallatin	< 6.5	6.5-13.5	13.5-17	> 17
Big Hole	< 7.5	7.5-14.5	14.5-18	> 18
Ruby	< 9	9-15.5	15.5-19	> 19
Jefferson	< 9	9-16	16-19.5	> 19.5
Yellowstone	< 9.5	9.5-16.5	16.5-20	> 20



Figure 3. Estimated growth curves for beavers (n = 193) from eight major river drainage in southwest Montana, USA, 2015–2017.

supported in the candidate set, and the retention of drainage as a variable in the top model suggests mass ranges specific to individual river drainages are more accurate (adjusted $R^2 = 0.67$; Table 4).

DISCUSSION

As expected, our results suggest beavers grow rapidly in the first 1-3 years of life then growth rates slow beyond three years of age. We could not reliably separate kits from one-year- old beavers using mass, but other authors have recommended kits vary from 3.2–11.4 kg (Table 1). Our top model predicted beavers less than one year old are generally less than 5 kg, which is within the range of other studies. The reliability of our estimates of mass ranges decreased as beavers got older (Table 2). While separation of one- and two-year-old beavers was highly reliable, separation of two- and three-year-old beavers as well as three- and four-year-old beavers was only moderately reliable. Our results are consistent with other studies that have found age determination difficult for live-captured beavers beyond three years of age (Layne 2003).

The age distribution of our sample was skewed towards younger animals, and it is unclear if this represents an accurate age distribution for southwest Montana beavers overall. The age distribution of beavers gathered from trappers may not represent actual age distributions in a given area. Larson (1967) suggested beavers harvested by trappers may be skewed toward larger animals as trappers target beavers with more valuable furs. However, Novak (1977) found no bias in age distribution from trapper harvests in Ontario, Canada. McTaggart (2002) observed a similar age distribution as ours in Illinois where beavers were trapped with a more systematic protocol. Larson (1967) also noted a similar age distribution in Maryland from trapper-submitted beaver carcasses, but noted a drop in the number of two-year-old beavers which he attributed to those beavers being missed by trappers due to dispersal. Unlike Larson's study, we found two- year-old beavers were the most common age submitted by trappers. Due

to low market prices for beaver furs during our study, a majority of the beavers in our sample were trapped due to property damage complaints. Stream sections where beavers must be trapped due to property damage are commonly recurring issues where it is likely young, naïve beavers are repeatedly moving into the sites that appear to be open habitat. It is therefore possible our sample was biased towards younger animals which are more likely to have recently dispersed and settled in areas where they are not tolerated by humans.

Beavers in the Yellowstone, Ruby, and Jefferson River drainages were larger than in other drainages. It is unclear why there were dissimilarities, but there are notable differences in environmental conditions among drainages. A large proportion of the beavers in the Yellowstone, Ruby, and Jefferson River drainages came from colonies in or near spring creeks. Beavers in spring creeks may take advantage of stable water temperatures that enhance plant growth and limit ice cover which allows access to quality forage for a longer portion of the year compared to other drainages. Year-round access to forage may allow beavers in the Yellowstone, Ruby, and Jefferson River drainages to maintain or put on weight in the winter, while beavers in other drainages may maintain or lose weight due to being ice-bound during the winter.

We compared our overall growth curve to those of Payne (1979) and Van Deelen (1991) and found beavers grew at a faster rate in our study area (Fig. 4). Payne (1979) examined beavers in Newfoundland but did not report on the food source or winter conditions associated with beaver habitat in his study area, making comparisons difficult. Van Deelen (1991) collected beavers in western Montana and incorporated data from Jackson (1990) in the same study area. Beavers in his study area live under similar climatic and habitat conditions to our study, with mountain streams flowing through willow-dominated riparian areas. Unlike Van Deelen (1991) a large portion of our sample came from spring creeks which may explain why our data resulted in faster estimated



Figure 4. Estimates of the age-mass relationship for beavers from three studies in North America.

growth rates.

This study provides regionally calibrated growth curves allowing for estimation of the age of beavers by mass. Researchers, trappers, wildlife managers, and stream restoration practitioners can use the results of this project to more reliably age live-captured beavers. While our growth estimates were calculated from a relatively large sample size, there is still wide variation in beaver mass across ages which is likely due to differences in habitat conditions among individual colonies in a given drainage that allows members of some colonies to grow faster than others. We recommend future researchers acquire colony-specific locations for beavers if trappers are willing to provide such information. Colony membership information would allow for statistical analyses that account for within versus cross-colony variation. The accuracy of age estimation may be increased if researchers gather other morphological measurements on captured beavers such as zygomatic breadth and tail dimensions (Patric and Webb 1960, Larson and Van Norstrand 1968, Layne 2003).

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