Comparing Population Growth Rates Between Census and Recruitment-Mortality Models

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ABSTRACT In forested ecosystems, estimating the abundance or trend of most wildlife populations is difficult. Therefore, vital rates are often used to model population change, but validating such models is important. Using data from woodland caribou (*Rangifer tarandus*), we compared estimates of population change (λ) based on vital rate models to λ based on aerial censuses. We modeled λ using Hatter and Bergerud's (1991) recruitment-mortality (R-M) equation (λ = survival/[1 − recruitment]). We estimated survival and recruitment from a sample of 317 radio-collared caribou from 9 subpopulations in British Columbia, Canada. In this ecosystem, woodland caribou have high sightability (>85%) in winter and thus are easy to census compared to most forest wildlife. We found that the R-M equation overestimated λ compared to census-based λ across most of the observed range of data (e.g., if R-M estimated λ of 1.1, census-based λ was 0.99, and if R-M was 0.90, census-based λ was 0.89). We then assessed whether recruitment, survival, a linear model of both parameters, or the R-M equation best predicted census-based λ. The R-M equation explained 60% of the variation in census-based λ, more than double the next-best approach (i.e., the simple linear model), even though identical parameters were included. Further, we simulated variability due to the unknown sex (M:F) ratio in the sample, and found that the R-M equation remained the best predictor of census-based λ. Although the R-M equation was the most precise and accurate approach, our results reaffirm that it is important to periodically validate trend estimates based on vital rate models with estimates of absolute abundance, particularly for species of management concern. © 2016 The Wildlife Society.

KEY WORDS age ratios, census, population trend, *Rangifer tarandus caribou*, recruitment, survival, validation, woodland caribou.

Estimating the abundance, distribution, and trend of wild populations is fundamental to many aspects of ecology (Krebs 2009). Such estimates are needed to identify limiting factors, set quotas for harvest management, and in the case of endangered species, to gauge the success of recovery actions (Caughley 1994). In ecosystems where the sightability of animals is poor (e.g., forest and marine environments) obtaining reliable population estimates can be a major challenge. Consequently, considerable effort has been devoted to developing and improving methods for estimating abundance (Boulanger et al. 2004, Efford 2011), trend

(Hatter and Bergerud 1991, DeCesare et al. 2012), and distribution (MacKenzie et al. 2002) of wild animals.

Caribou (*Rangifer tarandus*) are declining in many portions of their pan-Arctic distribution (Vors and Boyce 2009, Festa-Bianchet et al. 2011), and as a result are a species of conservation concern. Some populations and subspecies are relatively easy to count because they spend time in landscapes where they can be easily seen (e.g., on tundra or above treeline in the mountains; Wittmer et al. 2005*a*), but others live in forests where sightability is low and variable (DeMars and Boutin 2013). The boreal ecotype of woodland caribou (*R. t. caribou*) are notoriously difficult to count because they occur at low densities and live in forests year-round (Courtois et al. 2003). Many methods have attempted to estimate abundance or population trend of boreal caribou, including 2-stage aerial sampling to sequentially estimate occupancy and abundance (Courtois et al. 2003), mark-resight estimates

using collared animals to adjust for detectability in forested habitats (Schaefer et al. 1999), and DNA-based mark-recapture (Wasser et al. 2011, Hettinga et al. 2012). However, methods to estimate abundance are typically more costly and logistically challenging than those used to monitor population trend. Consequently, some jurisdictions have focused exclusively on monitoring population trend. For example, using the recruitment-mortality (R-M) equation (Hatter and Bergerud 1991), caribou trend has been monitored in the province of Alberta, Canada for nearly 2 decades (McLoughlin et al. 2003, Hervieux et al. 2013). This equation estimates the finite rate of change (λ) by the ratio of the recruitment rate to the adult mortality rate. The R-M equation is an algebraic rearrangement of the standard formula for λ ($\lambda = N_1/N_0$), where $N_1 = N_0 + R \, N_1 - M \, N_0$, R is the fraction of recruits at time t_1, and M is the adult mortality rate from time t_0, to t_1. The equation is similar to the life table and Leslie matrix approaches commonly used to calculate rates of change (Caughley 1977, Eberhardt et al. 1994, Hovey and McLellan 1996) for vertebrates but with the substantial advantage of not requiring age-specific fecundity and survival as inputs. DeCesare et al. (2012) compared estimates of λ for boreal caribou derived from the R-M equation to λ estimates from matrix models, and reported them to be nearly equivalent. However, as highlighted by Hatter and Bergerud (1991) an important shortfall of basing a management program solely on population trend is that in the absence of truthing provided by occasional abundance estimates (i.e., census or survey data), any error or bias in trend-based estimates compounds. Furthermore, conservation and recovery actions are often prioritized based on risk of extinction, and absolute abundance is helpful for such decisions (Schneider et al. 2010, Wittmer et al. 2010).

