COMPENSATORY RESPONSE TO CHANGES IN CALF SURVIVORSHIP: MANAGEMENT CONSEQUENCES OF A REPRODUCTIVE COST IN MOOSE

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ABSTRACT: Life history tradeoffs are a well-documented feature in many large mammal species but the management consequences of such tradeoffs usually are not explored. A cost to present reproduction, in terms of future reproductive success, for female moose was implied in recent work by Testa and Adams (*unpubl.*). In that paper, rump fat thickness differed in moose with and without a calf at heel in autumn, and was correlated in logistic regression models to subsequent calving. This suggests an energetic link that results in lower reproductive success for female moose in years after successfully rearing a calf to autumn. In the present paper, a model of their results linking present and future calving success through rump fat changes was favorably compared to a second sample of female moose for which reproductive histories in successive years was known. This individual cost of reproduction in moose may play a role in populations having high and variable rates of additive perinatal mortality due to predation. The cost for individual moose of having and rearing a calf to autumn was estimated, and incorporated into a population model in which perinatal mortality was manipulated to simulate managed reduction of predation rates on neonates. The expectation was that the tradeoff between current and future reproductive success in individuals could reduce the harvest benefits expected from reducing calf mortality. The estimated cost of successfully rearing a calf to the fall in this study was a 44% reduction in fecundity, which led to modeled reductions of 10-13% in the gains expected from better calf survival. This effect could be greater in years of unusually low reproduction, or after an increase in population density.

ALCES VOL. 34(1): 107-115 (1998)

Key words: *Alces alces*, population dynamics, population model, reproduction, reproductive costs

The cost of reproduction, in terms of future adult survival and reproduction, is a central tenet of life history theory (e.g., Reznick 1985, Clutton-Brock 1988, Partridge 1989). Such costs have been detected in several ungulate species (e.g., Albon *et al.* 1986, Cameron 1994, Clutton-Brock *et al.* 1996), and can be more prevalent at high densities or during periods of environmental stress (Clutton-Brock *et al.* 1983, 1996; Festa-Bianchet 1989). In southcentral Alaska, moose were found to have lower body energy stores, as indexed by rump fat measurements, and lower rates of pregnancy when accompanied by a calf in November (Testa and Adams, *in press*). Low rump fat measurements were also correlated with lower rates of pregnancy, calving and neonate survival (Testa and Adams, *in press*). The effect of reproductive success, defined as bearing and rearing a calf to fall, on future reproduction is likely mediated by body energy stores that are reduced by gestation and lactational demands and, in turn, reduce future reproductive success. Moose calf survival can vary substantially (Ballard *et al.* 1991, Gasaway *et al.* 1992), but the consequences of life history trade-offs in individuals are not usually included when interpreting population dynamics in a management context. My goal here was to explore the possible management and population dynamics consequences of the life history trade-off between current and future reproductive success in moose.

Moose populations in Alaska are an important resource, and their management has been near the center of controversies over predator management (Gasaway *et al.* 1983, Gasaway *et al.* 1992, Franzmann 1993). In Game Management Unit (GMU) 13, southcentral Alaska, the principle predator species on moose calves has been the brown bear (*Ursus arctos*), with over half of calves born from 1979-1984 being killed by this predator (Ballard *et al.* 1990). The current management plan for the area calls for the reduction of brown bear numbers through liberalized hunting regulations, with the objective of increasing moose calf survival and, as a result, hunter harvests of moose. The consequences of life history trade-offs may be important in this context. My first objective was to model the hypothetical link, via body condition, between present and future reproductive success reported by Testa and Adams (*in press*) by combining their statistical models, and comparing the result to a sample of reproductive histories in the same population. My second objective was to incorporate the estimated cost of reproduction, in terms of next year's calving probability, into a population model to predict its effect on the expected benefits of reducing predation mortality on neonates.

STUDY AREA

Moose were studied in the Nelchina Study Area (NSA), an area of approximately 4200 km^2 near the townsite of Nelchina (62°15'N, 147°15'W) in southcentral Alaska. Ballard *et al.* (1991) documented the recent management and ecological history of moose in GMU 13 from 1952-1984. Moose underwent a decline from 1963-1976, then an increase through 1984. In recent years, the population has stopped growing and declined slightly since the late 1980's (Testa *unpubl.*). Moose density in 1994 was 0.81 moose/km^2 (E. Becker, *in litt.*). Vegetation in the area was described by Skoog (1968). Previous studies in nearby areas suggest that an area this size could support 9-45 wolves in at least 3 packs (Ballard *et al.* 1987) and 80-120 adult brown bears (Miller *et al.* 1997).

METHODS

Forty adult female moose were captured from 6-28 March 1994, and equipped with VHF radiocollars. Twenty-four additional moose were captured and radiocollared from 7 November to 12 December 1994 . Twenty new adult female moose were captured during 7-8 November 1995, and 21 collared moose were recaptured on 9-10 November 1995. Except for 13 moose that were captured by helicopter net-gun on 16-17 November 1994, all captures were made by darting moose from a helicopter with a mixture of carfentanil-citrate and xylazine hydrochloride (Schmitt and Dalton 1987).

Radiocollared moose were located by airplane 1-2 times each month, except from mid-May to late June, when they were located daily, and July, when they were tracked 2-3 times per week. Daily radiotracking flights in May and June included visual sightings of all adult and 2-year-old moose to obtain parturition dates and rates. Parturition rates were calculated as the proportion of radiocollared females that were sighted at least once with a calf in a given year. Twinning rate was calculated as the proportion of adult females with calves that also had twins when first sighted with a calf (Testa and Adams, *in press*).

