



REVISITING THE RECRUITMENT-MORTALITY EQUATION TO ASSESS MOOSE GROWTH RATES

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ABSTRACT: Hatter and Bergerud (1991) developed a recruitment-mortality (R-M) equation to estimate the annual finite rate of change (λ) in a moose (*Alces alces*) population from a single estimate of calf recruitment and adult mortality. I present and assess an alternative formulation of the R-M equation and compare it with the original. A modification to the R-M equations is provided to accommodate early to mid-winter composition surveys where recruitment is measured when calves are less than 1 year-of-age. An example with the modified R-M equation illustrates estimation of λ for the female component of two moose populations under recent study in British Columbia, Canada. Due to potential biases with estimating recruitment and mortality rates, the calculation of λ with the R-M equation should be verified with periodic density surveys whenever possible. The R-M equation is most useful for estimating λ when moose density surveys are not feasible or an estimate of the adult survival rate is available.

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Key words: *Alces alces*, finite rate of change, mortality rate, population growth rate, recruitment-mortality equation, recruitment rate, survival rate

Hatter and Bergerud (1991) developed a recruitment-mortality (R-M) equation to estimate the finite rate of change or growth rate (λ) of an ungulate population from estimates of juvenile recruitment (R) and adult mortality (M) rates where $\lambda = (1-M)/(1-R)$. This equation has been used commonly with populations of moose (*Alces alces*) (e.g., Gasaway et al. 1992, Boertje et al. 1996, Kunkel and Pletscher 1999, Hayes et al. 2000, Kuzyk et al. 2019b, Severud et al. 2019), caribou (*Rangifer tarandus*) (e.g., Bergerud and Elliott 1986, Seip and Cichowski 1996, McLoughlin et al. 2003, Hebblewhite et al. 2007, Sorensen et al. 2008, Latham et al. 2011, DeCesare et al. 2012, Hervieux et al. 2013, 2014, Serrouya et al. 2017), elk (*Cervus elaphus*) (e.g., Kunkel and Pletscher 1999, DeVore et al. 2018), black-tailed deer (*Odocoileus columbianus*) (e.g., Hatter and Janz

1994), and white-tailed deer (*Odocoileus virginianus*) (e.g., Kunkel and Pletscher 1999, Patterson et al. 2002). Refinements have been made by several authors to improve its utility as an ungulate population assessment tool (DeCesare et al. 2011, Hervieux et al. 2013).

The primary utility of the R-M equation is that it calculates λ from a single estimate of recruitment provided that the adult mortality rate is known. It is particularly appropriate when there are few other cost-effective alternatives. One drawback of using the R-M equation with moose is that recruitment is commonly measured from composition surveys conducted during early or mid-winter before calves are recruited into the adult population at 1 year-of-age (Hatter and Bergerud 1991). This is because aerial spring surveys are generally impractical due to lack of snow-cover, poor visibility,

and dispersal of moose from winter ranges (Gasaway et al. 1986). The purposes of this paper were to review the original R-M equation (Hatter and Bergerud 1991), compare it with an alternative formulation, identify a modification that accommodates moose composition surveys before calves are 1 year-of-age, and provide an example of its use.

THE R-M EQUATION

The R-M equation enables the calculation of λ from annual recruitment and adult mortality rates. This equation expressed as a difference equation (Serrouya et al. 2017) is:

$$N_{t+1} = N_t + RN_{t+1} - MN_t \tag{1}$$

where R is the proportion of juveniles at the end of their first year of life (i.e., year t_1) and M is the adult (1+ year-old males and females) mortality rate during the year (i.e., from year t_0 to t_1). Rearranging Eq.1 and solving for $\lambda = N_{t+1}/N_t$ yields:

$$\lambda = (1 - M)/(1 - R). \tag{2}$$

As $1-M$ is the adult survival rate, Eq. 2 also equals:

$$\lambda = S/(1 - R) \tag{3}$$

where S is the annual probability of adult survival. Here, I refer to Eq. 3 as the Type 1 R-M equation. If hunting occurs, then S must account for both non-hunting (Mn) and hunting (Mh) mortality rates:

$$S = (1 - Mh) \times (1 - Mn) \tag{4}$$

Alternative formulations of the R-M equation where R is the juvenile:adult ratio and adults refer to both sexes combined (Guthery and Shaw 2013, DeVore et al. 2018) are:

$$N_{t+1} = N_t S(I + R) \tag{5}$$

and

$$\lambda = S(I + R) \tag{6}$$

I refer to Eq. 6 as the Type 2 R-M equation.

