

Population Ecology

Estimating Ungulate Recruitment and Growth Rates Using Age Ratios

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ABSTRACT Trends in population growth can be monitored with data for key vital rates without knowledge of abundance. Although adult female survival has the highest elasticity for ungulate population dynamics, the more variable recruitment rates are commonly monitored to track local variation in growth rates. Specifically, recruitment is often measured using late winter young:adult age ratios, though these age ratios are difficult to reliably interpret given the contribution of multiple vital rates to annual ratios. We show that the supplementation of age ratio data with concurrent radio-telemetry monitoring of adult female survival allows both retrospective estimation of empirical population growth rates and the decomposition of recruitment-specific vital rates. We demonstrate the estimation of recruitment and population growth rates for 1 woodland caribou population using these methods, including elasticity and life-stage simulation analysis of the relative contribution of adult female survival and recruitment rates to variation in population growth. We show, for this woodland caribou population, that adult female survival and recruitment rates were nearly equivalent drivers of population growth. We recommend the concurrent monitoring of adult female survival to reliably interpret age ratios when managing caribou and other ungulates. © 2011 The Wildlife Society.

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Monitoring population trends is fundamental to species conservation. Abundance estimates are ideal for monitoring population dynamics, but are often challenging to reliably obtain for species that are difficult to count due to rarity, uneven distributions, or poor detectability. Because knowledge of population trend may be as valuable for conservation as abundance per se, and estimates of trend do not necessarily require estimates of abundance, trend estimates are a common surrogate for abundance in conservation planning. Demographic models allow the estimation of population growth rates using vital rates without requiring knowledge of abundance, and in closed populations key vital rates can reduce to survival and recruitment (Hatter and Bergerud 1991, Danchin et al. 1995, White and Bartmann 1998, Caswell 2001).

Recruitment is commonly monitored with young:adult age ratios derived from harvest and survey data, particularly for populations of birds (Kaminski and Gluesing 1987, Menu et al. 2002) and ungulates (Roseberry and Woolf 1991, Monello et al. 2001, White et al. 2001, Bright and Hervert 2005, Hegel et al. 2010). Several authors have cautioned that age ratios alone are not sufficient for popula-

tion monitoring (Caughley 1974, McCullough 1994, White and Bartmann 1998), though they have been shown to be positively correlated with population growth rates for elk under some conditions (Harris et al. 2008). We consider age ratios collected near the end of the biological year (e.g., late winter for ungulates that birth in spring), when juveniles are considered as recruited to the adult population. These ratios are difficult to interpret with specific reference to population growth or vital rates given that they can be influenced by multiple contributing vital rates. The numerator, or number of young at the time of survey, is the product of the age-specific fecundity of adult females (which is itself the product of pregnancy rate, fetal survival, and litter size) and the survival of young to the time of survey, whereas the denominator, or number of adults at the time of survey, is affected by the age-specific survival rates of adults since the birth pulse. The interpretation of ungulate recruitment rates using age ratios is further complicated by an unknown age structure of breeding- and nonbreeding-aged adults, given a minimum age of first reproduction of 2-years-old. Trained observers may not be able to reliably differentiate nonbreeding yearlings (1 to 2-year-olds) and breeding-aged adults (≥ 2 -year-olds) in the total count of adult females, especially during aerial surveys (Smith and McDonald 2002).

Despite these complications in interpreting age ratios, Harris et al. (2008) found that 96% of the variation in

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simulated age ratios for elk (*Cervus elaphus*) was explained by variation in a single vital rate, calf survival. Consequently, in populations where calf survival is the vital rate most predictive of population growth rates (Gaillard et al. 2000, Raithel et al. 2007), age ratios alone may be suitable for monitoring population trends. For long-lived, iteroparous species such as ungulates, the elasticity of population growth rates is typically highest in adult female survival (Gaillard et al. 2000), but variation in this important vital rate is expected to be minimized by evolutionary adaptation (Pfister 1998, Gaillard and Yoccoz 2003). The survival, or recruitment, of young generally has higher variance than that of adults (Gaillard et al. 1998), which affords this vital rate subsequently greater correlation to realized population growth rates (Gaillard et al. 2000, Raithel et al. 2007). However, additional demographic analyses have revealed that the variance of vital rates and their resultant importance to population growth rates can vary across populations within species and across time or space within populations (Albon et al. 2000, Morrison and Hik 2007, Ezard et al. 2008, Nilsen et al. 2009, Johnson et al. 2010). Furthermore, the importance of adult survival in explaining ungulate population growth rates may be accentuated in declining or endangered populations experiencing patterns of adult survival that are lower or more variable than would have been evolutionarily stable (Owen-Smith and Mason 2005, Nilsen et al. 2009, Johnson et al. 2010). This highlights the potential importance of monitoring both recruitment and adult survival for complete depiction of population trend. We show that concurrent monitoring of adult survival using radio-telemetry supplements age ratio data sufficiently to alleviate the initial concerns of Caughley (1974) and McCullough (1994) and allows the estimation of both recruitment and population growth rates.

