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Efficacy of calf:cow ratios for estimating calf production of arctic caribou

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Abstract: Caribou (*Rangifer tarandus granti*) calf:cow ratios (CCRs) computed from composition counts obtained on arctic calving grounds are biased estimators of net calf production (NCP, the product of parturition rate and early calf survival) for sexually-mature females. Sexually-immature 2-year-old females, which are indistinguishable from sexually-mature females without calves, are included in the denominator, thereby biasing the calculated ratio low. This underestimate increases with the proportion of 2-year-old females in the population. We estimated the magnitude of this error with deterministic simulations under three scenarios of calf and yearling annual survival (respectively: low, 60 and 70%; medium, 70 and 80%; high, 80 and 90%) for five levels of unbiased NCP: 20, 40, 60, 80, and 100%. We assumed a survival rate of 90% for both 2-year-old and mature females. For each NCP, we computed numbers of 2-year-old females surviving annually and increased the denominator of the CCR accordingly. We then calculated a series of hypothetical "observed" CCRs, which stabilized during the last 6 years of the simulations, and documented the degree to which each 6-year mean CCR differed from the corresponding NCP. For the three calf and yearling survival scenarios, proportional underestimates of NCP by CCR ranged 0.046–0.156, 0.058–0.187, and 0.071–0.216, respectively. Unfortunately, because parturition and survival rates are typically variable (*i.e.*, age distribution is unstable), the magnitude of the error is not predictable without substantial supporting information. We recommend maintaining a sufficient sample of known-age radiocollared females in each herd and implementing a regular relocation schedule during the calving period to obtain unbiased estimates of both parturition rate and NCP.

Key words: composition counts; errors; fecundity; herd productivity.

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Introduction

Herd composition counts are commonly used in ungulate management (Bender, 2006), but the ratios obtained are the subject of ongoing debate (Caughley, 1974; McCullough, 1994; Bonenfant *et al.,* 2005; Harris *et al.,* 2008). Given the potential to provide ambiguous information on population dynamics (Caughley, 1974), these ratios require a number of restrictive assumptions for proper usage (McCullough, 1994). Composition counts may also be affected by unequal mixing of herd components (Bonenfant *et al.,* 2005). Nonetheless, late winter composition counts may adequately index overwinter calf survival and herd growth where 1) biased sampling is absent, 2) precise calf:cow ratios are available, 3) adult survival is precisely estimated, 4) the variance in juvenile survival swamps variance in subadult and adult survival, and 5) parturition is relatively constant (Hatter & Bergerud, 1991; Harris *et al.,* 2008; DeCesare *et al.,* 2012). However, it is not clear that these fairly restrictive assumptions can be consistently met for long-term field monitoring.

Within a few weeks after calving, the female segment of caribou (*Rangifer* tarandus granti) herds that calve north of the Arctic Circle (hereafter referred to as "arctic caribou") consists of sexually-mature individuals (with and without calves), sexually-immature 2-year-olds, and yearlings. Whereas yearling females typically are distinguishable from older females, it is nearly impossible to accurately classify 2-year-olds. Hence, 2-year-old and older females are combined in a single class called "cows" or, inappropriately, "adult females" for the calculation of CCRs.

In caribou herds that calve south of the Arctic Circle (hereafter called "subarctic caribou") up to 48% of 2-year-old females may be pregnant (*i.e.*, breed as yearlings at ca. 16 months of age; c.f. Bergerud *et al.,* 2008). In arctic herds, however, females rarely breed as yearlings and calve as 2-year-olds. For example, in the Porcupine herd (PCH) only 2 of 41 (5%) radiocollared and monitored 2-year-old females, 2004–2011, were observed to be parturient; and in only two of these years were any 2-year-olds parturient (J. Caikoski, ADF&G, pers. comm.). For the Central Arctic herd (CAH), only 3 of 94 (3%) radiocollared 2-year-old females monitored, 1994–2010, were parturient; and in only three of these years were any 2-year-olds parturient (Lenart, 2011). For the Teshekpuk caribou herd (TCH), only 3 of 46 (7%) radiocollared 2-year-old females monitored, 1993–2012, were parturient; and in only three of these years were any 2-year-olds parturient (Parrett, 2009). These values would be overestimates if less effort was invested in monitoring any nonparturient females located outside of the calving ground.