The R-M equation has also been used to estimate λ for the female segment of the population as growth rates are largely determined by females (Caughley 1977) and because many studies focus on adult female mortality rates (Hervieux et al. 2013, 2014, Kuzyk et al. 2019a, 2019b). Equations 7–12 apply specifically to females, although they are easily modified for males or both sexes combined (Hatter and Bergerud 1991). Recruitment in the Type 1 model is estimated as:

$$R = \frac{c \times J/F}{c \times J/F + 1} \tag{7}$$

and in the Type 2 model as

$$R = c \times J/F \tag{8}$$

where c is the proportion of recruited juveniles that are female and J/F is the ratio of juveniles/1+ year-old females.

Calf:cow ratios (J/F) for moose are usually measured in early or mid-winter when aerial survey conditions are optimal for determining herd composition and abundance (Gasaway et al. 1986). However, these surveys do not provide an accurate measure of recruitment at 1 year-of-age since calves die at a higher rate than cows during winter (Ballard et al. 1991, Kuzyk et al. 2019b). Failing to account for the differential winter mortality between calves and cows results in a biased estimate of R , which by definition is measured when calves are 1-year-of-age. Calf:cow ratios from these surveys

must be adjusted to account for this differential mortality.

The adjustment of R (R') for the Type 1 model is:

$$R' = \frac{c \times J/F \times Sf_w}{(c \times J/F \times Sj_w + Sj_w)} \tag{9}$$

and the adjustment for the Type 2 model is:

$$R' = c \times J/F \times Sj_w / Sf_w \tag{10}$$

where Sj_w is the winter calf survival rate and Sf_w is the winter cow survival rate. These survival rates must be measured from the end of the winter survey to just before calves become 1 year-of-age, and is typically accomplished through telemetry studies of radio-collared animals (Pollock et al. 1989). The finite rate of change for the Type 1 model is then estimated as:

$$\lambda = Sf(1 - R') \tag{11}$$

and for the Type 2 model as:

$$\lambda = Sf(1 + R') \tag{12}$$

where Sf is the annual cow survival rate. Figure 1 illustrates estimates of change in λ when there is differential overwinter mortality between cows and calves (Sj_w/Sf_w). For example, λ ranged from 0.98 ($Sj_w/Sf_w = 0.50$) to 1.06 ($Sj_w/Sf_w = 1.00$) when assuming $J/F = 0.35$, $c = 0.5$, and $Sf = 0.90$.

The above equations do not account for uncertainty in the parameters used to estimate λ . In order to determine the 95% CI for λ in Eq. 11 or 12, the SE must be measured for J/F , Sf , Sf_w , Sj_w , and c . A number of researchers including Caughley (1977), Gasaway et al. (1986), Skalski et al. (2005), and Pollock et al. (1989) provide methods and examples for making these calculations.