Annual population estimates of a threatened ungulate, woodland caribou (*Rangifer tarandus caribou*), would inform recovery planning under Canada's Species at Risk Act (SARA), but monitoring of woodland caribou abundance is difficult due to their low density, small group sizes, and low sightability in densely forested habitat. In Alberta and other jurisdictions, monitoring of woodland caribou has focused on the monitoring of adult female survival and age ratios, from which population growth rates have been estimated (McLoughlin et al. 2003). We use monitoring data from a population of woodland caribou in Alberta as a case study for developing demographic models of population growth with adult female survival and age ratio data. We demonstrate the estimation of population growth with 2 methods, Hatter and Bergerud's (1991) *R/M* equation and matrix population models. For use with matrix models, we show the proper adjustment of age ratio data to isolate adult female recruitment rates. Lastly, we use adult survival, age ratio, and age of first reproduction data to conduct a life-stage simulation analysis (LSA; Wisdom et al. 2000), assessing the relative importance of each vital rate to population growth for a single woodland caribou population.

STUDY AREA

We studied vital rates and population growth for the A la Pêche woodland caribou population in the Rocky Mountains of west-central Alberta. The A la Pêche population traditionally migrates between an alpine summer range in protected areas (Jasper National Park and the Willmore Wilderness Area) and a forested foothill winter range east of park boundaries, though individuals can exhibit sedentary behavior in both winter and summer ranges (McDevitt et al. 2009). The eastern portion of the range has been modified by industrial land use such that 59% of the population's range outside of protected areas is within 500 m of an anthropogenic feature (e.g., road, seismic line, or forest harvest unit; Alberta Sustainable Resource Development and Alberta Conservation Association [ASRD and ACA] 2010). Wolf (*Canis lupus*) population control was conducted to benefit a neighboring caribou population in an area overlapping the eastern boundary of the A la Pêche winter range during 2006–2009 (ASRD and ACA 2010). Caribou are protected from hunting within the national parks, and licensed hunting of the A la Pêche population, when outside of the park, was discontinued in 1981. Forested habitats included upland lodgepole pine (*Pinus contorta*), spruce (*Picea* spp.) and aspen (*Populus tremuloides*) mixed forests, and lowland black spruce (*Picea mariana*) muskegs.

METHODS

The *R/M* Equation

Hatter and Bergerud (1991) derived the following equation (the *R/M* equation) as a means of retrospectively estimating population growth (λ), recruitment (R), or either mortality (M) or survival ($S = 1 - M$) rates for a given year, when at least 2 of these 3 rates are known:

$$\lambda = \frac{(1-M)}{(1-R)} = \frac{S}{(1-R)} \quad (1)$$

The *R/M* equation was originally proposed as a complementary means for estimating growth rates in concert with surveys of abundance (e.g., Patterson et al. 2002), but has since been applied to monitor populations lacking abundance data. It has been used to estimate population trends for deer (*Odocoileus* spp.; Patterson et al. 2002), elk (Kunkel and Plotscher 1999), moose (*Alces alces*; Hayes et al. 2000), and caribou (McLoughlin et al. 2003, Hebblewhite et al. 2007, Sorensen et al. 2008), and is a cornerstone of Alberta's caribou monitoring and recovery plan (ASRD and ACA 2010). Although Hatter and Bergerud (1991) specified both male- and female-based models, we focus specifically on female-only models.

This model is conveniently designed to estimate the recruitment rate, R_{RM} , using age ratio data collected at the end of a biological year, when the survival of juveniles is assumed to become equal to that of adults (Hatter and Bergerud 1991). The age ratio, X , is commonly estimated as the number of juveniles, n_j , per adult female, n_{af}

observed at the end of a measurement year, such that

$$X = \frac{n_j}{n_{af}}, \text{ and } \frac{X}{2} = \frac{n_{jf}}{n_{af}} \quad (2)$$

where $X/2$ estimates number of female juveniles, n_{jf} per adult female assuming a 50:50 sex ratio. Although studies of caribou population trend have occasionally treated $X/2$ and R_{RM} as equal (McLoughlin et al. 2003, Hebblewhite et al. 2007), proper adjustment of $X/2$ to a juveniles/(juveniles + adults) ratio is necessary, according to

$$R_{RM} = \frac{n_{jf}}{n_f} = \frac{(X/2)}{1 + (X/2)} \quad (3)$$

where $n_f = n_{jf} + n_{af}$, or the total number of females of all age classes, including juveniles, counted at the end of the measurement year. Failure to make this adjustment has resulted in overestimates of recruitment and optimistic estimates of population growth.

