



Research Article

# Quantifying Telemetry Collar Bias When Age Is Unknown: A Simulation Study With a Long-Lived Ungulate

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**ABSTRACT** Radiotelemetry collars are frequently used to estimate demographic parameters of animals, such as annual survival and parturition rates. If animals are collared for multiple years and statistical adjustments are not made, these estimates can be biased by an unrepresentative age structure and individual variability of collared animals. To quantify the effects of different factors on the magnitude of these potential biases, we created a computer simulation of the female portion of a barren-ground caribou (*Rangifer tarandus granti*) herd and then randomly assigned collars to individuals within the simulated population. Under our default model, based on the Western Arctic Herd monitoring program, caribou were collared randomly from all females aged 2 years and over, and they remained collared for a mean of 7 years. Our simulations revealed that survival rates were underestimated by approximately 3.4% and parturition rates were overestimated by approximately 3.3%. The magnitude of these biases increased when individuals remained collared for longer periods. Increased individual variability in the population resulted in only small increases in survival and parturition rates. Because the magnitude of the bias increased steadily during the first years of the study, we found a substantial risk of incorrectly identifying a significant decline in survival in the first 7 years after marking. Including the number of years individual animals have been collared as a covariate in analyses can reduce the biases in demographic parameters and should be considered for inclusion in analyses when animal age is unknown. Actual survival rate estimates from telemetry data for the Western Arctic Herd were generally consistent with the results of these simulations. These potential biases should be considered when interpreting demographic parameters from multi-year collaring studies. © 2012 The Wildlife Society.

**KEY WORDS** Age structure, Alaska, caribou, parturition rate, *Rangifer tarandus*, statistical bias, survival rate, telemetry.

Radiotelemetry collars revolutionized wildlife biology and analysis of data from these collars is currently the primary method for estimating many demographic parameters in wild ungulate populations (White and Garrott 1990, Murray 2006). Estimates of demographic parameters can be biased because of issues such as negative effects of collar weight (Brooks et al. 2008, Venturato et al. 2009), unknown fates (Heisey and Fuller 1985), individual variability (Zens and Peart 2003, Murray 2006), and unrepresentative samples (Murray 2006). Although statistical techniques exist to deal with these potential sources of bias, difficult-to-obtain information is often required to correct these estimates.

Many large mammals display a distinct pattern in survival and reproduction; low survival and reproduction is typical of subadults, high and relatively constant survival rates and peak reproductive potential typify prime-aged animals, and de-

creasing survival and senescence occur in older age classes (Siler 1979, Eberhardt 1985, Adams and Dale 1998, Weladji et al. 2010). Therefore, the age structure of a sample may have a large influence on estimated demographic rates. Many telemetry studies collar a random sample of animals within the population, and in each successive year that collared sample becomes older than the general population. This increasingly unrepresentative age structure of the collared sample is responsible for 1 potential source of bias (age structure bias) that is present in various degrees in most studies that maintain telemetry collars on the same animals for multiple years. The problem of age structure bias has long been recognized (Eberhardt 1985, Tsai et al. 1999), and various statistical procedures are available to estimate accurate demographic parameters when the ages of animals are known (Murray 2006). In many telemetry studies, the age of study animals is unknown, and data from all adult animals are pooled to estimate demographic parameters.

In addition, a great deal of variation may exist among individual animals in behavior and performance (e.g.,

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body mass, body fat, body size, parasite loads, range use), even within a cohort. These individual characteristics will be reflected in variable probability of survival and productivity among individuals. Poor quality individuals may die early in a study, leaving a collared sample that over-represents high quality individuals (individual variability bias). This could, over time, bias estimates of demographic parameters (Zens and Peart 2003).

The magnitude of age-structure and individual variability biases would presumably change because of many factors, including the age-specific survival or fertility curves of the population, the length of time the collars are deployed, the amount of individual variability in the population, and annual changes in demographic parameters (i.e., process variation) of the population.

The objectives of our analyses were to 1) determine the magnitude of biases in survival and parturition rate estimates from unknown age animals and how these biases change with the number of years individual animals remain collared, 2) determine how these estimates change with varying levels of individual variability, 3) assess the potential for detecting false trends in demographic parameters when age-structure bias is not accounted for, and 4) determine whether including the length of time individuals have been collared as a covariate in analyses can correct for the effects of age structure bias.

# STUDY AREA

We loosely based our analysis on the collaring plan for the Western Arctic Herd (WAH), a barren-ground caribou (*Rangifer tarandus granti*) herd numbering roughly 350,000 and inhabiting northwestern Alaska (J. Dau, Alaska Department of Fish and Game, unpublished data; Dau 2009). The herd ranged over 360,000 km<sup>2</sup> and used extensive areas of tundra, boreal forest, rugged mountains, and the Arctic coastal plain among other ecosystems. For a detailed description of the herd's range, see Dau (2009) or Joly (2011).

# METHODS

We used a simulation model to explore potential biases, determine their importance, and explore various factors that influence their magnitude. Alaskan caribou typically start producing offspring at 3 years of age and can live 15 years or more. Management of the WAH is fairly typical of many other caribou herds and other ungulate populations in Alaska, although its remote range imposes some additional logistical constraints on management. A long history of telemetry-based research on the WAH (Dau 2009) is available to compare to the results of our computer simulations.

For our default simulation, we modeled the herd undergoing modest growth ( $\lambda = 1.02$  for the female portion of the herd), with mean survival and parturition rates based on estimates for the WAH (Dau 2009). We created a simple stochastic age-classified time-step model with Microsoft Excel 2007 (Microsoft Corporation, Redmond, WA) in which the population of each cohort declines each year based on an age-specific mortality rate and the number of offspring produced by a cohort is determined by the spring population

and an age-specific parturition rate. For the purpose of our analyses, we only modeled the female portion of the population. Because age-specific survival and parturition rates are not known for the WAH, we based our age-specific parturition rates on results from the Denali Herd in central Alaska where peak parturition occurred from age 7 to 13 (Adams and Dale 1998) and derived age-specific survival rates by averaging rates for the Beverly Herd in central Canada (Thomas and Barry 1990) and the George River Herd in eastern Canada (Messier et al. 1988), as reported by Taylor (1991). We multiplied all of the age-specific parturition and survival rates by constant proportions so that the mean values of the population approximated the mean values for the WAH over the period 1986–2008 (Dau 2009). We began the model with a female population size of 100,000 animals and the beginning age structure of the population set at the equilibrium age structure for the population assuming constant demographic parameters (Table 1).