Potential biases that could affect outcomes from the R-M equation are those related to estimating its 2 parameters: survival and recruitment. Because this technique is used routinely for monitoring boreal woodland caribou populations, DeCesare et al. (2016) tested for biases associated with telemetry-based survival estimation including non-random right censoring, interval censoring, and poor detection probabilities. They did not detect significant biases for 5 caribou populations in Alberta with sufficient data to examine these potential problems (DeCesare et al. 2016). Similarly, Wasser et al. (2011) postulated that a consistent underestimate of recruitment from aerial surveys would overestimate the rate of decline using the R-M equation, particularly because this bias would be multiplicative over time when estimating multi-year realized population declines from annual estimates of λ. Subsequently, Hervieux et al. (2013) and DeCesare et al. (2016) disputed that such biases existed for Alberta's monitoring program, and reiterated that empirical, widespread caribou declines were demonstrated.

In many cases, even the cost of collaring and monitoring adult survival has been prohibitive, so agencies have relied on a more basic metric, the ratio of recruits to adult females. This metric can be readily obtained from aerial or hunter surveys. However,

the ability of this simple metric to predict population change has been mixed and can be misleading (Caughley 1974, McCullough 1994). For example, if the number of recruits and adult females decline at the same rate because of a common mortality agent (Caughley 1974, Wittmer 2004), the ratio would be constant but the population decline would be missed. Nonetheless, some studies have reported that age ratios explained a significant component of population change (Harris et al. 2008), especially if survival rates for juveniles versus adults diverge over time.

Although there have been many rigorous approaches to address biases and validate trend monitoring for cryptic species (Harris et al. 2008; DeCesare et al. 2012, 2016; Hervieux et al. 2013), it has been difficult to corroborate these findings independently for woodland caribou because actual population estimates have been challenging to obtain. Few mark-recapture studies have been successfully applied to boreal caribou (Hettinga et al. 2012), and sightability trials have had limited success (Fuller and Keith 1981, Stuart-Smith et al. 1997, DeMars and Boutin 2013). However, 2 woodland caribou ecotypes that live in mountainous areas adjacent to boreal caribou have been censused repeatedly since the mid-1990s (Fig. 1), providing a basis for empirical estimates of λ (λ_{census}; Wittmer et al. 2005a). These ecotypes include a deep-snow ecotype (often referred to as mountain caribou; Heard and Vagt 1998), and a shallow-snow ecotype (referred to as Northern caribou; Stuart-Smith et al. 1997, Heard and Vagt 1998, Serrouya et al. 2012). Sightability of the deep-snow ecotype usually exceeds 90% when the snowpack in the subalpine is >300 cm (Flaa and McLellan 1999, Wittmer et al. 2005a; Appendix A, available online in Supporting Information) because this depth provides the lift needed for animals to access their late-winter forage (i.e., arboreal lichen that grows in the canopy of conifers; Edwards et al. 1960, Serrouya et al. 2007). In late March during these deep-snow winters, almost all animals are in open, subalpine forests where their tracks are obvious and can be followed from a helicopter until the animals are seen and counted (Wittmer et al. 2005a). Populations from both ecotypes have been monitored with radio-collars since at least 1992 to identify causes of mortality, survival rates, and to develop sightability values for late-winter population estimates. Consequently, we were able to compare estimates of the finite rate of change based on aerial censuses (λ_{census}) and predicted by the R-M equation (λ_{RM}). If estimates derived from these 2 approaches deviated from a 1:1 relationship, our objective would be to elucidate the causes for such an over- or under-estimation produced by the R-M equation based on the predicted directions of the various biases discussed above. If λ_{RM} was a reasonable predictor of λ_{census} for the mountain caribou ecotype, then our confidence in λ_{RM} that is necessarily used with the boreal ecotype (because there is no reliable census method) would be increased.