Additionally, for ungulates the count n_{af} includes both breeding adult females and nonbreeding yearlings and subadults, given that the age of first reproduction is ≥ 2 -years old. The R/M model does not require knowledge of age structure or age-specific fecundity and instead growth rates are estimated treating recruitment as the simple proportion of recruits in the total population of females (equation 3). Thus, the inclusion of nonbreeding-aged adults in the recruitment denominator is appropriate for this model. However, this inclusion of both breeding-aged and nonbreeding-aged adults in the denominator of age ratios complicates estimation of stage-specific recruitment rates necessary for using structured demographic models such as stage- or age-based matrix population models.

Matrix Population Models

We also estimated population growth rates using matrix models, which can project age- or stage-structured female-only populations using survival and recruitment vital rates (Caswell 2001). If we assume, as we do when using the R/M equation, that survival is equal across all nonjuvenile age classes, then the appropriate dimensions of a stage-based matrix for ungulates are a function of age-specific fecundity, or more simply the age of first reproduction. Though yearling pregnancy in caribou can approach 100% under optimal conditions (Ouellet et al. 1997), caribou on average may have an older age of first reproduction than typical of other ungulates. Studies of both woodland and tundra-dwelling caribou have found 3-years old to be the most common age of first reproduction (range 2–6; Parker 1981, Messier et al. 1988, Fancy et al. 1994, Adams and Dale 1998).

For simplicity of presentation we treat age of first reproduction as 2-years-old and begin with a 2-stage, pre-birth pulse, female-only matrix model \mathcal{A} , for a given time step, t , and a stage-structured population vector, $n(t)$. We estimate caribou population growth according to

$$\lambda(t) = \frac{\mathcal{A}(t) \times n(t)}{n(t)} \quad (4)$$

$$\mathcal{A}(t) = \begin{bmatrix} 0 & F_a p_f S_j \\ S_y & S_a \end{bmatrix} = \begin{bmatrix} 0 & R_{2\text{-stage}} \\ S_a & S_a \end{bmatrix} \quad (5)$$

and

$$n(t) = \begin{bmatrix} p_y(t) \\ p_a(t) \end{bmatrix} = \begin{bmatrix} p_y(t) \\ 1 - p_y(t) \end{bmatrix} \quad (6)$$

where the survival of yearlings, S_y is assumed to be equal to adult survival, S_a , the recruitment of 12-month-old females to the population, $R_{2\text{-stage}}$, is the product of adult female fecundity, F_a , the proportion of juveniles that are female, p_f and the first-year survival of juveniles, S_j , and the age structure of the population $n(t)$ is a function of the proportion of the population entering the time step as nonbreeding yearlings, $p_y(t)$, and breeding adults, $p_a(t)$. For retrospective assessment of population growth with matrix models given a set of empirical vital rates, equation 4 is preferable to estimating the dominant eigenvalue of a given projection matrix because it specifies a transient population age structure rather than assuming an asymptotic stable age structure (Fox and Gurevitch 2000).

DeCesare et al. (2011) showed that R for matrix models should be estimated as the number of juveniles at the end of the time step per breeding adult present at the beginning of the time step. They decreased the numerator of caribou age ratios to account for a 50:50 sex ratio and the survival of juveniles from the time of survey to the completion of the time step, and they increased the denominator using the survival rate of adults from the beginning of the time step to the time of survey. Assuming, as we did above for the R/M equation, that survival of all age classes is equivalent to adult survival for the remainder of the biological year after the time of survey, this adjustment reduced to $\hat{R} = (X/2) \times \hat{S}_a$ (DeCesare et al. 2011). However, although DeCesare et al. (2011) attempted to identify and exclude yearlings in the collection of their age ratio data, the denominator in most ungulate age ratio data includes yearling females in the count of adults (Smith and McDonald 2002), which were incapable of giving birth at the beginning of the time step. Although suitable for estimating recruitment when using the R/M equation, the inclusion of yearlings is inappropriate for our matrix model (equation 5), which requires an estimate of the per-capita contribution to recruitment of breeding females, specifically. Thus, an additional adjustment is required to remove the proportion of yearlings, or perceived adults which have not reached the age of first reproduction, to estimate the appropriate recruitment rate of breeding-age adults as

$$\hat{R}_{2\text{-stage}} = \frac{(X/2)}{((1 - p_y)/\hat{S}_a)} \quad (7)$$

The proportion of yearlings entering a given time step, t , can be estimated using the adjusted age ratio of the previous time step, $t - 1$, where