We then simulated different collaring scenarios and ran 3,000 simulations for each scenario. In each simulation, we randomly selected a sample of caribou each year to collar according to the specified criteria. Each caribou was randomly assigned an age at collaring (based on the age structure of the population that year), an individual variability score representing that individual's relative health (from a standard normal distribution), a length of time the collar would transmit in years (a random normal variable with an assigned mean [default = 7] and a SD = 1), and a body weight at capture based on the animal's age and its individual variability score. In each successive year, new animals were collared and each existing collared caribou was randomly assigned as either a mortality, a transmitter failure or removal, or actively transmitting based on their respective probabilities.

**Table 1.** Initial demographic parameters used in the default model of a simulated caribou herd. Only caribou 2 years old and older were collared so mean survival rate estimates of the collared sample were compared to actual values for caribou 2 years of age and older and parturition rates of the collared sample were compared to actual rates for caribou 3 years of age and older.

| Age               | % of population | Survival rate | Parturition rate |
|-------------------|-----------------|---------------|------------------|
| 0                 | 20.5            | 0.57          | 0.00             |
| 1                 | 11.5            | 0.95          | 0.00             |
| 2                 | 10.7            | 0.93          | 0.15             |
| 3                 | 9.7             | 0.92          | 0.59             |
| 4                 | 8.7             | 0.90          | 0.65             |
| 5                 | 7.7             | 0.89          | 0.68             |
| 6                 | 6.7             | 0.88          | 0.70             |
| 7                 | 5.8             | 0.86          | 0.75             |
| 8                 | 4.9             | 0.84          | 0.75             |
| 9                 | 4.0             | 0.82          | 0.75             |
| 10                | 3.2             | 0.79          | 0.75             |
| 11                | 2.5             | 0.75          | 0.75             |
| 12                | 1.8             | 0.69          | 0.75             |
| 13                | 1.2             | 0.57          | 0.75             |
| 14                | 0.7             | 0.31          | 0.60             |
| 15                | 0.2             | 0.05          | 0.53             |
| 16                | 0.0             | 0.00          | 0.45             |
| Mean <sup>a</sup> |                 | 0.860         | 0.688            |

<sup>a</sup> Means calculated from ages 2 to 16 for survival and 3 to 16 for parturition and weighted by the proportion of the population.

Although WAH caribou are not recaptured, the calculations would be the same if a single collar functioned for a mean of 7 years or if a single animal was re-collared multiple times with a mean total marked history of 7 years. Each run simulated a 20-year period.

We also assumed that all caribou were  $\geq 2$  years old when collared and were randomly selected from all female caribou in the herd except that unhealthy animals (we defined this as the lowest 1% of the individual variability score in the sample) would not be collared (Dau 2009). In the first year, 100 collars were deployed, and in each successive year, 22 additional collars were deployed to replace collars lost to mortalities or battery failure and to keep an active sample of about 100 collars throughout the 20-year simulation under the default model. In some other models (e.g., lower adult survival), the mean sample size varied from 100, resulting in increased or decreased variation around the estimated mean bias.

To simulate the effect of individual variability on telemetry-based estimates of survival and the potential effects of this on independence assumptions among years, we adjusted the survival probability of each collared caribou according to a randomly generated individual variability score. Because few empirical data were available to estimate the effect of individual variability on the annual probability of survival, we used a simple linear model with upper and lower constraints. We assumed in our default model that each standard deviation (SD) from the mean would change the annual probability of survival for that individual by 2%. We truncated the upper 1% of the distribution because we assumed that after a certain increase in the individual variability score, survival would be influenced more by stochastic events such as predation, hunting mortality, and accidental death than by individual health. In fact, hunting mortality may be greater for high quality caribou (Lyver and Gunn 2004). Therefore, we constrained the change in survival due to individual variability in our default model to be between  $-4.7\%$  and  $4.7\%$  and to be symmetric about zero. We felt this was a reasonable estimate, but we also tested other levels to determine the sensitivity of the results to this variable.

We simulated individual variability in parturition rates using a similar method but incorporated available literature on the relationship between body weight and parturition in caribou. Cameron et al. (2000) used caribou weight and parturition data from the Central Arctic Herd and the Porcupine Caribou Herd to derive a logistic model describing the probability of parturition based on body weight. This was a nonlinear relationship, where the probability of parturition increased more rapidly at moderate body weights and slowly at high and low weights. In other words, heavy animals would have a smaller increase in the probability of parturition than caribou of average weight for the same increase in body weight.

We replicated this relationship by assigning each collared caribou a mean weight based on the mean probability of parturition for its age. We then increased or decreased its weight based on its randomly generated individual variability

score and calculated the probability of parturition based on the adjusted weight and the logistic model of Cameron et al. (2000). Cameron et al. (2000) reported SDs of weights of sexually mature female caribou of different ages roughly in the range of 7.5–10 kg. Much of this variation can likely be explained by age of the caribou, so we used a smaller SD of 4 kg as the default value in our age-specific model. As with survival, we also constrained the individual variability in weight to exclude the bottom 1% of the population that was unhealthy and unlikely to be collared. We used the same individual variability score for both survival and parturition, because high quality individuals are more likely to both survive and reproduce.

After developing the model, we varied values for the mean number of years individuals were collared, the mean population adult survival and parturition rates, and individual variability, 1 at a time. In this way, we determined the sensitivity of the magnitude of the bias to a range of possible values of the input parameters.