Caribou CCRs remain commonly used to index the product of parturition rate and calf survival (proportion of all ≥ 2-year-old cows that gave birth and retained calves by the survey date) of caribou herds in Alaska (*e.g.*, Boertje *et al.,* 1996; Valkenburg *et al.,* 2004). Typically, stratified random or systematic surveys are conducted on the calving grounds shortly after the peak of calving, and caribou are classified as bulls, cows, yearlings, and calves. The CCR for any particular survey is estimated as the number of calves observed per 100 cows observed.

A more explicit and ecologically relevant term than CCR is "net calf production" (NCP, the proportion of sexually-mature females observed with surviving neonates ~1–4 weeks after calving). For any arctic herd, NCP can be confidently estimated as the proportion of a sample of radiocollared females, known to have been fecund previously or at least 3 years old, that are accompanied by calves (Whitten *et al.,* 1992; Cameron *et al.,* 1993; 2005).

A CCR derived from survey counts is an underestimate of NCP for arctic herds, owing to observer inability to distinguish between 2-year-old females that are rarely parturient and sexually-mature females with parturition rates typically in the range of 70–90% (PCH, 2005–2011, J. Caikoski, pers. comm.; CAH, Cameron *et al.,* 2005). Including 2-year-olds artificially increases the CCR denominator, resulting in an underestimate of NCP. High survival rates of calves (prior-year) and yearlings would further inflate the CCR denominator, exacerbating underestimates of NCP by CCR. In contrast, for subarctic caribou herds in which a highly variable proportion of yearlings may breed (*e.g.*, 8–48%; Bergerud *et al.,* 2008), underestimation of NCP by CCR may be reduced in some years. However, quantifying such bias in CCRs would require precise annual estimates of 2-year-old female parturition rates, and these data are rarely available.

Dilution of the CCR denominator by sexually-immature 2-year-old females is intuitively obvious; yet status assessments of herds based on CCRs seldom make reference to the bias, perhaps because the data necessary for calibration (*i.e.*, proportion of all ≥ 2-year-old females that are sexually- immature 2-year-olds) are rarely available. In some cases, potential bias in CCRs has been acknowledged in the context of demographic modeling when the age composition of the female component of the population fluctuated with cohort-specific changes in survival. For example, Boulanger et al. (2011) encountered difficulties interpreting a decline in apparent calf recruitment in the Bathurst herd (Canada) based on CCRs and appropriately recognized the possibility of biased estimates of fecundity when the denominator in CCR included a substantial proportion of females in the relatively unproductive young and old age classes. Regardless, sexually-mature females are the most appropriate denominator for calculating NCP because they are the most numerically stable of the sex-age classes (McCullough, 1994; Harris *et al.,* 2008) and the only class of arctic caribou females likely to give birth.

With the increasingly widespread use of very high frequency (VHF) radio collars, NCPs can now be estimated by relocating sexually-mature females during the calving period and observing their maternal status. Even so, some biologists continue to routinely conduct separate calving ground and/or postcalving surveys to estimate CCRs, particularly when the number of radio collars deployed is considered insufficient.

Our objectives were to 1) document the magnitude and range of underestimates of NCP by CCR for arctic caribou using deterministic simulation modeling based on three survival scenarios for calves and yearlings, and 2) evaluate the utility of NCP as an estimator of herd growth status, given variable survival; and, by implication, the additional uncertainty introduced by CCR underestimates.

Methods

We conducted 10-year deterministic simulations using three different scenarios of overwinter calf and annual yearling survival (respectively: low, 60 and 70%; medium, 70 and 80%; high, 80 and 90%). We assumed 50% females among yearlings and assigned a constant 90% annual survival for females ≥ 2 years old. For each scenario, we projected annual numbers of surviving yearlings and 2-year-old females at five levels of NCP (20, 40, 60, 80, and 100%) and sequentially totaled the 1) number of females ≥ 3 years old and assumed to be sexually-mature (*i.e.*, the denominator for calculation of NCPs) and 2) number of sexually-mature females plus sexually-immature 2-year-old females (*i.e.*, the denominator of CCRs).