$$p_y(t) = \frac{(X_{t-1}/2)}{1 + (X_{t-1}/2)} \quad (8)$$

Thus, an adjusted recruitment term for use in matrix models, $R_{2\text{-stage}}$, is estimable for all years when the age ratio is available for both the year of interest and the previous year. With the assumption that survival is equal across nonjuvenile age classes (i.e., $S_y = S_a$), as held in equation 5, all age structure ($p_y[t]$) terms cancel out when estimating λ , and equation 4 becomes numerically equivalent to equation 1, the R/M equation. In other words, population growth rate estimates from equations 4–7 are insensitive to age structure when the included matrix population model lacks age-specific differences in vital rates. For each pair of annual estimates of $S_a(t)$ and $X(t)$, equivalent estimates of λ can be achieved using either equation 1 or equation 4 (substituting any value for $p_y[t]$). However, the recruitment term itself, $R_{2\text{-stage}}$, which varies according to $p_y(t)$, will not be interpretable without consecutive years of age ratio data to properly estimate $p_y(t)$ using equation 8. Interpretable estimates of $R_{2\text{-stage}}$ will be necessary if the user wishes to isolate the contribution of recruitment parameters from those of age structure and S_a to age ratios, or to estimate means or process variances of recruitment parameters, specifically.

To treat age of first reproduction as 3-years-old, these methods can be extended to a 3-stage matrix model by adding an additional nonbreeding subadult stage, such that

$$A = \begin{bmatrix} 0 & 0 & R_{3\text{-stage}} \\ S_a & 0 & 0 \\ 0 & S_a & S_a \end{bmatrix} \quad (9)$$

$$n(t) = \begin{bmatrix} p_y(t) \\ p_s(t) \\ 1-p_y(t)-p_s(t) \end{bmatrix} \quad (10)$$

$$\hat{R}_{3\text{-stage}} = \frac{(X/2)}{(1-p_y-p_s)/\hat{S}_a} \quad (11)$$

and

$$p_s(t) = \frac{p_{y,t-1}}{1 + (X_{t-1}/2)} \quad (12)$$

where $p_y(t)$ is estimated using equation 8, and the proportion of subadults that entered the time step, $p_s(t)$, is estimated using the age ratio and estimate of $p_y(t-1)$. In total, estimation of an interpretable value of $R_{3\text{-stage}}$ requires 3 consecutive years of data, though population growth rates can still be estimated with vital rates for a single year using equations 4 and 9–11. Annual population growth rates estimated with the 2-stage (equations 4–7) or 3-stage (equations 4 and 9–11) models will be equivalent, but recruitment rates will vary according to the proportion of the perceived adult population assumed to be of actual breeding age.

Case Study: Estimating λ for Woodland Caribou

Empirical vital rates and growth rates.—We monitored the survival and recruitment of the A la Pêche woodland caribou population during 1998–2009. We monitored survival of ≥ 1.5 -year-old females by capturing animals using helicopter

net gunning and fitting captured animals with very high frequency and global positioning system telemetry collars (ASRD and ACA 2010). Animal use protocols were approved by the University of Montana Institutional Animal Care and Use Committee; Animal Use Protocol 059-09MHWB-122209. We monitored recruitment with late winter helicopter surveys documenting calf/cow age ratios with the counts of cows including both yearling and adult females (Smith and McDonald 2002, ASRD and ACA 2010). Recruitment surveys targeted caribou groups containing at least 1 radio-collared adult female and included an average of 99.7 (SD = 26.0) individuals in 14.2 (SD = 4.0) groups per year.

We estimated annual adult female survival rates, $S_a(t)$, for each biological year (1 May–30 April) using Pollock et al.'s (1989) staggered-entry modification of Kaplan and Meier's (1958) survivorship model. We estimated caribou age ratios according to equation 2 and estimated recruitment for use with the R/M equation and matrix models according to equations 3 (R_{RM}), 7 ($R_{2\text{-stage}}$), and 11 ($R_{3\text{-stage}}$). For 2 years (1998 and 1999) when only late fall survey data were available, we reduced calf counts by an additional 15% as estimated by comparing years with both late fall and late winter survey data (Smith 2004). When adults counted during surveys were not classified according to sex (due to dense forested cover and low sexual dimorphism; Geist and Bayer 1988), we partitioned unclassified adults as 65% female and 35% male following Smith (2004). Linear regression revealed no significant bias in annual age ratio estimates caused by annual variation in the proportion of unclassified adults ($\beta = -0.057$, $P = 0.34$). We estimated annual population growth rates using each demographic model and used the geometric mean of annual growth rates to estimate the overall average annual growth rate. In addition to estimating empirical growth rates for the A la Pêche population, we also simulated a range of survival and recruitment values observed in other woodland caribou populations in Alberta (ASRD and ACA 2010) to visually depict the potential range of transient population growth rates given input vital rates.