Our second objective was to determine how well recruitment alone predicted λ_{census}. The relationship between recruitment and population growth likely varies among systems. Adult female survival generally has more
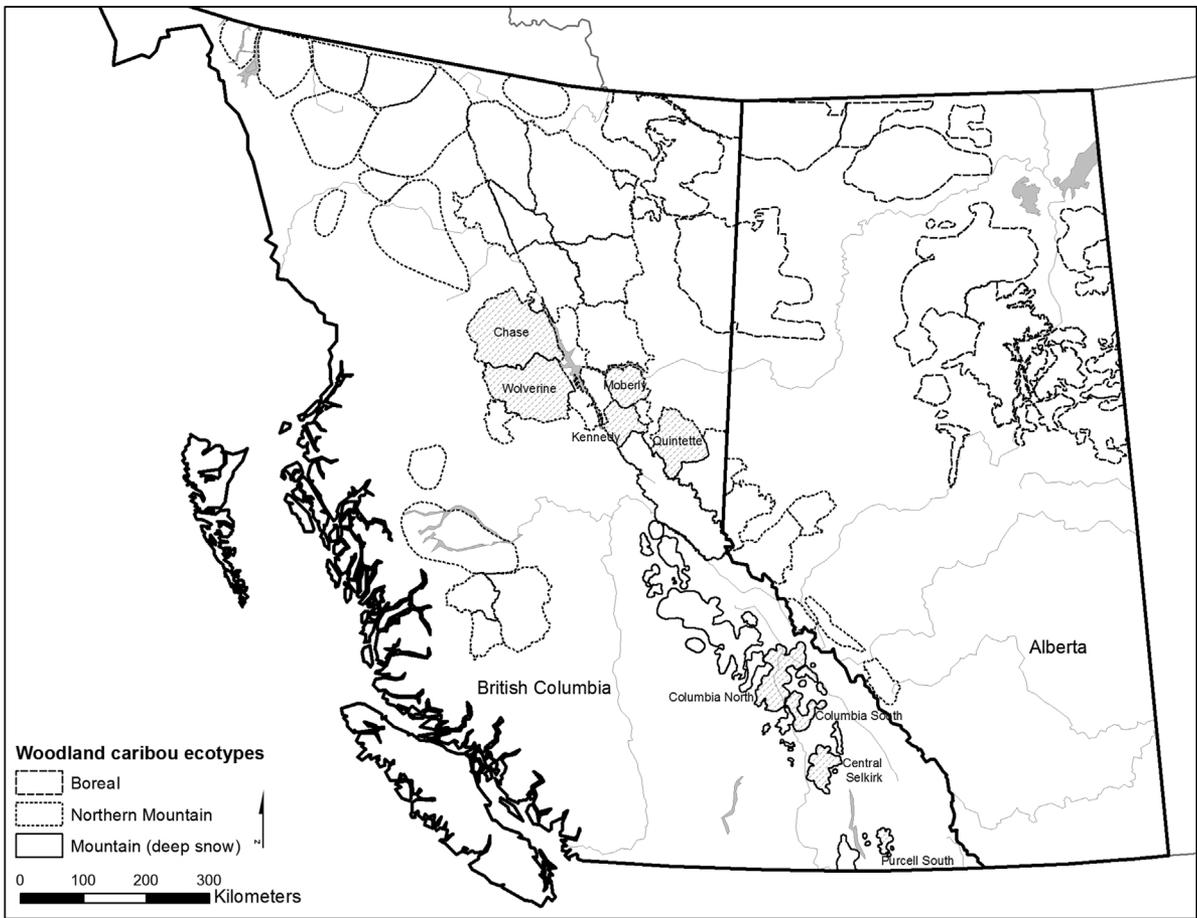
Figure 1. The distribution of 3 ecotypes of woodland caribou in Alberta and British Columbia, Canada. Subpopulations analyzed in this study are named and shown with diagonal shading.

influence on λ than does recruitment for k-selected organisms (Hovey and McLellan 1996, Gaillard et al. 1998). Therefore, when recruitment is correlated with survival, it is likely a good predictor of λ, but when recruitment is not correlated with survival, it will have less influence on population change (i.e., is less elastic). Recruitment and survival are more likely to be correlated when predation is the dominant source of mortality (Bergerud 1988, Wittmer 2004) and less likely to be correlated when mortality factors (e.g., spring weather) affect recruitment but not adult survival (Post and Stenseth 1998, Hegel et al. 2010). Such empirical tests are important, because many jurisdictions routinely collect recruitment or age ratio data and plan management based on these metrics in the absence of survival rates, but the reliability of age-based indices is still debated and may be context-dependent (Caughley 1974, Harris et al. 2008, DeCesare et al. 2012).

STUDY AREA

The study occurred in mountainous areas of British Columbia, Canada. Major mountain ranges included the Columbia, Rocky, and Cariboo mountains. This area encompasses 2 ecological zones: deep snow areas of the Columbia and Cariboo Mountains (200 cm annual precipitation), and the Rocky Mountains, which are characterized by lower snow depths (65 cm annual precipitation). Elevations in the study area range from 450 m in valley bottoms to 3,519 m. Temperatures in the deep-snow zone range from 25.1°C in July to −6.1°C in January (City of Revelstoke, BC), whereas in the Rocky Mountains portion, temperatures are colder (22.2°C to −12.9°C; Mackenzie, BC). These 2 montane zones provide habitat for 2 ecotypes of caribou (mountain and northern ecotypes), adjacent and to the west of boreal caribou ranges (Serrouya et al. 2012). Both ecotypes of woodland caribou spend all or most of the year in the mountains.

In the deep snow zone, dominant tree species at low elevation include western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*), whereas at high elevations Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) dominate, although mountain hemlock (*Tsuga mertensiana*) is common in some stands (Meidinger and Pojar 1991). Interspersed at all elevations are <30-year-old regenerating clear-cut forests. In the shallow snow zone, dominant tree species at low elevation include lodgepole pine (*Pinus contorta*) and black spruce (*Picea mariana*), whereas Engelmann spruce and subalpine fir are

most common at high elevations (Meidinger and Pojar 1991).

Common predators of caribou in British Columbia include grizzly bears (*Ursus arctos*), American black bears (*U. americanus*), wolves (*Canis lupus*), and cougars (*Puma concolor*; Kinley and Apps 2001). Moose (*Alces alces*), white-tail deer (*Odocoileus virginianus*), and mule deer (*O. hemionus*) are common, but caribou occur at low densities (Wittmer et al. 2005*b*).