The magnitude of the age-structure bias will increase annually in the first years after initiation of a collaring program. Under our default model, the bias is initially zero, then increases during the first years of the study and then, because some new collars are added each year, stabilizes and remains constant near the maximum size. This pattern has implications for interpretation of annual estimates and for detecting trends.

The magnitude of the biases will be greater in later years, but this changing bias in early years could also, in theory, result in researchers observing a trend in demographic parameters that is caused solely by a change in the bias rather than an actual change in the mean demographic parameters for the population. We therefore tested the probability of detecting false linear trends (type I error) in survival rates with year of the study based on simulated collar data when the modeled population's survival rate was constant. Based on collar battery life and observed patterns in mean estimates, we tested 2 time periods: years 1–7 when the magnitude of the bias in survival rates increased steadily (and estimated survival rates declined); and years 11–17 when mean estimates and the magnitude of the bias remained constant. For each period, we ran logistic regression models on the simulated data with survival (i.e., yes or no) as the response variable and year as a covariate. For each period, we ran this analysis on 3,000 simulations and recorded the slope coefficient and *P*-values, and estimated survival rates.

We also added the number of years individuals had been collared as a covariate in the model to determine if inclusion of this variable could correct for age-structure bias and reduce the probability of a type I error to the nominal value of 0.05 (for  $\alpha = 0.05$ ). We reran the above analyses, but included the number of years individuals have been collared as both a linear and quadratic term and calculated the estimated survival rate at collar age equal to zero (i.e., the year each collar was deployed). If including the number of years individuals have been collared in the analysis corrects for age-structure bias, the estimated survival rate when collar age is set to zero should be an unbiased estimate of the true survival rate.

Because we used a constant survival rate, the slope of the relationship between survival rate and year should be zero for an unbiased model. We used the results of these simulations to estimate the probability of detecting a false trend at  $\alpha \leq 0.05$  and to determine if including the number of years individuals have been collared would successfully correct the bias in the estimate.

We also compared simulation results to actual, telemetry-based survival data for the WAH (Dau 2009). We estimated mean annual survival rates for 672 female WAH caribou collared between 1979 and 2009. Caribou aged 2 years or older were selected randomly (except obviously sick or injured caribou were not included) and collared from a boat while crossing the Kobuk River during fall migration in September each year (Dau 2009). Teeth were not collected for aging. Enough collars were added each year to maintain a sample size of approximately 100 collared caribou. The mean battery life was 5.79 years, somewhat less than the 7-year value used in our default model. Because of the considerable logistical constraints of tracking caribou throughout northwest Alaska, mortality can only be reliably assigned to annual time-steps. We estimated the mean annual survival rate of all collared caribou and the mean survival rate of caribou by collar duration (number of years an individual caribou had been collared). For comparison with the simulation output, survival rates were estimated as the number of collar-years of surviving caribou in a group divided by the total number of collar-years for that group. Caribou were not included in calculations in years in which transmitter failure occurred.

## RESULTS

Under our default model for collaring, the age structure of the collared sample contained more middle-aged and old caribou and fewer young caribou than the population at large (Fig. 1). The mean survival rate of this collared sample was 82.6% (SD = 3.9%), whereas the actual mean survival rate of the simulated population (age 2 and older) was 86.0%. The mean parturition rate of this collared sample (age 3 and

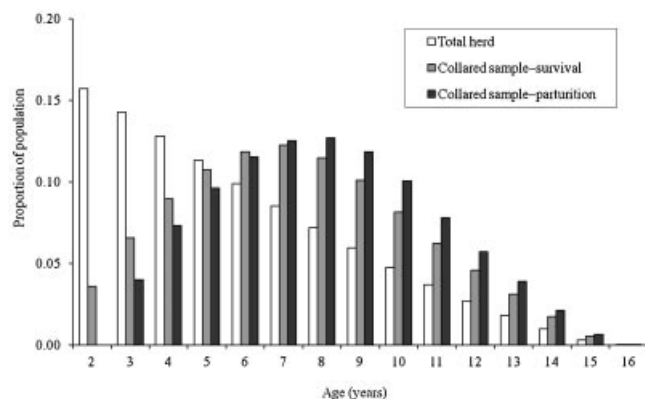


**Figure 1.** Age structure of a simulated caribou herd (total herd; >1-year-old) and the mean age structure of the simulated collared sample of the caribou herd calculated immediately after autumn collaring (for survival analysis) and in the spring (for parturition analysis) for year 20 of the simulations. Values were estimated from 3,000 simulations, simulating 20 years of the collaring program.

older) was 72.0% (SD = 5.3%), whereas the actual mean parturition rate of the population (age 3 and older) was 68.8% (Table 1).

The sample of collared animals is representative of the actual population in year 1 when 100 animals are collared randomly, but in each subsequent year the animals collared in previous years get older, thus gradually skewing the age structure of the collared sample towards older animals (Fig. 2). In our default model, the aging of the first 100 animals collared at the beginning of the study resulted in increasing biases in survival and parturition estimates (decreased mean estimated survival rate and an increased mean estimated partition rate) during the first 7 years of the study (Fig. 2). After 7 years, most of the initial 100 animals collared had died or their collars had ceased transmitting, and the biases in survival and parturition decreased slightly. Eventually, if the collaring strategy and demographic parameters remained constant, the age structure of the collared population approached equilibrium; newly collared caribou offset caribou that were lost because of mortality, collar retrieval or battery exhaustion, and the biases remained constant. The magnitude of the biases at this equilibrium level depended on many factors, including the age-specific demographic parameters, the mean collar longevity, and the amount of individual variability (Table 2).