Elasticity and life-stage simulation analyses.—We calculated analytical elasticities of adult survival and recruitment vital rates using a 2-stage matrix model (equation 5) parameterized with the geometric mean survival and recruitment values of the A la Pêche woodland caribou population. We conducted elasticity analysis using the MATLAB (The MathWorks, Natick, MA) code vitalsens.m, provided by Morris and Doak (2002). We used life-stage simulation analysis (LSA) to incorporate empirical measures of vital rate variation into the assessment of vital rate importance (Wisdom et al. 2000). We used LSA to estimate the relative contribution of adult survival, recruitment, and age of first reproduction to deterministic, or asymptotic, population growth rates.

Stochastic simulations of vital rates, as conducted with LSA, should simulate the variation of vital rates according to the process, or environmental, variance after excluding the contribution of sampling error to raw estimates of variance (White 2000). We isolated the process variance of adult

survival among years using program Kendall.m in MATLAB v.7.9.0 (Kendall 1998, Morris and Doak 2002). To account for censoring in our survival data, we first estimated the within-year means and variances of adult female survival using nonparametric methods (Greenwood 1926, Pollock et al. 1989), and we then adjusted the input annual sample sizes of animals and survival events to produce equivalent mean and variance estimates using a binomial variance estimator (Morris and Doak 2002). We tested sets of 2,500 possible means and variances with each run of Kendall.m, and we iteratively re-ran the program manually refining the limits on means and variances until we reached a consistent best estimate. To estimate the within-year variance of recruitment, we treated each group of animals observed during an annual survey as the sample unit (Bowden et al. 1984). We then removed the effect of adult survival and age structure from age ratio data by adjusting the numerators and denominators of the calf/cow ratios of each group observed during annual surveys to group-specific estimates of $R_{2\text{-stage}}$ according to equation 7. We then used the variance of ratios estimator (Cochran 1977, Krebs 1989) to estimate the variance of the recruitment term, $R_{2\text{-stage}}$, per year as

$$\text{Var}(R) = \frac{(1-f)}{n_g \bar{n}_{af}^2} \times \frac{(\sum n_{jf}^2) - 2\hat{R}_{2\text{-stage}}(\sum n_{jf} n_{af}) + \hat{R}_{2\text{-stage}}^2(\sum n_{af}^2)}{n_g - 1} \quad (13)$$

where n_{jf} and n_{af} are counts of juveniles and adult females per group, n_g = the number of groups surveyed and $f = n_g/N_g$, or the sampling fraction of the number of groups surveyed divided by the total number of groups in the population. For each annual estimate of f we calculated N_g by dividing a reported population estimate of 150 individuals in the A la Pêche population (ASRD and ACA 2010) by the mean number of animals per group for a given year. For 1 year (2002) when per-group age ratio data were unavailable we estimated within-year variance using the mean value of all other years. We then isolated the process variance of $R_{2\text{-stage}}$ according to White (2000) using program White.m in MATLAB v.7.9.0, as provided by Morris and Doak (2002).

We created beta distributions for adult survival and recruitment with mean and process variance estimates and drew a set of 100,000 stochastic vital rate combinations using program MATLAB (Morris and Doak 2002). We used previously published data (Adams and Dale 1998) to estimate the frequency of age of first reproduction values of 2- (22.5%), 3- (58.3%), 4- (14.8%), 5- (3.0%), and 6-years old (1.5%) for female caribou, after accounting for animals that did not breed before either death or the end of the study. We estimated asymptotic population growth rates (λ_1 ; Morris and Doak 2002) from the set of 100,000 stochastic S_a and $R_{2\text{-stage}}$ values by inserting them into 2-, 3-, 4-, 5-, and 6-stage matrix models, with respective matrix model frequencies according to this distribution in age of first reproduction. For each matrix model, recruitment was set to zero for all age classes except the oldest one, for which we

parameterized recruitment by stochastic values of $R_{2\text{-stage}}$. Our distribution of $R_{2\text{-stage}}$ recruitment values specifically estimated the contribution of breeding-aged adults to annual recruitment assuming an age of first reproduction of 2-years old, but we applied stochastic $R_{2\text{-stage}}$ values to 2 to 6-stage matrices to assess the effect of age of first reproduction given equal distributions of recruitment per breeding-aged adult. This created a data set of population growth rates accounting for empirical estimates of environmental variance in all 3 vital rates. We then used linear regression to assess the coefficient of determination, r^2 , for 3 models predicting simulated population growth rates as a function 3 vital rates (adult survival, recruitment, and a set of indicator variables for the age of first reproduction) to assess the percentage of variability in population growth rates explained by each vital rate (Wisdom et al. 2000).