METHODS

Estimating Survival

We used data from 9 caribou subpopulations, 4 from the mountain and 5 from the northern ecotype (Fig. 1). Based on extensive telemetry studies (Wittmer et al. 2005*a*), including those that monitored juveniles (van Oort et al. 2011) and corroborated with population genetics (Serrouya et al. 2012), movement among these subpopulations is very rare. To compare estimates of λ_{RM} and λ_{census}, the period between censuses had to coincide with the period during which caribou survival was monitored using radio-collars. For some subpopulations and inter-census periods, there were insufficient radio-collared caribou to estimate survival (i.e., <5 collared animals/yr), so we used the next census date as the boundary of the monitoring period to include more collared caribou-years. To adjust for differing sample sizes of collared individuals between subpopulations and periods, we weighted all analyses by the collared caribou sample size (see below). Most animals were radio-collared in March and fitted with lightweight very high frequency (VHF) collars (LMRT-4; Lotek Wireless, Newmarket, Ontario, Canada) or global positioning system (GPS) collars (Lotek Wireless and Televilt, Lindesburg, Sweden). All animal captures had to be approved and permitted by the Provincial wildlife veterinarian who reviewed protocols for safe and ethical animal care. Monitoring of radio-collared caribou survival occurred every 2–4 weeks. Although some authors have argued that monitoring intervals >1 month can bias survival estimates (Murray 2006), knowing the exact date of death is less relevant when cause-specific mortality is not being estimated. In this case the parameter of interest is the proportion of animals surviving to the next reproductive cycle (i.e., caribou have an annual birth-pulse life history, and all animals are collared in Mar prior to the parturition cycle), so a less frequent monitoring schedule was adequate. As a case in point, demographic analyses of caribou survival in Alberta used similar or much less frequent monitoring intensity (median of 52 days; DeCesare et al. 2012, Hervieux et al. 2013), which produced a negligible effect on survival estimates (DeCesare et al. 2012).

Within each subpopulation and monitoring period, we calculated daily survival as 1 − (no. deaths)/(days monitored) for 2 risk periods: winter (i.e., Nov–Apr) and summer (May–Oct). To produce seasonal survival rates for winter and summer, we exponentiated daily survival rates by 181.25 for winter and 184 for summer (i.e., no. days in each period). We then calculated annual survival as the product of the 2

seasonal risk periods (Heisey and Fuller 1985). Several authors argue for alternative approaches such as cumulative incidence functions (Heisey and Patterson 2006, Murray 2006), but because we were not using any covariates to explain variation in survival, the Heisey–Fuller method was appropriate and is still commonly used in survivorship studies (Sparkman et al. 2011).

Lambda Calculations

We calculated annual population growth rates from aerial censuses as $\lambda = (N_t/N_0)^{(1/t)}$, where N was the population estimate, and t was the interval (i.e., no. years) between estimates (Caughley 1977). We corrected survey estimates for sightability using program NOREMARK (White 1996) by correcting for missed animals (Wittmer et al. 2005*a*) unless snow conditions allowed for high sightability (i.e., >300 cm snow depth equating to >90% sightability of marked animals; Supplementary Appendix A), in which case we adjusted numbers positively by 10% as the Provincial standard (Supplementary Appendix A). We did not use census data if there were an insufficient number of radio-collars (<10) to provide a mark-resight estimate when snow depth was <300 cm (Supplementary Appendix A). Additional census details are provided in Wittmer et al. (2005*a*).

We calculated λ from the R-M equation as $\lambda = S/(1 - R)$, where S is the annual survival rate and R is the recruitment rate. DeCesare et al. (2012) presented an adjustment to this equation to account for the proportion of females in the population by estimating the ratio of juvenile females to the number of juvenile + adult females as a component of recruitment. This adjustment was appropriate because λ was female-based and the population size was not available for boreal caribou, so they had to fly and locate groups of collared females and count adults and juveniles to estimate recruitment. However, we assumed this adjustment was not needed in our case because we estimated calves as a percent of the total population surveyed in March, which was our definition of recruitment; however, we performed simulations to assess the importance of this assumption in our system (below). This definition of recruitment matched the original formulation of the R-M equation, where R was the proportion of the population that was calves (Hatter and Bergerud 1991). If multiple recruitment estimates existed for the monitoring period (which occurred if the monitoring period exceeded 1 year), we re-sampled from the period's recruitment values to calculate λ_{RM} across 5,000 Monte-Carlo simulations, and using the percentile method, report the mean and 95% confidence intervals of these values.

We grouped males and females for survival estimation, as per Hatter and Bergerud's (1991) Example 1 with moose in Alberta. Furthermore, we included both sexes in survival estimation because caribou population censuses included both sexes, and the ratio of adult males to females was not known because females and young males can have similar antler size and shape. Flying close enough to observe the vulva patch on females was thought to be excessively invasive for endangered animals and could cause them to move into risky avalanche terrain (Wittmer et al. 2005*a*). One exception

to the unknown sex ratio was for the subpopulation in Kennedy Siding, where intensive camera trapping on a concentrated winter range in 2014 and 2015 resulted in an estimate of 69 males/100 females (D. C. Heard, Tithonus Wildlife Research, unpublished data).