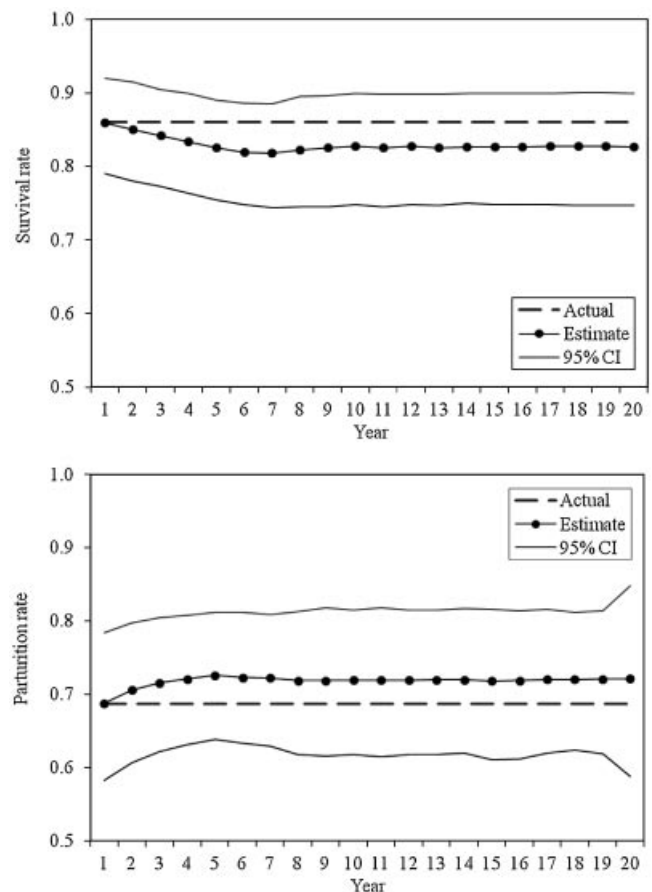


**Figure 2.** Actual mean population survival and parturition rates of a simulated caribou herd and mean estimated rates (95% CI) from simulated collared samples over a 20-year period. Means estimated from 3,000 simulations under the default collaring scenario.

**Table 2.** Estimated bias in demographic parameters calculated from collar deployments on caribou based on 3,000 simulations and modification of different associated variables. Values were estimated from years 15 to 20 of the simulations.

| Variable modified          | Values used          | Survival       |      | Parturition    |      |
|----------------------------|----------------------|----------------|------|----------------|------|
|                            |                      | Average bias % | SD % | Average bias % | SD % |
| Mean adult survival        | 82%                  | -2.92          | 4.37 | 3.11           | 5.44 |
|                            | 86% <sup>a</sup>     | -3.36          | 3.88 | 3.32           | 5.33 |
|                            | 90%                  | -3.88          | 3.35 | 3.20           | 4.72 |
|                            | 59%                  | -3.27          | 3.93 | 2.99           | 5.57 |
| Mean parturition rate      | 69% <sup>a</sup>     | -3.36          | 3.88 | 3.32           | 5.33 |
|                            | 79%                  | -3.44          | 3.79 | 3.46           | 4.23 |
|                            | 0%/SD                | -3.47          | 3.88 |                |      |
|                            | 2%/SD <sup>a</sup>   | -3.36          | 3.88 |                |      |
| Individual variability     | 4%/SD                | -3.08          | 3.82 |                |      |
|                            | 0 kg/SD              |                |      | 3.01           | 5.04 |
|                            | 4 kg/SD <sup>a</sup> |                |      | 3.32           | 5.33 |
|                            | 8 kg/SD              |                |      | 3.95           | 5.11 |
| Average collaring duration | 3 years              | -1.31          | 4.88 | 1.91           | 6.59 |
|                            | 5 years              | -2.33          | 4.13 | 2.81           | 5.52 |
|                            | 7 years <sup>a</sup> | -3.36          | 3.88 | 3.32           | 5.33 |
|                            | 9 years              | -4.33          | 3.75 | 3.47           | 4.83 |

<sup>a</sup> Default model.

The length of time animals remained collared (either based on battery life of a single collar or repeated recollarings of an individual) had the largest impact on the magnitude of the biases for both survival and parturition rates (Fig. 3, Table 2). The longer individual animals remained collared, the older

the collared sample was relative to the population, and the larger the biases became. The degree of individual variability in the population had relatively small effects on survival or parturition estimates at the levels we simulated (Table 2). Increasing the mean survival rate of the population increased the size of the bias in survival rate but had an inconsistent effect on the bias in parturition rates (Table 2). Increasing the mean parturition rate of the population increased the size of the biases in both survival rate and parturition rate (Table 2).

Tests of trends in the first 7 years of collaring indicated a significant probability of falsely detecting a negative trend in survival rates (type I error) when not accounting for changes in age structure. Of our 3,000 default model simulations, 2,571 (85.7%) estimated a declining survival rate (slope < 0) during the first 7 years. A large number, 558 (18.6%), showed a significant ( $\alpha \leq 0.05$ ) linear decline in survival rates, whereas only 4 (0.1%) indicated a significant increase in survival, for an overall type I error rate of 18.7%. Overall, the mean intercept was 1.793 (SD = 0.184) and the mean value of the year parameter was -0.054 (SD = 0.049); this corresponded to a mean annual estimated decline in the survival rate of 0.75%/year over that period. In the worst case scenario, where 100 collars were deployed in the first year, no new collars were deployed after that, and all caribou remained collared until they died, the probability of falsely detecting a significant declining trend in survival over the first 7 years was 42.4%.