RESULTS

We documented 19 mortalities of 87 captured individuals and monitored an average of 23 adult female woodland caribou per year (range 18–32) during 1998–2009. The geometric mean of annual survival rates was 0.912 and 11% of the total variance ($\text{Var}[S_a] = 0.00488$) was attributed to process variance ($V_c[S_a] = 0.000526$). Late winter composition surveys included an average of 100 individuals of all sex and age classes, with a geometric mean calf/cow ratio of 0.166 either-sex calves per cow (range 0.068–0.303). Calf/cow ratio data resulted in 3 different geometric mean estimates of recruitment depending on the demographic model used ($R_{RM} = 0.0796$, $R_{2\text{-stage}} = 0.0867$, and $R_{3\text{-stage}} = 0.0898$; Table 1). We attributed 73% of the total variance ($\text{Var}[R_{2\text{-stage}}] = 0.00109$) in recruitment rates to process variance ($V_c[R_{2\text{-stage}}] = 0.000795$). Population growth rates using each method were equivalent (Table 1), with a geometric mean annual growth rate of 0.998 (range 0.862–1.078). The distribution of potential transient growth rates varied according to both vital rates (Fig. 1).

Elasticities of recruitment and adult survival for the 2-stage matrix model were 0.0744 and 0.926, respectively. Coefficients of determination (r^2) from our life-stage simulation analysis revealed that 54.0% of the variation in deterministic growth rates was explained by the adult survival rate, followed by 43.3% explained by the recruitment rate, and 1.7% explained by the age of first reproduction.

DISCUSSION

We demonstrated that age ratios could be used to retrospectively estimate empirical population growth rates using Hatter and Bergerud's (1991) R/M equation and 2- and 3-stage matrix population models when combined with estimates of adult female survival. Age ratios result from the combination of multiple vital rates, including the proportion of yearlings in the population, the survival of adults, and those rates affecting recruitment of juveniles. Concurrent monitoring of adult survival allowed us to remove its effect in age ratio data, and consecutive years of age ratio data allowed us to estimate and remove the effects of age structure. In

Table 1. Estimates of adult female survival (S_a) and March calf/cow ratios (X), the proportion of yearlings ($p[y]$) and subadults ($p[s]$) in the female population, and recruitment rates (R) and transient population growth rates (λ) estimated over a single time step using Hatter and Bergerud's (1991) R/M equation and 2- and 3-stage matrix population models for the A la Pêche woodland caribou population in west-central Alberta, 1998–2009.

Years	S_a	X	$p[y]$	$p[s]$	R_{RM}	$R_{2\text{-stage}}$	$R_{3\text{-stage}}$	λ_{RM}	$\lambda_{2\text{-stage}}$	$\lambda_{3\text{-stage}}$
1998	0.100				0.048					
1999	0.918	0.303	0.048		0.132	0.146		1.057	1.057	1.057
2000	0.870	0.263	0.132	0.041	0.116	0.132	0.138	0.984	0.984	0.984
2001	0.950	0.175	0.116	0.116	0.080	0.094	0.108	1.033	1.033	1.033
2002	0.952	0.247	0.080	0.107	0.110	0.128	0.145	1.070	1.070	1.070
2003	0.861	0.179	0.110	0.071	0.082	0.087	0.094	0.938	0.938	0.938
2004	1.000	0.155	0.082	0.101	0.072	0.085	0.095	1.078	1.078	1.078
2005	0.952	0.068	0.072	0.076	0.033	0.035	0.038	0.985	0.985	0.985
2006	0.836	0.232	0.033	0.070	0.104	0.100	0.108	0.933	0.933	0.933
2007	0.944	0.115	0.104	0.030	0.054	0.060	0.063	0.999	0.999	0.999
2008	0.780	0.211	0.054	0.098	0.095	0.087	0.097	0.862	0.862	0.862
2009	1.000	0.120	0.095	0.049	0.057	0.067	0.070	1.060	1.060	1.060

in these cases, we were able to isolate the portions of age ratios relevant for recruitment alone, and estimate the mean and variance of the recruitment term in matrix models. This method allowed the estimation of process variance of recruitment from age ratio data, for use in stochastic matrix model projections and a life-stage simulation analysis.

Our results supported previous findings that adult female survival has the highest elasticity for population growth in ungulates (Gaillard et al. 1998). Previous research has also shown that annual differences in population growth of ungulates can be better explained by more variable recruitment, or juvenile survival, rates despite their low elasticity (Hatter and Janz 1994, Gaillard et al. 2000, Raithel et al. 2007). In our study, a life-stage simulation analysis suggested that high variation in recruitment caused it to explain a greater percentage of population growth rates (43%) than might be expected from its low elasticity (0.07). However, adult female survival still explained comparatively more of the variation (54%) in annual estimates of λ than that has been shown in other ungulate populations (Gaillard et al. 2000, Raithel et al. 2007). This may suggest an effect of recent disturbances

to caribou demography (e.g., Sorensen et al. 2008) because vital rates that are both highly elastic and variable would not have been sustainable over evolutionary time (Pfister 1998, Johnson et al. 2010). Further analysis across multiple caribou populations may be necessary to fully describe the relationships between human disturbance, vital rate variance, and caribou population growth. Age of first reproduction can vary among species (Cole 1954), populations (Langvatn et al. 1996), cohorts (Langvatn et al. 1996), and individuals within a population (Festa-Bianchet et al. 1995), and has been theoretically described as the key vital rate underlying maximum growth rates achievable by species (Hone et al. 2010). Simulations of caribou population growth accounting for a level of variation in age of first reproduction observed in barren-ground caribou (*R. t. granti*; Adams and Dale 1998) revealed that this vital rate explained a relatively small percentage (1.7%) of the variation in population growth estimates, similar to results from other woodland caribou population simulations (Wittmer et al. 2010).