The R-M approach assumes the radio-collared adults are a representative sample of the population, including both sexes. Although we did not target only females when collaring animals, we wanted to determine the potential influence of various adult sex ratios on our estimates of λ_{RM}. We therefore conducted 5,000 Monte Carlo simulations, drawing from a uniform distribution of sex ratios ranging from 0.4 to 0.7 males/female, which spanned the range observed in wild, unhunted caribou populations in adjacent areas in Alberta (D. Hervieux, Government of Alberta, unpublished data). For each Monte Carlo simulation, we used the sex ratio generated to calculate the percentage of adult females expected in the total population and the juvenile:adult female ratio (X). We then calculated the per-female recruitment rate (R_{RM}) as ($[X/2]/[1+\{X/2\}]$) for all the estimates for that subpopulation and period (DeCesare et al. 2012). We then randomly sampled from all the R_{RM} estimates generated for that period (i.e., all estimated R_{RM} within a Monte Carlo simulation had the same adult sex ratio) and calculated the R-M estimate of λ using the DeCesare et al. (2012) females-only adjustment, $S/(1-R_{RM})$. We also restricted survival estimates (S) to only adult females. We subsequently generated mean and 95% confidence intervals for λ_{RM} with varying adult sex ratios from the percentile values of the resulting distribution for comparison with unadjusted R-M estimates based on the original formulation by Hatter and Bergerud (1991).

If the R-M equation is an accurate prediction of λ_{census}, the slope of λ_{census} on λ_{RM} should be 1 with an intercept of 0. Deviations from those expected outcomes are measures of over- or under-estimation by the R-M equation. We used a linear regression weighted by monitoring effort (see below) to evaluate the relationship between the 2 λs. We converted λ to the instantaneous rate of change (r) to avoid Jensen's inequality (i.e., variance inflated by non-linear relationships), with r calculated as the natural log of λ. We also transformed recruitment and survival rates using the logit link (ln ($p/[1-p]$)), where p is a recruitment or survival parameter. We indexed monitoring effort by the number of radio days (no. caribou × no. days they were monitored) divided by the product of the population size and interval length (yr) between population estimates (i.e., $\bar{x}$ radio-days/individual/yr). We calculated the population size as the mean value of the censused estimates at the endpoints of the monitoring period, and summed the radio-days across all caribou during the monitoring period. This monitoring index accounts for the intensity of monitoring (i.e., radio-days) relative to the population size, and the length of the monitoring period. To report magnitude and effect size, we back-transformed all values to λ, survival, or recruitment rates to allow for standard inferences.

We considered but did not use mixed-effects models to account for repeated measures across subpopulations because a parallel analysis using the same weighting and variables produced standard errors that were only marginally different (i.e., $SE = 0.118$ for the mixed effects vs. 0.125 for the standard regression; Appendix B, available online in Supporting Information), and variance for the random effect was low (i.e., 0.003; Supplementary Appendix B) suggesting that repeated measures within subpopulations did

Table 1. Comparison between population change (λ) from census (λ_{census}) and λ from the recruitment-mortality (λ_{RM}) equation, for caribou subpopulations in British Columbia, Canada, 1994–2013. Two formulations of λ_{RM} are shown: 1 based on the original example by Hatter and Bergerud (1991), and the second based on the DeCesare adjustment for females only, with male:female ratios that we simulated to determine the sensitivity of this unknown parameter on λ_{RM}. Also shown are population parameters for each monitoring period (S = adult survival) and sample size of collared caribou (n).

Subpopulation	Monitoring period	S	Monitoring-days	Deaths	n	Pop size[a]	λ_{RM}	95% CI	λ_{RM}, M:F[b]	95% CI	λ_{census}
Kennedy	2002–2011	0.855	32,555	14	42	44	0.964	0.885–1.068	0.939	0.875–1.030	0.895
Kennedy	2011–2012	1.000	1,302	0	8	41	1.171	1.171–1.171	1.132	1.120–1.145	0.932
Moberly	1997–2011	0.778	13,065	9	19	35	0.913	0.824–1.027	0.882	0.811–0.982	0.886
Moberly	2011–2012	0.574	1,315	2	7	25	0.607	0.607–0.607	0.591	0.585–0.596	0.714
Quintette	2008–2013	0.913	19,985	5	43	100	0.930	0.866–1.021	0.901	0.848–0.983	0.896
Columbia South	1994–1996	0.916	8,253	2	12	103	1.045	1.045–1.046	1.016	1.007–1.026	0.938
Columbia South	1996–2002	0.811	12,153	7	13	34	0.918	0.811–0.979	0.886	0.802–0.938	0.831
Columbia South	2002–2009	0.764	6,770	5	12	14	0.884	0.779–0.941	0.860	0.779–0.912	0.881
Columbia North	1994–1996	0.807	8,564	5	18	167	1.000	0.998–1.001	0.857	0.829–0.909	0.900
Columbia North	1996–2002	0.785	24,040	16	40	145	0.905	0.883–0.923	0.879	0.858–0.900	0.977
Columbia North	2002–2004	0.783	7,436	5	17	129	0.892	0.871–0.910	0.874	0.853–0.896	0.943
Columbia North	2004–2006	0.872	7,966	3	14	138	1.002	0.978–1.023	0.956	0.933–0.980	1.034
Columbia North	2006–2008	0.857	4,717	2	10	166	0.979	0.955–0.998	0.924	0.901–0.946	1.097
Purcell South	1994–1996	0.779	5,841	4	12	38	0.823	0.808–0.842	0.725	0.714–0.741	0.839
Purcell South	1996–2002	0.754	7,730	6	19	14	0.845	0.772–0.913	0.779	0.726–0.836	0.847
Central Selkirk	1996–1999	0.835	18,191	9	29	155	0.916	0.905–0.930	0.892	0.880–0.910	0.977
Chase	2007–2009	0.698	11,157	11	49	399	1.053	1.005–1.101	0.917	0.898–0.953	0.962
Wolverine	2007–2010	0.882	14,526	5	31	253	0.987	0.963–1.008	0.981	0.954–1.006	0.843