We began each simulation with 100 sexually-mature females, calculated numbers of current-year calves for each NCP level, and calculated future totals for yearlings, 2-year-old females, and sexually-mature females based on the set of survival rates specified. We totaled the accrued sexually-mature females with the surviving previous-year sexually-mature females; the sum was then used as the basis for calculating numbers of calves present at the specified NCP and for projecting numbers of mature females surviving through the following winter. We repeated that same procedure for each successive year through year 10. For each level of NCP and survival scenario, we summed sexually-mature and 2-year-old females to obtain a denominator typically used for CCR calculations. We then produced a series of hypothetical "observed" CCRs, computed a geometric mean CCR for the last six years of the simulation, and documented the degree to which each of those means differed from the corresponding NCP.

Finally, for each NCP, we computed a geometric mean annual rate of change in the number of sexually-mature females generated

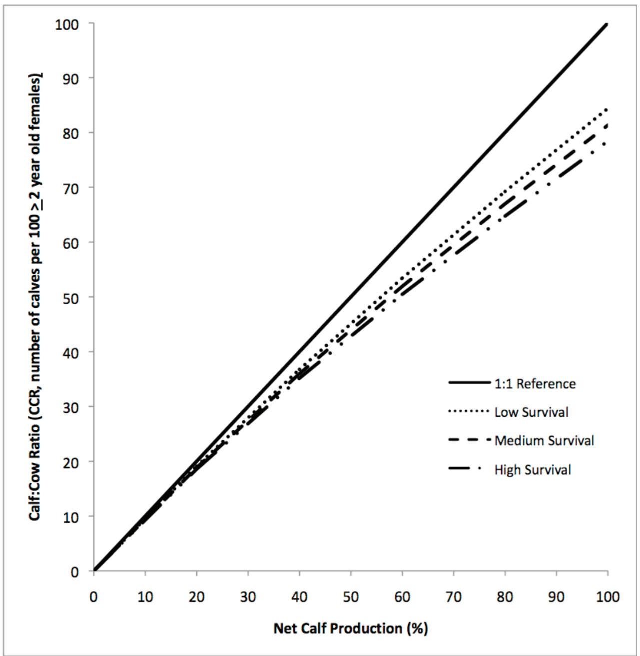

Fig. 1. Calf:cow ratios (CCR; *i.e.*, where the denominator includes sexually-immature 2-year-olds) in relation to net calf production (NCP; *i.e.*, where the denominator includes only ≥ 3-year-old sexually-mature females) at low (60, 70%), medium (70, 80%), and high (80, 90%) levels of overwinter calf and annual yearling survival, respectively (see Table 1).

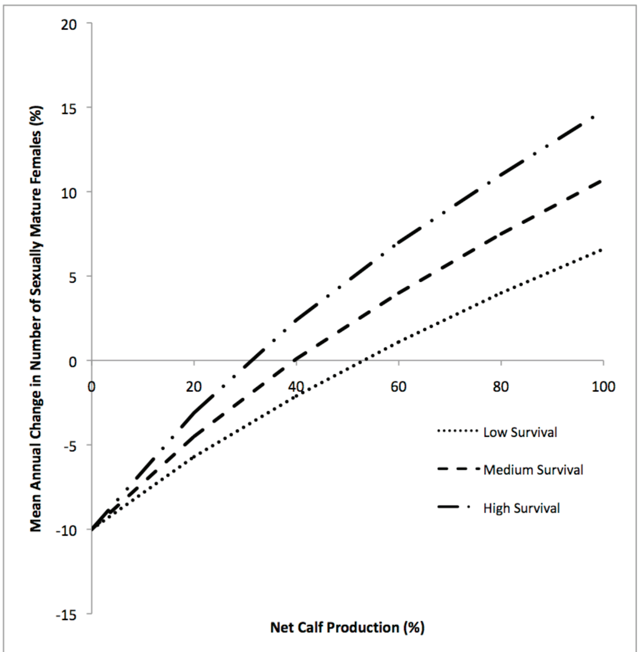

Fig. 2. Mean annual rates of change in the number of sexually-mature females in relation to net calf production at low (60, 70%), medium (70, 80%), and high (80, 90%) levels of overwinter calf and annual yearling survival, respectively (see Table 1).

by the simulations and described those trends within each of the three survival scenarios. We restricted our analyses to the last six years of the simulations in order to attain a stable age distribution.