During years 11–17 after collaring began, the magnitude of the bias had stabilized and there was little chance of falsely detecting a trend. We found significant trends in 167 simulations (5.6%). These were about evenly split between positive (90; 3.0%) and negative (77; 2.6%) rates. Overall, the mean intercept was 1.55 (SD = 0.69) and the mean value of the year parameter was 0.0016 (SD = 0.053), indicating essentially no change in the estimated survival rate over time. The probability of a type I error (5.6%) was very close to the nominal level (5%). During this period, the magnitude of the bias was the greatest, however, so although

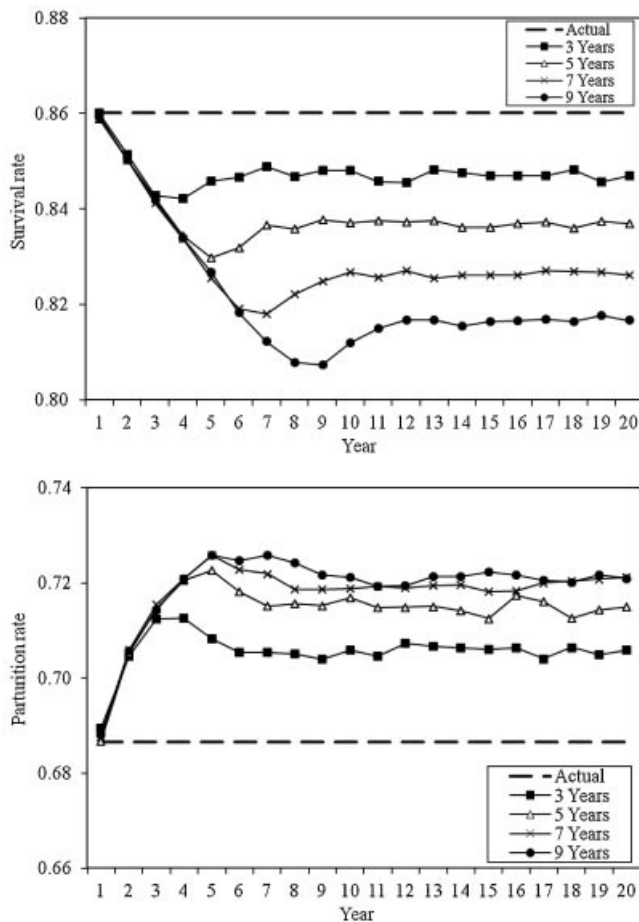


**Figure 3.** Actual mean population survival and parturition rates of a simulated caribou herd and mean estimated rates for collared samples with different numbers of years that caribou remained collared.

**Table 3.** Results of logistic regression analyses of 3,000 simulations to test for apparent declines in survival with different models including year and number of years collared.

| Data set                          | Model                                             | Average survival rate % (SD) <sup>a</sup> | Percent significant ( $\alpha = 0.05$ ) |                |                             |
|-----------------------------------|---------------------------------------------------|-------------------------------------------|-----------------------------------------|----------------|-----------------------------|
|                                   |                                                   |                                           | Year                                    | Collared years | Collared years <sup>2</sup> |
| Years 1–7 (increasing bias phase) | Intercept Only                                    | 83.47 (1.27)                              |                                         |                |                             |
|                                   | Year                                              | 85.58 (2.25)                              | 18.7                                    |                |                             |
|                                   | Year, Collared Years                              | 86.06 (2.23)                              | 4.8                                     | 36.9           |                             |
|                                   | Year, Collared Years, Collared Years <sup>2</sup> | 85.98 (2.52)                              | 5.0                                     | 1.1            | 5.2                         |
| Years 11–17 (constant bias phase) | Intercept Only                                    | 82.75 (1.42)                              |                                         |                |                             |
|                                   | Year                                              | 82.61 (2.67)                              | 5.6                                     |                |                             |
|                                   | Year, Collared Years                              | 85.97 (2.75)                              | 5.6                                     | 53.1           |                             |
|                                   | Year, Collared Years, Collared Years <sup>2</sup> | 85.72 (3.18)                              | 5.7                                     | 7.0            | 5.8                         |
| Years 1–17 (total)                | Intercept Only                                    | 83.10 (0.86)                              |                                         |                |                             |
|                                   | Year                                              | 83.93 (1.55)                              | 8.7                                     |                |                             |
|                                   | Year, Collared Years                              | 86.13 (1.62)                              | 5.3                                     | 87.5           |                             |
|                                   | Year, Collared Years, Collared Years <sup>2</sup> | 85.95 (1.83)                              | 5.2                                     | 12.5           | 5.3                         |

<sup>a</sup> Mean is calculated at the intercept (number of years collared = 0 and year = 0) to correct for potential biases. Actual survival rate for simulated population = 86.01%.

estimates of trends would be largely accurate, the annual survival rate estimates would have substantial biases.

When the number of years individuals have been collared was included in the analysis, the mean survival rate (86.06%, SD = 2.23%) was unbiased (actual mean = 86.01% for model population) and the probability of detecting a false trend by year dropped to 4.8%, very close to the expected level of 5%. Including the number of years individuals have been collared as a quadratic term only improved the model slightly; the mean survival rate was 85.98%, but the SD was slightly greater (2.52%; Table 3).

The mean survival rate estimated from empirical data from WAH female caribou declined as the number of years individuals had been collared increased from 1 to 7 years. The rate of decline over this range of collar durations was similar to the decline projected from the simulations (Fig. 4). The mean survival rate from WAH caribou data increased slightly for collared times over 7 years, whereas the simulations predicted a more rapid decline in mean survival. Few collars transmitted longer than 7 years, so the sample sizes ( $n = 104$  collar-years) were small for collars over 7 years old.

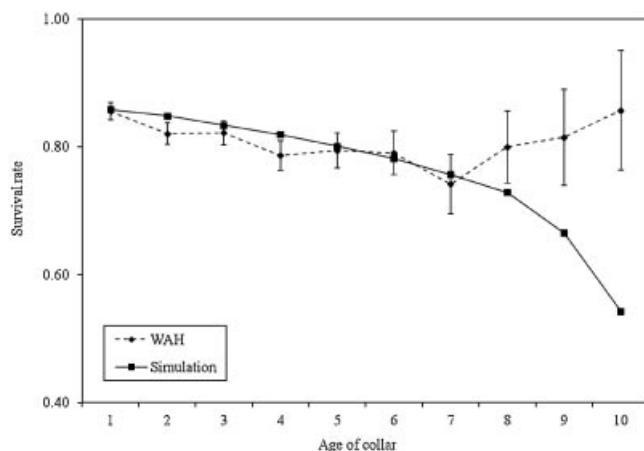


**Figure 4.** Mean survival rate ( $\pm$ SE) of 672 female Western Arctic Herd (WAH) caribou collared between 1979 and 2009 as a function of number of years collared and the predicted mean survival rate estimated from simulations.