[a] Population size at the end of the monitoring period.
[b] The survival rate (S; adult F), monitoring days, deaths, and sample size (n) corresponding to the estimates of λ_{RM} presented in this table that included the M:F simulations, are shown in Appendix C, available online in Supporting Information.

not inflate precision as expected if pseudo-replication was a problem. Subsequently, we chose standard regression because it provides the usual R^2 value that is easy to interpret.

Many caribou subpopulations of all ecotypes are managed in the absence of survival data, with only annual recruitment surveys available, so we also tested the efficacy of recruitment rates alone for predicting λ_{census}. We again used a Monte Carlo approach by randomly selecting an observed recruitment value for each subpopulation within each monitoring period, using 5,000 iterations. Using linear models weighted by monitoring effort as described above, we then compared these 4 approaches to predicting λ_{census}: recruitment, survival, recruitment + survival, and the R-M equation. We compared the effectiveness of these approaches based on the amount of variance explained (R^2) and parsimony (i.e., corrected Akaike's Information Criterion [AIC_c]).

RESULTS

We radio-collared 317 caribou (286 F, 31 M) and monitored them for 563 caribou-years to estimate survival rates. Some individuals were monitored across sampling periods (Table 1). Estimated annual adult survival rates ranged from 0.57 to 1.0 across subpopulations and study periods (Table 1), and annual recruitment ranged from 0 to 0.24. Adult survival was more variable than recruitment ($CV = 53.9$ vs. 34.4, respectively, based on logit transformed values).

The R-M equation was positively correlated with, and predicted 60% of the variation in λ_{census} (Table 2). By back-transforming dependent and independent variables, we determined that the R-M equation under- or over-estimated λ_{census} (Fig. 2a), depending on the range of data (i.e., λ_{RM} below or above 0.88). This pattern was caused by the positive y-intercept and slope that was significantly <1 (Table 2; Fig. 2a). For λ_{RM} values of 1.1, 1.0, 0.90, 0.88, and 0.80, corresponding λ_{census} would be 0.99, 0.94, 0.89, 0.88, and 0.84. Because 1 datum had large leverage (Fig. 2a), we also bootstrapped the weighted regression ($n = 5,000$) and found that the relationship was robust to the range of data (median slope = 0.497, 95% CIs = 0.191–0.723). The median bootstrapped slope of 0.497 was similar to the deterministic slope of 0.505 (Table 2). No obvious pattern emerged from the

plot of residuals versus fitted values (Supplementary Appendix B).

The simulated sex ratio of adults in the population had a slight effect on λ_{RM}, but even including variability in male: female ratios, the mean (and 95% CI) regression relationships of λ_{RM} to λ_{census} remained positively correlated (Table 2; Fig. 2b; Appendix C, available online in Supporting Information). By varying the adult sex ratio from 40 to 70 males/100 females, the mean slope predicting λ_{census} from λ_{RM} was 0.481 (median = 0.462, 95% Monte Carlo CIs 0.421 to 0.501), similar to the slope of 0.505 (SE = 0.103) that was based on the original formulation by Hatter and Bergerud (1991).

The relationship between recruitment and λ_{census} was positive ($P = 0.18$), but recruitment explained only 11% of the variation in λ_{census} (Table 2). This effect size indicates that an increase in recruitment yields a relatively small increase in λ_{census} (e.g., a recruitment increase from 0.15 to 0.25 yields an increase in λ from 0.90 to 0.93). This example is a generalization because the relationships are non-linear: r is back-transformed to yield λ, and recruitment is back-transformed from the logit link to a proportion. Adult survival had a marginally greater influence on λ_{census}, with a change in survival from 0.80 to 0.90 producing a change in λ from 0.88 to 0.92 (Table 2). The linear combination of survival and recruitment ($R + S$) was more predictive of λ_{census} than was recruitment alone but less so than recruitment and survival combined as the R-M equation (Table 2). Comparing these approaches to prediction of λ_{census}, the R-M equation explained twice as much of the variation as the next-best approach, and was more parsimonious by 10 or more AIC_c units compared to all other approaches (Table 2).