Asymptotic projections of vital rates can be used to estimate long-term deterministic growth rates given a set of vital rates,

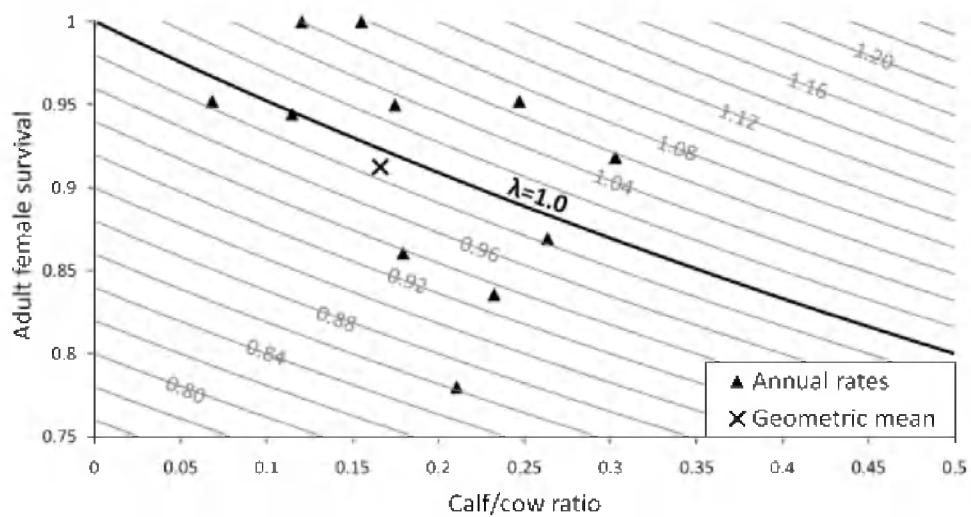


Figure 1. Contour plot depicting the range of possible transient population growth rates (λ) and empirical annual estimates for the A la Pêche woodland caribou population according to the paired values of adult female survival and late winter calf/cow ratios as estimated equivalently by both Hatter and Bergerud's (1991) R/M equation and the projection of 2- and 3-stage population matrix models over a single time step, Alberta, Canada, 1998–2009.

but these methods assume stable age distributions and may be less appropriate for recovery monitoring (Fox and Gurevitch 2000, Yearsley 2004). We have shown that transient population growth rates for a single time step can be estimated consistently without knowledge of the age of first reproduction, but these ad hoc rates are not necessarily representative of long-term trends due to a simplified treatment of age structure and age of first reproduction (Danchin et al. 1995). Future projections of vital rates to estimate long-term trends may be best conducted using stochastic matrix models (Boyce et al. 2006). Specifically, projections should simulate the variation of vital rates according to empirical estimates of their means and environmental variances, and be parameterized to account for population age structure and age-specific vital rate variation (Gaillard et al. 1994, Ezard et al. 2010). Stochastic population projections should also address the potential for within- and among-year correlation of vital rates, which can affect realized growth rates (Coulson et al. 2005). Our equations are based on 2- and 3-stage population models, and incorporation of age-specific vital rates into age-based matrix models offers an alternative when data are available (Raithel et al. 2007). We recommend our methods for retrospective interpretation of monitoring data, but encourage the use of stochastic, age-structured models for predicting future trends for caribou (e.g., Walsh et al. 1995, Wittmer et al. 2010, DeCesare et al. 2011) and other species.

Ungulate population monitoring designs exist on a continuum from trend monitoring with composition counts alone (McCullough 1994) to individual-based studies of sex- and age-specific vital rates (Coulson et al. 2001, Nussey et al. 2009). Our methods reduce ungulate population dynamics to 2 key parameters and reflect a trade-off between what is commonly measurable given the costs and extent of monitoring ungulate populations and what is necessary for baseline estimates of population trend (Bowden et al. 2000). Specifically in the case of woodland caribou, recovery planning faces the challenge of monitoring a threatened subspecies that occurs in >164 populations across 9 jurisdictions (Thomas and Gray 2002), and our methods reflect those recently adopted for broad-scale monitoring of population trends in Alberta (Alberta Woodland Caribou Recovery Team 2005). We reiterate Hatter and Bergerud's (1991) caution that the reliability of trend estimates using our methods depends strongly on the precision of input survival and recruitment vital rate estimates. For example, the precision of adult female survival estimates incorporated into these models is dependent on both the sample size of radio-collared individuals and the process mean of the adult survival vital rate (White and Bartmann 1998). We recommend incorporation of estimates of precision about vital rates into our equations by estimating growth using both vital rate means and confidence limits or using Monte Carlo simulation of vital rates and growth estimates (Patterson et al. 2002).