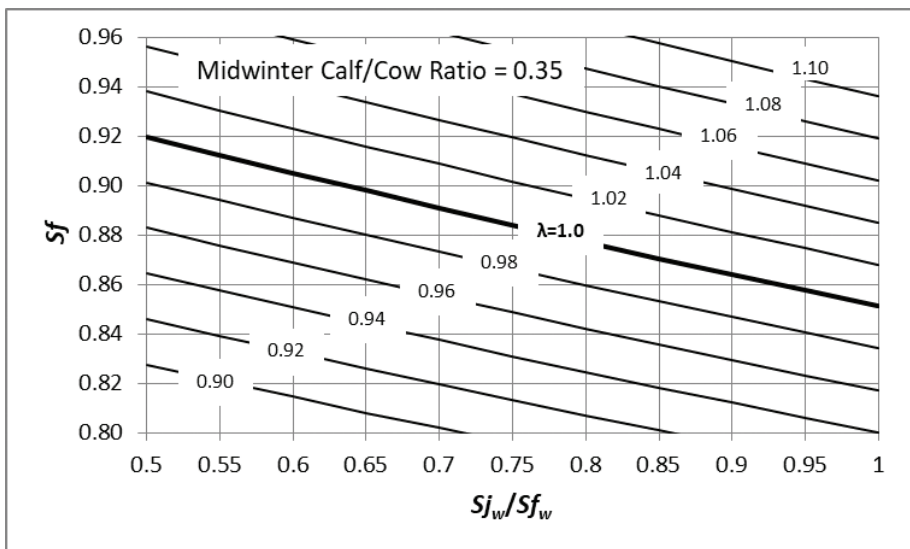


Fig. 1. Contour plot depicting the range of population growth rates (λ) based on plausible ranges in annual cow survival (Sf) and differential winter mortality between calves and cows (Sj_w/Sf_w). The midwinter calf:cow ratio (J/F) was 0.35, and the calf sex ratio was 50:50.

Following Latham et al. (2011) and Hervieux et al. (2013), one method of estimating the 95% CI for λ is to randomly draw from each year’s annual survival and recruitment distributions (i.e., \bar{x} and SE) a large number of times (e.g., 10,000) using Monte Carlo simulation. Survival rates should be drawn from a beta distribution (values range from 0–1) and calf:cow (J/F) ratios from a lognormal distribution (values > 0).

For a quick and simple comparison, the normal approximation may be used to determine if two estimates (est) (e.g., J/F , Sf , Sf_w , Sj_w , or λ) are significantly different using

$$|Z| = \frac{(est_1 - est_2)}{\sqrt{(var(est_1) + var(est_2))}} > 1.96$$

where $var = SE^2$ (Sinclair et al. 2006). If estimates are not significantly different, they may be merged to produce a more precise estimate of λ using the procedure outlined by Sinclair et al. (2006:234).

An example

Factors affecting moose population declines in British Columbia, Canada are currently being investigated with population dynamics studied intensively (Kuzyk et al. 2019a, 2019b). Estimates of J/F , Sf , Sf_w , and Sj_w were available for 3 consecutive years in the Bonaparte study area (2016–17 to 2018–19) and 2 consecutive years in the Prince George South study area (2017–18 to 2018–19) (Table 1), and the proportion of 8-month-old female calves (c) was documented from the sex ratio of radio-collared calves from 2016–17 to 2019–20. Calf sex ratios were not significantly different from 50:50 in either study area (Bonaparte: $\chi^2 = 0.45$, $P = 0.50$, $n = 80$; Prince George South: $\chi^2 = 0.24$, $P = 0.62$, $n = 66$), so c was set equal to 0.5. Differential winter survival (Sj_w/Sf_w) varied from 0.47–0.89 in the Bonaparte study area and from 0.78–0.87 in the Prince George South area.

Growth rates based on unadjusted recruitment rates from the Hatter and

Table 1. Moose population parameters including calf:cow ratio (J/F), annual cow survival rate (Sf), winter cow survival rate (Sf_w), and winter calf survival rate (Sj_w) within the Bonaparte and Prince George South study areas of British Columbia, Canada; data is from Kuzyk et al. (2019). Merged refers to combined estimates for 2017–18 and 2018–19.