DISCUSSION

Estimating population trend or abundance of animal populations is a central challenge for researchers and managers alike, and as a result the choice of metric and methodology is a topic of ongoing debate with broad implications for management and conservation (Walters 2003; Peacock and Garshelis 2006; Wasser et al. 2011, 2012; Boutin et al. 2012). Our analysis indicated that the R-M model overestimated λ across a specific range of values

Table 2. Predicting estimates of population change (λ) from census data (λ_{census}) based on 4 different approaches for caribou subpopulations in British Columbia, Canada, 1994–2013. Model fit (R^2) and corrected Akaike's Information Criterion (AIC_c), number of parameters (K), slopes, and P-values are presented. Coefficients are based on logit-transformed values for recruitment and survival, and λ from the recruitment-mortality (R-M) equation has been transformed to the instantaneous rate of increase (r).

Method	R^2	AIC_c	ΔAIC_c	K	Equation	P
Recruitment (R)	0.11	−27.0	13.0	3	$r = 0.0632R - 0.0219$	0.18
Adult survival (S)	0.25	−30.0	10.0	3	$r = 0.0545S - 0.200$	0.04
$S + R$	0.30	−28.0	12.0	4	$r = 0.0487S + 0.0437R - 0.098$	0.065, 0.32[a]
R-M equation (RM)[b]	0.60	−40.0	0.0	4	$r = 0.505RM - 0.0627$	0.0002
R-M equation (RM) M:F[b,c]	0.61			4	$r = 0.481RM - 0.040$	0.0001

[a] For S, then R, respectively.
[b] Recruitment-mortality equation from Hatter and Bergerud (1991).
[c] AIC_c values are not shown in the table because these are based on different data sets (i.e., the inclusion of M:F simulations); thus, models are not directly comparable. The AIC_c value is −39.7.
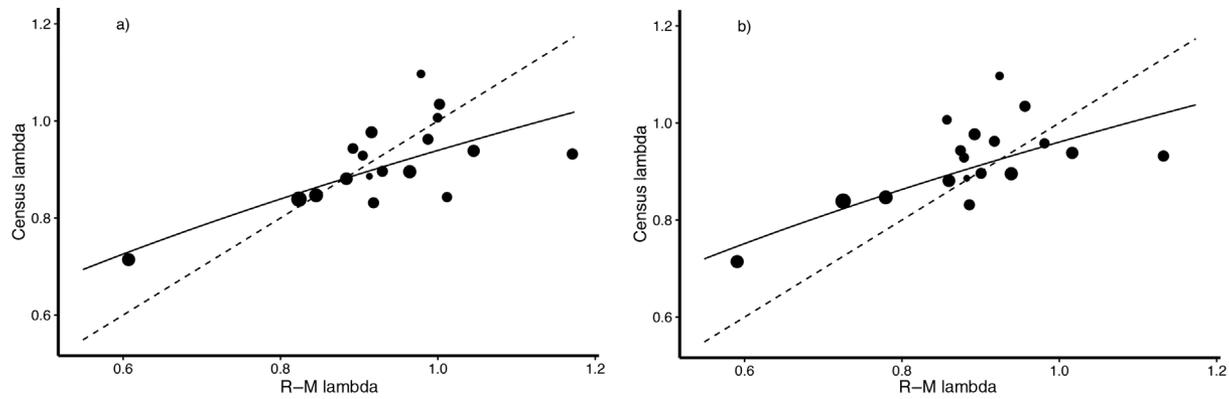
Figure 2. Observed and predicted relationship between the recruitment-mortality (R-M) equation and population change (lambda) based on aerial censuses of caribou in British Columbia, Canada, 1994–2013. Predicted line (solid) is based on (a) the R-M equation from Hatter and Bergerud (1991; $R^2 = 0.60$), and (b) the R-M equation with Monte Carlo simulations of male:female ratios ($R^2 = 0.61$). The dashed line represents the 1:1 best-fit line. The relative weight of each data point is shown by the area of the symbol. The values have been back-transformed to λ from the analysis based on the instantaneous rate of change (r). Bootstrapping the regression revealed that the slope was robust to sampling error and outlying data.

(i.e., $\lambda_{RM} > 0.88$) based on data from caribou ecotypes in British Columbia. This relationship was robust to whether the adult sex ratio was accounted for (i.e., formula used in Hatter and Bergerud [1991] or correction used in DeCesare et al. [2012]). In parts of Alberta, where conditions make validation using census data impractical, the R-M equation predicts λ to be >0.88 for 9 of 11 boreal populations (range $= 0.884$–1.001; Hervieux et al. 2013). Therefore, values of λ_{RM} for these 9 populations in Alberta are likely overestimates of λ_{census}. Although the quantitative relationship (Fig. 2) may not apply to the boreal ecotype, the magnitude of the overestimate suggests caution in management because a λ_{RM} of 1.0 equates to a λ_{census} of 0.94, indicating that trend-based estimates signifying stability or moderate decline could mask steeper underlying population declines because of this positive bias. We recognize that across some of the data ($\lambda_{RM} < 0.88$) the predicted relationship underestimated λ_{census}, but this pattern occurred over a narrow range of sampled populations (3 of 18).