## DISCUSSION

Telemetry collars are one of the few tools currently available to obtain accurate measures of demographic parameters in highly mobile animals living in remote locations, such as caribou. Financial and logistical considerations often prevent researchers from gathering large sample sizes from wild populations, which reduces the power to detect small changes in mortality (Murray 2006). These constraints often dictate the quality and quantity of data that can be gathered.

In many cases it is logistically advantageous to maintain collars on a sample of animals for multiple years and, therefore, the sample will become less representative of the general population over time. In these cases where it is not feasible to design a study to collect unbiased estimates, it is important to understand these biases and correct for them to the extent practicable. Our analyses assessed the effects of unrepresentative age samples and individual variability on demographic estimates from multi-year telemetry studies. An unrepresentative age sample may result in serious errors in estimated demographic parameters (e.g., estimating a declining population from a population experiencing modest growth) if not corrected, whereas the individual variability bias appeared to have minimal effect on estimates and can be ignored in many situations.

Our simulations were based on a simplified caribou population with constant demographic parameters and a stable age structure. In a real population, natural variability in demographic parameters could affect these biases in various ways. A dynamic age structure would affect the actual population survival and parturition rates as well as the bias of the estimates based from a collared sample. In an aging population, the mean survival rate should decline even if the age-specific survival rates stay the same, but the size of the bias should be less than it otherwise would be because the aging of the collared sample will be partially offset by the simultaneous aging of the population. The reverse would be true for a population with an age structure that is getting younger. The collared sample would get older while the population would get younger, causing an increasing bias. In cases where

a large mortality event dramatically reduces survival for a single year, the change in the magnitude of the age structure bias would depend on whether the mortality occurred evenly across all age classes or was focused on young and/or old animals.

For survival rates in our model, individual variability bias acted in the opposite direction of age structure bias, reducing bias. For parturition rates in our model, the 2 biases were additive. The magnitude of individual variability bias would depend on the degree of variability in the population and the strength of the correlations among specific traits and demographic parameters. In caribou, body condition in fall is strongly correlated with parturition rate the following spring (Cameron et al. 1993, 2000; Cameron and Ver Hoef 1994), the timing of calving (Cameron et al. 1993), and calf growth and survival (Skogland 1984, Cameron et al. 1993, Adams 2003). To the degree body condition is also related to survival, caribou with greater than average parturition rates are also likely to be over-represented in a multi-year collaring study. The results of this simulation suggested that at this level of variability and with this collaring schedule, the magnitude of the individual variability bias in both parturition and survival would be low. Some larger sources of individual variability such as that caused by pooling data from males and females can result in biased estimates after a large portion of the sample have died (Murray 2006).

Various telemetry studies have reported potential effects of age structure bias on calculations of demographic parameters. Jenkins and Barten (2005) found that parturition rates from aerial surveys of caribou were 5–10% less than parturition rates estimated from observations of collared caribou and concluded that part of the difference may have been due to older females in the collared sample. Delguidice et al. (2006) used white-tailed deer (*Odocoileus virginianus*) data to simulate the size of the bias in the estimated population growth rate caused by pooling all female adult deer and found that the estimate was biased ( $\lambda = 1.03$  vs.  $\lambda = 1.07$ ), but concluded that, under their study design, the magnitude of the bias was low compared to the uncertainty of the estimates. Dividing animals into 2 groups (age 1–7 and >7 years) decreased the magnitude of the bias substantially ( $\lambda = 1.06$  vs.  $\lambda = 1.07$ ; Delguidice et al. 2006), suggesting that, in some situations, even imprecise estimates of age can correct for a substantial portion of age structure bias.

Haskell and Ballard (2007) modeled the population growth of the WAH based on demographic parameters estimated from telemetry data (Dau 2003). They concluded that the estimated parameters from telemetry data were too low to explain the observed population growth in the herd. To explain this discrepancy, they hypothesized that the weight of telemetry collars reduced parturition rates of collared caribou. The existence of age structure bias in survival rates from the telemetry data could also explain some of this observed discrepancy, although some evidence exists that collars may also have negative effects on animals. The WAH animals with heavier collars had lower survival rates than caribou with lighter collars (Dau 2009). Collar weight has also been correlated with lower movement rates during

foraging in zebras (*Equus burchelli antiquorum*; Brooks et al., 2008) and greater mortality rates in pheasants (*Phasianus colchicus*; Venturato et al. 2009).

We could not locate published age-specific survival rates for male caribou, but breeding male reindeer (*Rangifer tarandus tarandus*) lost 34% of their ingesta-free body mass during the rut (Barboza et al. 2004) and male caribou had lower annual survival rates (Fancy et al. 1994, Carroll 2007, Dau 2009) and lower overwinter survival rates (Bergerud 1971) than females. This probable sharp decline in the survival rates of adult bulls should result in a larger bias in survival rates for males than for females.

We found that, in our simulations, the probability of falsely detecting a trend in survival would likely be high for new collaring programs as the age structure of the sampled caribou changes and the magnitude of the bias increases. In the first 7 years, the probability of falsely detecting a declining trend in survival in our modeled population was high (18.6%). In a study in which no new collars were deployed and all caribou remained collared until they died, this probability rose to 42.4%. This suggested that failure to account for age structure bias could result in erroneous conclusions about parameter trends early in collaring programs; however, the probability of falsely detecting a statistically significant trend would be less in practice than suggested by our model because of inter-annual variability of survival rates in ungulate populations, which will lower statistical power. In many cases, researchers will consider a suite of different models describing the trends in demographic parameters. This additional complexity of the analysis will have an unpredictable impact on the probability of detecting a false trend. When additional covariates explain large portions of the interannual variability in parameters, they will increase the probability of detecting a false trend due to changing bias levels. But, if the other covariates are correlated with the duration of collaring covariate, they may reduce the probability of detecting false trends. After the age structure of the collared sample reached equilibrium (after 10 yr in our simulation), the probability of falsely detecting a trend was low but the magnitude of the bias remained high.