a. Bonaparte Study Area

Year	Calf:Cow ratio			Annual cow survival			Winter cow survival			Winter calf survival		
	J/F	SE	n	Sf	SE	n	Sf_w	SE	n	Sj_w	SE	n
2016–17	0.13	0.028	208	0.91	0.057	79	0.96	0.028	52	0.45	0.051	20
2017–18	0.32	0.047	256	0.98	0.022	53	0.96	0.022	52	0.85	0.069	20
2018–19	0.28	0.056	148	0.95	0.026	70	0.95	0.028	63	0.80	0.073	20
Merged	0.30	0.036		0.97	0.017		0.96	0.017		0.83	0.050	

b. Prince George South Study Area

Year	Calf:Cow ratio			Annual cow survival			Winter cow survival			Winter calf survival		
	J/F	SE	n	Sf	SE	n	Sf_w	SE	n	Sj_w	SE	n
2017–18	0.34	0.040	375	0.79	0.049	54	0.90	0.041	40	0.70	0.071	20
2018–19	0.31	0.056	168	0.79	0.052	55	0.85	0.052	47	0.74	0.076	19
Merged	0.33	0.033		0.79	0.036		0.88	0.032		0.72	0.052	

Bergerud (1991) R-M equation were higher than those based on adjusted recruitment rates (Table 2). Estimates of λ based on adjusted recruitment rates were identical between the Type 1 and Type 2 R-M equations. The 95% CI for λ , based on adjusted recruitment rates, ranged from <1.0 to >1.0 for each year in both populations, except for 2017–18 in the Bonaparte study area. In this area estimates of λ were lower in 2016–17 than in 2017–18 ($Z = 2.64$, $P = 0.008$) and also between 2016–17 and 2018–19 ($Z = 1.82$, $P = 0.068$). Growth rates were not different between 2017–18 and 2018–19 ($Z = 1.00$, $P = 0.32$). Merging these years produced a more precise estimate of λ (Table 2). Growth rates were similar in the Prince George South area between 2017–2018 and 2018–19 ($Z = 0.034$, $P = 0.97$); merging these years also produced a more precise estimate of λ . Estimates of growth rates from density surveys in the Bonaparte study area during 2013–18 ($\lambda = 0.97$) were

within the range calculated from recruitment and mortality ($\lambda = 0.93$ – 1.12), and estimates of population growth from density surveys in the Prince George South study area during 2012–17 ($\lambda = 0.91$) were comparable to the R-M equation ($\lambda = 0.90$).

DISCUSSION

The original formulation of the R-M equation developed by Hatter and Bergerud (1991) requires an adjustment to the recruitment rate when calf:cow ratios are measured in early-to-mid winter. This adjustment accounts for differential overwinter survival of calves and adults which may be made using either the Type 1 or Type 2 R-M equations. Failure to account for differential survival results in an overestimate of λ . Users of the R-M equations may prefer the Type 2 model since most moose biologists define calf recruitment as the calf:cow ratio rather than % calves and because calculations are simpler.

Table 2. Moose recruitment (R), adjusted moose recruitment (R'), and population growth rates (λ) with Monte Carlo simulated confidence intervals (95% CI) for the Type 1 and Type 2 R-M equations within the Bonaparte and Prince George South study areas of British Columbia, Canada. Merged refers to combined estimates for 2017–18 and 2018–19.

a. Bonaparte Study Area

Year	R-M equation ¹		Type 1 R-M equation		Type 2 R-M equation		Type 1 & 2
	R (Eq. 7)	λ (Eq. 3)	R' (Eq. 9)	λ (Eq. 11)	R' (Eq. 10)	λ (Eq. 12)	95% CI
2016–17	0.061	0.97	0.030	0.93	0.030	0.93	0.79–1.02
2017–18	0.138	1.13	0.124	1.12	0.142	1.12	1.04–1.18
2018–19	0.123	1.08	0.105	1.06	0.118	1.06	0.98–1.14
Merged	0.132	1.11	0.116	1.09	0.131	1.09	1.04–1.14

¹Estimated using the original R-M equation from Hatter and Bergerud (1991).

b. Prince George South Study Area

Year	R-M equation ¹		Type 1 R-M equation		Type 2 R-M equation		Type 1 & 2
	R (Eq. 7)	λ (Eq. 3)	R' (Eq. 9)	λ (Eq. 11)	R' (Eq. 10)	λ (Eq. 12)	95% CI
2017–18	0.145	0.93	0.117	0.90	0.133	0.90	0.77–1.01
2018–19	0.134	0.91	0.119	0.90	0.135	0.90	0.76–1.02
Merged	0.142	0.92	0.119	0.90	0.135	0.90	0.81–0.98

¹ Estimated using the original R-M equation from Hatter and Bergerud (1991).