Results

CCR underestimates of NCP increased with the progressive addition of 2-year-old females to the simulated population, from 0.046, 0.058, and 0.071 at 20% NCP to 0.156, 0.187, and 0.216 at 100% NCP for low, medium, and high rates of survival, respectively (Table 1, Fig. 1). Annual rates of change in the number of sexually-mature females were positively correlated with NCP for each of the three survival classes, increasing from ca. –3 to –6% at 20% NCP to ca. 7 to 15% at 100% NCP (Table 1, Fig. 2).

Discussion

Our intent was to illustrate the source, direction, and magnitude of biases incurred in the estimation of CCRs from survey observations at calving for arctic herds specifically. It was not our objective to offer a practical means of correcting those biases. Doing so would require annual overwinter survival estimates for calves, yearlings, and females ≥ 2 years old from a comprehensive radiotracking program. With those data, CCR underestimates could be calculated, and NCPs derived with some confidence. If one did have access to such data, however, NCPs could be estimated directly, and correcting CCRs would become a superfluous exercise.

Nonetheless, for the manager limited to the use of CCRs and interested in approximating the attendant errors, we do identify the component variables and structure of a simple model suited for those calculations. One could, for example, further align one or more of the age class survival rates to the estimated or suspected value(s) and compute a herd- and year-specific

Table 1. Underestimates of net calf production (NCP) by calf:cow ratios (CCR) and changes in the number of sexually-mature females derived from 10-year simulations.

Survival scenario	Net calf production (NCP, calves per 100 ≥ 3-year-old females) (%)[a]	Calf:cow ratio (CCR, calves per 100 ≥ 2-year-old females) (%)	Proportion of CCR denominator that is 2-year-old females	Proportional underestimate of NCP by CCR[b]	Annual change in number of sexuall mature females (%)[c]
Low[d]	20	19.1	0.053	0.046	−5.7
	40	36.8	0.105	0.081	−2.1
	60	53.4	0.154	0.110	1.1
	80	69.2	0.201	0.135	4.0
	100	84.4	0.245	0.156	6.6
Medium[e]	20	18.8	0.067	0.058	−4.5
	40	36.0	0.129	0.101	0.1
	60	51.9	0.186	0.135	4.0
	80	67.0	0.238	0.163	7.5
	100	81.3	0.287	0.187	10.7
High[f]	20	18.6	0.083	0.071	−3.1
	40	35.2	0.154	0.121	2.4
	60	50.5	0.217	0.159	7.0
	80	64.8	0.274	0.191	11.0
	100	78.4	0.325	0.216	14.8

[a] Percentage of sexually-mature (≥ 3 years old) females accompanied by calves ca. 3 weeks postpartum.
[b] Differences between each mean calf:cow ratio (CCR) and the corresponding net calf production (NCP).
[c] Mean percentage change between successive years; sexually-mature females are ≥ 3 years old.
[d] Calves, 60%; yearlings, 70%; females ≥ 2 years old, 90%.
[e] Calves, 70%; yearlings, 80%; females ≥ 2 years old, 90%.
[f] Calves, 80%; yearlings, 90%; females ≥ 2 years old, 90%.
NOTE: At NCP = 0, all mean CCRs and proportional underestimates = 0, and all mean annual changes in the number of sexually-mature females = –10% (*i.e.*, reflecting a constant survival rate of 90%).

estimate of bias for guidance. Or the fecundity of yearling females (*i.e.*, 2 years of age at calving), here assumed to be zero, could be raised if there was appropriate evidence for a significant parturition rate for this age class. The bias we document here would be reduced in direct proportion to the proportion of 2-year-old females that are parturient in a particular situation; and our use of adult survival of 90%, admittedly optimistic, indicates that our documentation of the underestimation of NCP by CCR is conservative. Likewise, our use of 60% as the low value for overwinter survival of calves implies much lower annual survival of calves (early calf mortality is subsumed in NCP) and minimizes bias in CCR.

The constraints imposed by our deterministic simulation are clearly artificial because both fecundity and survival are inherently variable; and for calves and yearlings, there are 2- and 1-year lags, respectively, before survivors become 2-year-old females that are incorporated into the CCR denominator. Thus, an investigator will rarely know the magnitude of bias in a CCR estimated from field surveys without substantial supplemental information.