When collected in tandem with adult female survival rates, age ratio data may provide a suitable alternative for managers interested in documenting recruitment and growth rates.

However, further study of the component vital rates of recruitment (pregnancy, litter size, and fetal and juvenile survival) may be necessary to understand mechanistic relationships between factors such as density dependence, climate, predation, and net recruitment rates. The majority of variation in age ratios for primiparous species such as elk or woodland caribou is often attributed to juvenile survival (Harris et al. 2008) given fixed litter sizes and relatively invariable pregnancy rates (Wittmer et al. 2005, Raithel et al. 2007). Studies of juvenile woodland caribou survival using radio-collared calves are rare (Gustine et al. 2006), yet such studies would be beneficial for conservation by assessing cause-specific juvenile mortality and the link between recruitment and anthropogenic disturbance. For multiparous ungulates, age ratios contain added variation in litter size, which further complicates the interpretation of age ratio-based recruitment rates with specific reference to component vital rates.

Age ratio data can suffer from other potential sources of error, such as misclassification of female juvenile and adult age classes (Smith and McDonald 2002) as well as the potential misidentification of sex during adult female counts. This latter problem may be especially relevant for caribou, given the capacity of both females and young males to carry antlers into late winter. Although female caribou and reindeer typically carry antlers until parturition (Esmark 1971), antlerless females can also be common, particularly within woodland caribou populations and those in poor condition (Reimers 1993). Consistent errors in identifying the sex of adults may lead to biases in recruitment estimates either by the inclusion of males in the female count, which would bias estimates of recruitment low, or the exclusion of antlerless females from the female count, which would bias estimates of recruitment high.

Monitoring vital rates allows managers to estimate trends in population growth as well as study mechanistic relationships between environmental factors and specific components of population demography not possible with estimates of abundance alone (Todd and Rothermel 2006). However, estimates of actual abundances may be necessary to compare risk among populations (e.g., Wittmer et al. 2010), assess recovery goals (Gerber and Hatch 2002), and to validate trends measured with vital rates alone (McCullough 1994). For woodland caribou, traditional aerial survey methods can be used successfully when counting caribou in open alpine or shrubland habitats (Seip 1990, Mahoney et al. 1998, Wittmer et al. 2005). However, the application of such methods to monitor caribou in dense boreal forest habitats suffers due to low sightability and grouping behavior (Stuart-Smith et al. 1997). Hierarchical, 2-tier approaches may provide an effective, but expensive alternative (Courtois et al. 2003). Genetic monitoring may provide another means of estimating woodland caribou population abundance (Hettinga 2010), though the feasibility of applying genetic techniques to monitor caribou populations over provincial or federal scales is uncertain. A quantitative assessment of the costs and power of monitoring strategies (sensu Bowden et al. 2000) for woodland caribou including all forms of abundance and vital rate

estimation would benefit recovery planning for this and other endangered species.

In addition to methodological implications of our results, we also portray a stable trend for the A la Pêche population of woodland caribou over the past decade. Woodland caribou are federally classified as threatened in Canada as a component of woodland caribou occurring within the Southern Mountain National Ecological Area (Committee on the Status of Endangered Wildlife in Canada 2002). As most woodland caribou populations are in decline in Alberta (Schneider et al. 2010), conservation of the A la Pêche population may be particularly important for the species' persistence at the provincial or even national scale. A recovery strategy for woodland caribou should include collection of survival and recruitment data similar to those used in our analyses as important components of population monitoring.

MANAGEMENT IMPLICATIONS

The value of age ratios for population monitoring has been both questioned (Caughley 1974, McCullough 1994) and supported (Harris et al. 2008) in previous research. We show how concurrent monitoring of adult female survival and age ratios allows both retrospective estimation of empirical population growth rates and the decomposition of recruitment-specific vital rates. We also use the A la Pêche woodland caribou population as an example population for which adult survival and recruitment parameters have contributed nearly equally to population growth rates over the past decade. White and Bartmann (1998) recommended that monitoring schemes for ungulates include both fawn survival and adult survival data. Similarly, we recommend the concurrent monitoring of adult female survival to complement age ratio data when managing caribou and other ungulates. This recommendation is partially due to the potential role of both vital rates in driving ungulate population growth rates, and additionally due to the important ability to isolate relevant recruitment terms from age ratios for stochastic modeling of future dynamics.

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