There are 4 primary methods currently used to estimate λ for moose populations. The growth rate may be measured from 2 or more population surveys over time (Van Ballenberghe 1983), from calf recruitment and adult mortality rates (Hatter and Bergerud 1991), from survival and fecundity schedules (Van Ballenberghe 1983), or from fitting population models to multiple sources of observed data (Kuzyk et al. 2018). The primary advantage of the R-M model is that it provides an estimate of λ from a single, late winter herd composition survey when the annual adult mortality rate is known. It may also be preferred where moose density surveys are not feasible, such as in densely forested areas or where moose occur at very low density (Severud et al. 2019).

Guthery and Shaw (2013) note that the R-M equation is a tautology and thus inevitably true and does not require empirical verification. However, survey timing and survey bias can affect the accuracy of λ calculations. Serrouya et al. (2016) compared population growth rates for caribou between abundance surveys and the R-M equation and found that the R-M equation overestimated λ compared to survey-based λ . They proposed 3 possible reasons including: 1) measurement of recruitment at 10-months of age rather than as 1 year-old, 2) adult survival estimates that are biased towards more mature animals, and 3) errors in herd composition surveys (e.g., sightability differences between barren females and those with offspring). They found that the R-M equation explained 60% of the variation in survey-based λ and was a better predictor of this parameter compared to other approaches.

Users of the R-M equation should ensure that herd composition surveys are representative of the population and measure recruitment just before calves become 1 year-of-age. Alternatively, the modified R-M equation may be used to account for differential

winter mortality between calves and adults when survival estimates are available. In addition, users need to be careful to ensure that estimates of adult survival from radio-collared animals include a representative sample of their standing age distribution. This may require estimating survival rates over multiple years.

In Alberta, the population trend for boreal caribou was monitored using the R-M equation based on annual surveys of recruitment and an ongoing, intensive radio-telemetry program with adult females (Hervieux et al. 2013). Annual changes in λ were used to calculate realized population change, which were the successive product of λ calculated from the first year of monitoring up to and including the most recent year's λ calculation. Because this approach may compound errors in relative abundance over time (Serrouya et al. 2017), periodic surveys of absolute abundance should be performed to help validate long-term population trends based on the R-M equation.

The R-M equation may provide relatively large confidence intervals for λ . In order to improve the accuracy and precision of λ , it is important to ensure that samples of recruitment and mortality rates are representative and that sample sizes are sufficiently large. DeCesare et al. (2012) employed elasticity and life-stage simulation analysis for a woodland caribou population in Alberta and found that adult female survival and recruitment rates were nearly equivalent drivers of population growth. This suggests that increased sampling to improve precision of λ should be directed towards both population parameters. Alternatively, annual estimates of J/F , S_f , S_{f_w} , and S_{j_w} may be merged over multiple years to improve precision, providing these parameters are not significantly different between years.

Biologists have been tasked with ensuring moose objectives for both conservation

and sustainable use are met. These challenges have recently intensified with broad scale moose declines occurring in parts of North America (Timmermann and Rodgers 2017, Kuzyk et al. 2018). The R-M equation provides a simple and relatively inexpensive method to rapidly assess moose population trends when adult survival rates are available. However, numerous biases may exist in estimating recruitment and mortality rates that can substantially affect estimates of λ (Serrouya et al. 2017, Severud et al. 2019). Thus, it is important to assess the accuracy and precision of both parameters when calculating λ using the R-M equation and to ensure that over-winter differential mortality between cows and calves is incorporated. If the R-M equation is used to monitor trends over multiple years, then estimates of λ should be validated periodically with surveys of absolute abundance.

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