Why does the R-M equation overestimate lambda for some caribou populations? There are at least 4 possible reasons. First, recruitment is estimated in March when snow makes survey conditions possible, but calves are only 10-months old so still have 2 months to die before they are recruited to the yearling age class. This scenario likely applies to many ungulate populations and would lead to an overestimate of recruitment, if recruits continue to die at a higher rate than adults for the remaining (i.e., un-monitored) months (Hatter and Bergerud 1991). Second, few yearlings were collared in caribou studies, so adult survival estimates are likely biased towards more mature animals. If the survival rate of yearlings is lower than older adults, then not sampling yearlings would positively bias survival and thus λ_{RM}. Third, there may be behavioral differences (i.e., differences in habitat selection) between barren females and those with offspring (Poole et al. 2007, Serrouya 2010), or those whose offspring died before a census occurred (DeMars 2015). These differences in space use are most pronounced shortly after birth and less likely during winter. However, in the montane ecosystems of our

study areas, R. S. McNay (Wildlife Infometrics, personal observation) noted a higher proportion of non-maternal caribou in thick pine forests during winter, in contrast with higher proportions of maternal females on open mountain ridges, perhaps because of the nutritional benefit afforded in pine forests and lack of predators at higher elevations (Bergerud et al. 1990). A final possibility is that the aerial censuses are somehow negatively biased over time or as populations get smaller, providing an underestimate of the true λ. This bias is unlikely to occur because of the generally high detection rate of these animals. If anything, we consider the potential for such a bias to operate in the opposite manner, because when there are few animals and groups, there is much less chance of track confusion and counting only 1 group when there were actually 2 groups.

Although recruitment alone was positively correlated with λ_{census}, managers should refrain from relying solely on this metric to infer population change in caribou. First, recruitment explained only a small component of variation in λ_{census}, the magnitude of the relationship was very modest, and not significantly different from 0 ($P = 0.18$). In comparison, adult survival explained twice the variation in λ_{census}, whereas the R-M equation's combination of survival and recruitment explained 5 times as much variation in λ_{census}. This result parallels many findings for k-selected organisms (i.e., slow life-history paces), where adult survival typically has higher elasticity than juvenile survival or recruitment within a population (Crowder et al. 1994, Hovey and McLellan 1996, Gaillard et al. 1998). However, no quantitative comparisons should be made between our results and other studies regarding the effect of recruitment or survival on λ (Crowder et al. 1994, Hovey and McLellan 1996, Gaillard et al. 1998, DeCesare et al. 2012) because our study design was focused on different goals than is typical. In this study, our goal was to statistically predict variation in λ_{census} among populations and time periods using 4 different methods to estimate population trends from vital rates. Because the vital rates we examined were not involved in estimates of λ_{census}, our calculations of which vital rates are most predictive of λ_{census} are

not analogous to an elasticity analysis. Therefore, inferences are not directly comparable between our work and studies using elasticity analyses to understand effects of vital rates on growth rates derived from vital rates.

The generalization that inter-annual variability is higher for recruitment than adult survival holds for most populations of ungulates (Gaillard et al. 1998) and other long-lived mammals (Hovey and McLellan 1996). This pattern is one reason why the matrix simulations performed by Harris et al. (2008) suggested that age ratios could index population change, because if adult survival is relatively constant but recruitment varies, it follows that changes in recruitment could track population trend. However, in the case of declining or endangered species, these conclusions may not hold, either because adult survival is no longer high and constant, or because recruitment is consistently low. For example, woodland caribou are probably unique among ungulates in that adult survival is apparently more variable than recruitment, particularly across populations (e.g., this study), and in some cases within populations through time (Wittmer et al. 2005a). Moreover, if recruitment is consistently low, then the variation needed for strong relationships between recruitment and λ would be lacking, as was the case in this study. Furthermore, if age classes share causes of mortality, then age ratios will be much less likely to detect changes in population size (Caughley 1974). Wittmer (2004) reported a strong correlation between adult survival and recruitment among 18 woodland caribou subpopulations, suggesting that these vital rates are correlated, and that age ratios, in the absence of data on other vital rates, should have limited utility for predicting population trends.

MANAGEMENT IMPLICATIONS

Our results re-affirm the elegance and utility of the R-M equation. Compared to simple linear models of recruitment or survival, or both additively, the R-M equation explained more than twice the variation in λ_{census}. Because the R-M equation was derived from first principles (i.e., from population ecology theory) and thus reflects a mechanistic interplay between recruitment and survival, its performance was superior to the univariate or simple additive statistical approaches. Although the variation explained by the R-M equation was only 60% of λ_{census}, the same direction in trend between the 2 approaches increases our confidence that the R-M equation is appropriate to use for species of management concern, particularly when there are few cost-effective alternatives. However, when using the R-M equation in the context of monitoring species that are cryptic or of management concern, 2 factors should be considered: occasional population abundance estimates should be performed to help validate the rate of change, and a representative sample of adults (including yearlings) should be radio-collared when estimating demographic parameters to reduce potential bias in the survival parameter.

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