Annual rates of change in the number of sexually-mature females (here, a surrogate for herd size) relative to NCP (Fig. 2) include a plausible range of herd growth rates, lending credence to the choice of numerical input variables. In reality, however, NCPs < 40% are unlikely, unless parturition rate is low and early postnatal mortality is extreme due to disease, starvation, or heavy predation. A 1-year reproductive pause is sufficient for mature females to regain body condition and resume breeding (Cameron, 1994; Cameron & Ver Hoef, 1994); hence, alternate-year breeding imposes a lower limit of 50% on parturition rate of sexually-mature females. An NCP of 100%, indicating parturition status of all sexually-mature females and no early calf mortality, is improbable as well.

Our calculated underestimates of NCP by CCR are not trivial. For NCPs of 40 and 100%, which easily encompass the range commonly observed in arctic caribou, CCRs projected over the range of survival rates evaluated (high to low) were 35–37 calves/100 cows and 78–84 calves/100 cows, respectively, yielding proportional underestimates ranging 0.081–0.216 (Table 1). Hence, CCRs are reasonable estimates of NCP when parturition and/or calf survival rates are low (ca. <40%), but the bias increases progressively thereafter, with CCRs becoming little more than approximations of NCP at the upper end of the scale (Fig. 1).

Counterintuitive results may also occur. For example, very low overwinter survival of yearlings would reduce the proportion of sexually-immature 2-year-old females subsequently entering the population at calving, which would reduce the negative bias that these animals typically impose and yield a relatively inflated CCR. This might falsely suggest that increased productivity had compensated for earlier reduced survival of younger age classes when, in fact, the increase in observed CCR was an artifact of previously-reduced survival.

Even direct estimates of NCP are of limited value for monitoring population trend because of uncertainty introduced by the range of plausible, but unknown survival rates for the various age classes. At an NCP of 40%, estimates of annual herd growth ranged −2 to 2%, depending upon the survival values applied in the simulations; while at an NCP of 90%, the range in growth rate increased to 5–13% (Table 2). Through a broad range of NCP, ~30% to ~60%, herd growth or decline is ambiguous if the mean and variance in survival are not known (Fig. 2).

Clearly, even NCPs offer only generalizations on herd trend; parturition rate and early calf survival are confounded in NCP, making it difficult to identify the limiting season without substantial supplemental information. Relying solely on CCRs would exacerbate the problem by biasing estimates of NCP downward, thereby underrating herd productivity and suggesting more conservative management strategies than warranted, increasingly more so as calf production increased. For the same reasons, CCRs are unsuitable as response variables in the evaluation of ecological processes or for population modeling.

Although our analysis was restricted to bias in CCRs, it should be noted that yearling:cow ratios are subject to identical problems with the ratio denominator. In addition, representative sampling may be quite challenging. Surveys conducted during the calving period must be broadened sufficiently beyond the calving grounds to include any yearlings located elsewhere, commonly in groups with bulls (R.D. Cameron & L.S. Parrett, unpubl. data). Similarly, sex-age composition counts of large postcalving aggregations and rutting concentrations, daunting enough under the best of circumstances owing to non-uniform distribution, are further complicated by increasing difficulty distinguishing between yearlings and 2-year-old females as the season progresses.

Despite problems with sampling and interpretation, CCRs are routinely used as indices of early calf survival (*e.g.*, Boertje *et al.,* 1996; Valkenburg *et al.,* 2004) and subsequent recruitment (*e.g.*, Dau, 2009; Parrett, 2009). In both of the above applications, making inferences on either long- or short-term trends in population "productivity" is hampered by the presence of an unknown proportion of sexually-immature females in the CCR denominator. Further, estimating the relative contributions of fecundity and survival to recruitment is not possible because the CCR numerator is a product of those two variables.

For a monitoring program, we recommend maintaining a sample of known-age radiocollared females, marked as yearlings (collars replaced as necessary, where practical), and implementing a relocation schedule appropriate to study objectives or management needs. If resources are insufficient for a sample size that yields adequate analytical power, we suggest a target of ~25 collars, the minimum required by many peer-reviewed journals to report proportions. Relocations during the calving period would provide estimates of parturition rate and NCP (and, by difference, early calf survival) without the bias introduced when using CCRs. Additional relocations during autumn and early spring would be desirable to estimate subsequent survival of calves, yearlings, and adult females.

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