We based our model on the largest caribou herd in Alaska (approx. 350,000 caribou). In this case, the proportion of collared animals is very small (approx. 0.03%) and therefore the uncollared portion of the herd was essentially the same as the entire population. The estimated biases would be different in small populations where a large proportion of the entire population is collared. In these cases, the proportion of the population that remains uncollared in any year will tend to be younger than the entire population. Randomly selecting a sample to collar from this younger uncollared population will therefore result in reducing the overall age of the collared sample. This will have the effect of decreasing the magnitude of the biases.

One way to collar known age animals without extracting teeth for aging is to collar yearlings. These caribou will be of known age and age-specific demographic parameters can be estimated. Calculating demographic parameters for large numbers of yearlings has additional advantages because

young animals are likely to show a stronger correlation with recent forage and weather conditions (Skogland 1985, Adams and Dale 1998, Eberhardt 2002). Yearling caribou are not always easily identifiable, however, and larger yearlings may be incorrectly classified as 2-year-olds, resulting in a different bias. This is especially true when collaring occurs later in the summer as it does for the WAH.

The problem of estimating demographic parameters from unknown age animals over long collaring periods is somewhat analogous to the problem of deriving nest survival estimates when nests are not discovered until sometime after nest initiation and high levels of individual heterogeneity exists among nests (Natarajan and McCulloch 1999, Dinsmore et al. 2002). Borrowing methodologies from this field, we found that including the collaring duration in analyses can correct for age structure bias and avoid inflated type I error rates when testing for trends, but it may not work as well in more complex situations with changing demographic parameters. The number of years individuals have been collared could easily be incorporated along with other covariates into analyses with Program MARK (White and Burnham 1999) and model selection procedures can be used to test the explanatory power of this covariate and select the most parsimonious model.

Data on age-specific survival are scarce and sometimes contradictory. We used rates reported by Messier et al. (1988) and Thomas and Barry (1990) that showed that survival rates were greatest for yearlings and declined for all older animals. Hearn et al. (1990) found that survival rates of female yearlings were less than for female caribou aged 2 and older in the George River Herd. Fancy et al. (1994) found high survival rates of both yearlings and 2-year-olds for the Porcupine Caribou Herd. Because we did not include yearlings in our analyses, whether or not yearlings have lower survival would not affect the bias in the default model, but if 2-year olds have lower survival than adults, it would reduce the magnitude of the bias. In general, the lack of good age-specific survival and parturition data for caribou was a limitation in this type of modeling exercise. Additional work should be conducted to estimate the pattern of age-specific survival and parturition in various caribou herds and assess how this varies among herds and over time within the same herd.

The fact that the results from actual WAH caribou data were generally consistent with our predicted bias estimates from simulations provided some evidence that our model provided a reasonable approximation of the potential biases in estimates of demographic parameters for that herd. It is unclear why mean survival rates increased for WAH animals that had been collared more than 7 years (Fig. 4). These caribou may have had physical traits or behavioral strategies that allowed them to maintain high survival even at advanced ages, or it could have been an artifact of small samples sizes of caribou collared for this length of time.

In many situations, such as short-term deployments of collars or monitoring programs that rely primarily on trend analysis, these biases may be sufficiently small relative to other sources of error to have little impact on many man-

agement decisions, but the biases may be large enough to have substantial impacts on the results of population modeling exercises. The estimated annual survival rate in the WAH has varied between 72% and 92% (Dau 2009), but the estimated bias in the mean survival rate estimate in our default model was large enough to make a substantial difference in the modeled population trajectory. If studies rely on a single, initial collar deployment without additional recollaring in subsequent years, the bias will be substantially larger and may be large enough to impact management decisions.

## MANAGEMENT IMPLICATIONS

Age structure bias is caused by a sample of collared animals that becomes increasingly unrepresentative of the general population over time. Whenever feasible, ungulate researchers should maintain a representative sample of animals in a study, but when collars are deployed for multiple years, some degree of age structure bias will exist as the collared animals age. In these cases, researchers should attempt to determine the age of collared animals and incorporate that information into analyses of demographic parameters. When age information is not available, researchers should be aware of potential biases introduced via age structure and individual variability effects and alter their telemetry deployment plan or adjust demographic estimates accordingly. In long-term studies when age is unknown, length of time an animal has been collared should be considered as a potential covariate in analyses of survival and parturition rates.

Understanding the magnitude of the potential biases will allow researchers to weigh the logistical benefits of multiple year deployments versus the potential for collecting biased data. The exact size of these biases will vary for each population, for each study design, and may vary annually, but our simulations provided information on the magnitude and direction of the biases and the factors that most strongly influence their magnitude. This simulation approach also provides a framework for quantifying biases from other data sources and management scenarios.

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## LITERATURE CITED

- Adams, L. G. 2003. Marrow fat deposition and skeletal growth in caribou calves. *Journal of Wildlife Management* 67:20–24.
- Adams, L. G., and B. W. Dale. 1998. Reproductive performance of female Alaskan caribou. *Journal of Wildlife Management* 62:1184–1195.
- Barboza, P. S., D. W. Hartbauer, W. E. Hauer, and J. E. Blake. 2004. Polygynous mating impairs body condition and homeostasis in male reindeer (*Rangifer tarandus tarandus*). *Journal of Comparative Physiology B* 174:309–317.

- Bergerud, A. T. 1971. The population dynamics of Newfoundland caribou. *Wildlife Monographs* 25:3–55.
- Brooks, C., C. Bonyongo, and S. Harris. 2008. Effects of Global Positioning System collar weight on zebra behavior and location error. *Journal of Wildlife Management* 72:527–534.
- Cameron, R. D., D. E. Russell, K. L. Gerhart, R. G. White, and J. M. Ver Hoef. 2000. A model for predicting the parturition status of arctic caribou. *Rangifer Special Issue* 12:139–141.
- Cameron, R. D., W. T. Smith, S. G. Fancy, K. L. Gerhart, and R. G. White. 1993. Calving success of female caribou in relation to body weight. *Canadian Journal of Zoology* 71:480–486.
- Cameron, R. D., and J. M. Ver Hoef. 1994. Predicting parturition rate of caribou from autumn body mass. *Journal of Wildlife Management* 58:674–679.
- Carroll, G. M. 2007. Unit 26A, Teshekpuk caribou herd. Pages 262–283 in P. Harper, editor. Caribou management report of survey and inventory activities 1 July 2004–30 June 2006. Federal Aid in Wildlife Restoration, grants W-33-3 and W-33-4, project 3.0. Alaska Department of Fish and Game, Juneau, Alaska, USA.
- Dau, J. 2003. Units 21D, 22A, 22B, 23, 24 and 26A (Northwest Alaska) Western Arctic Herd caribou management report. Pages 204–251 in C. Healy, editor. Caribou management report of survey and inventory activities 1 July 2000–30 June 2002. Grants W-27-4 and 5. Alaska Department of Fish and Game, Juneau, Alaska, USA.
- Dau, J. 2009. Units 21D, 22A, 22B, 22C, 22D, 22E, 23, 24A, 24B, 24C, 24D and 26A Western Arctic Herd caribou management report. Pages 176–239 in P. Harper, editor. Caribou management report of survey and inventory activities 1 July 2006–30 June 2008. Grants W-35-5 and W-33-6. Alaska Department of Fish and Game, Juneau, Alaska, USA.
- Delguidice, G. D., J. Fieberg, M. R. Riggs, M. C. Powell, and W. Pan. 2006. A long-term age-specific survival analysis of female white-tailed deer. *Journal of Wildlife Management* 70:1556–1568.
- Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83:3476–3488.
- Eberhardt, L. L. 1985. Assessing the dynamics of wild populations. *Journal of Wildlife Management* 49:997–1012.
- Eberhardt, L. L. 2002. A paradigm for population analysis of long-lived vertebrates. *Ecology* 83:2841–2854.
- Fancy, S. G., K. R. Whitten, and D. E. Russell. 1994. Demography of the Porcupine caribou herd, 1983–1992. *Canadian Journal of Zoology* 72:840–846.
- Haskell, S. P., and W. B. Ballard. 2007. Modeling the Western Arctic caribou herd during a positive growth phase: potential effects of wolves and radiocollars. *Journal of Wildlife Management* 71:619–627.
- Hearn, B. J., S. N. Luttich, M. Crête, and M. B. Berger. 1990. Survival of radio-collared caribou (*Rangifer tarandus caribou*) from the George River herd, Nouveau-Québec—Labrador. *Canadian Journal of Zoology* 68:276–283.
- Heisey, D. M., and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. *Journal of Wildlife Management* 49:668–674.
- Jenkins, K. J., and N. L. Barten. 2005. Demography and decline of the Mentasta Caribou Herd in Alaska. *Canadian Journal of Zoology* 83:1174–1188.
- Joly, K. 2011. Modeling influences on winter distribution of caribou in northwestern Alaska through use of satellite telemetry. *Rangifer Special Issue* 19:75–85.
- Lyver, P. O' B., and A. Gunn. 2004. Calibration of hunters' impression with female caribou body condition indices to predict probability of pregnancy. *Arctic* 57:233–241.
- Messier, F., J. Huot, D. Le Henaff, and S. Luttich. 1988. Demography of the George River herd: evidence of population regulation by forage exploitation and range expansion. *Arctic* 41:279–287.
- Murray, D. L. 2006. On improving telemetry-based survival estimation. *Journal of Wildlife Management* 70:1530–1543.
- Natarajan, R., and C. E. McCulloch. 1999. Modeling heterogeneity in nest survival data. *Biometrics* 55:553–559.
- Siler, W. 1979. A competing-risk model for animal mortality. *Ecology* 60:750–757.
- Skogland, T. 1984. The effects of food and maternal conditions on fetal growth and size in wild reindeer. *Rangifer* 4:39–46.
- Skogland, T. 1985. The effects of density-dependent resource limitations on the demography of wild reindeer. *Journal of Animal Ecology* 54:359–374.
- Taylor, M. 1991. Analysis of the standing age distribution and age-specific recruitment rate of the George River and Beverly barren-ground caribou populations. *Rangifer Special Issue* 7:60–66.
- Thomas, D. C., and S. J. Barry. 1990. A life-table for female barren ground caribou in north-central Canada. *Rangifer Special Issue* 3:177–184.
- Tsai, K., K. H. Pollock, and C. Brownie. 1999. Effects of violation of assumptions for survival analysis methods in radiotelemetry studies. *Journal of Wildlife Management* 63:1369–1375.
- Venturato, E., P. Cavallini, P. Banti, and F. Dessi-Fulgheri. 2009. Do radio collars influence mortality and reproduction? A case with ring-necked pheasants (*Phasianus colchicus*) in central Italy. *European Journal of Wildlife Research* 55:547–551.
- Weladji, R. B., H. Åystein, J.-M. Gaillard, N. G. Yoccoz, A. Mysterud, M. Nieminen, and N. C. Stenseth. 2010. Age-specific changes in different components of reproductive output in female reindeer: terminal allocation or senescence? *Oecologia* 162:261–271.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (Suppl.): 120–138.
- White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-telemetry data. Academic Press, New York, New York, USA.
- Zens, M. S., and D. R. Peart. 2003. Dealing with death data: individual hazards, mortality and bias. *Trends in Ecology and Evolution* 18:366–373.

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