Modeling Reproductive Cost

Reproductive cost is defined here as the percentage decline in reproductive rate that results in the year following successful rearing of a calf to autumn. Testa and Adams (*in press*) estimated the logistic relationship between maximum rump fat thickness measured in November using ultrasonography, and the probability of bearing a calf the subsequent spring. Similarly, a negative correlation was found between the presence of a calf "at heel" in November and rump fat thickness. I used the distribution of rump fat thickness within each category (with or without calves at heel), to model the proportion of females having calves the next year. I multiplied that distribution by the logistic relationship between rump fat (x) and calving probability of an individual;

$$\mathrm{P} = e^{(1.339+0.0868bx)} \ / \ (1+e^{(-1.339+0.0868x)}),$$

given by Testa and Adams (*in press*). I varied the mean of the sampling distribution across a range of rump fat measurements to produce a second curve that describes the relationship between mean rump fat measurements in fall and expected proportion of adults calving the next spring. This provides a translation between the logistic relationship describing individual probabilities, and the population variable, proportion calving. The mean rump fat measurements from our samples of moose with and without calves at heel were then used directly with this graph to predict the proportion of females calving. The prediction of calving proportion in each group was tested against the calving histories in a sample of moose followed from winter, 1994, to spring, 1996. This second sample included no data used to derive the logistic relationship described above. It did include 24 moose (roughly 1/3 of the total sample) used in the rump fat study in another year.

Loglinear categorical models were used to test categorical tables for independence (Agresti 1990). Because count data can produce asymmetric sampling distributions, bootstrap confidence intervals (95% C.I.) were calculated for all proportions, and for the cost of reproduction, based on 1000 simulated samples drawn from the data (Efron 1982).

Modeling the Management Consequences of Reproductive Cost

To assess the population consequences of reproductive cost, a stage-structured population model of female moose was developed, based on the parameterization of Eberhardt and Siniff (1977), and values estimated in the NSA (Testa, *unpubl. data*). The conditions of interest were rates of growth and potential harvest that are produced when calf survival improves, such as may occur if predation on calves is reduced (Ballard and Miller 1990). The parameters of Eberhardt and Siniff (1977) were expanded to create biannual time steps. In this way, neonatal survival could be varied in the model without changing winter parameters, and model output would include harvest and herd composition in the fall, when hunting and aerial surveys occur, as well as spring composition and reproductive rates. Remaining annual survival parameters for yearlings, and older moose were divided equally between the two time steps ($\text{survival}^{-1/2}$). Baseline parameter values were adjusted within their observed confidence limits to reflect recent conditions in the NSA: a stable population under current conditions of no female harvest, with model output of calves/100 cows in the fall near the observed average of 25 (Table 1). Of greatest interest was the population's productivity, in terms of calf recruitment and possible harvest of female moose older than calves, as calf survival from spring to fall increases. This was the "optimistic" model of reduced calf mortality used as a baseline.

To assess the possible consequences of known life history tradeoffs in moose to this management scenario, the model population of adults was divided into those having

Table 1. Parameters and their values used in a stage projection model of female moose in the Nelchina Study Area (NSA). Values were estimated from a population of radiocollared moose (Testa, *unpubl. data*), adjusted within their respective confidence limits to produce a stable population with composition comparable to that observed in the NSA.

Parameter Description	Baseline Value
calf survival from birth to autumn (P_1)	0.33
calf survival from autumn to spring (P_2)	0.90
annual yearling survival rate (P_Y)	0.75
annual adult survival rate (P_A)	0.91
average calving rate (F)	0.80
twinning rate	0.12
age of first reproduction	3

Table 2. Average calving rate without an explicit cost of rearing a calf to autumn, and comparative calving rates under assumptions that a 20, 40 or 60% reduction in calving probability occurs if a calf is reared. Probabilities of giving birth the subsequent spring are shown for female moose without (F_0) and with (F_1) an accompanying calf in autumn. Values shown produce an average calving rate of 0.80 under the starting model assumption of a stationary population.

Cost of Rearing a Calf	F_0	F_1
0	0.80	0.80
20%	0.84	0.67
40%	0.89	0.53
60%	0.94	0.37

a calf at heel in November, and those that did not, so that different calving rates could be applied. Rates for the two groups were selected to reflect 20, 40 and 60% reduction in calving rate for females with a calf, in comparison to the maximum calving rate by females without a calf in fall. The rates were selected to produce the average adult reproductive rate assumed by the baseline model with normal composition (Table 2). In this way, starting conditions for models without a cost of reproduction, and those with a wide range of such costs produced identical results until neonatal calf mortality was manipulated. The expectation was that increased calf survival in one year would entail compensatory changes in female productivity the following year that would partly offset gains in calf survival. The range of reproductive costs being modeled reflected the range actually measured in the NSA. Model outputs were those that might be estimated in a real population: calves:100 cows in fall, population growth rate (λ) in fall, the percent harvest (H) of adult females that would prevent population growth (λ=1.0), and average adult calving rate in spring (F).

RESULTS

Reproductive Cost

Application of the observed sampling distributions of autumn rump fat to the logistic relationship between rump fat thickness and calving probability for individuals yielded the relationship shown in Fig. 1. Mean rump fat thickness of females with and without a calf at heel was 29 and 42 mm with a pooled S.E. of 11.0 (Testa and Adams, *in press*), yielding predicted reproductive rates of 0.74 and 0.90 (Fig. 1). Reproductive data from the same years of the rump fat study, but excluding data used to derive the relationship in Fig. 1, yielded almost identical results. Ninety percent of females without a calf at heel had calves the following spring, while only 73% of those with a calf subsequently calved, thus supporting the assessment of reproductive cost through the energetic link of rump fat.

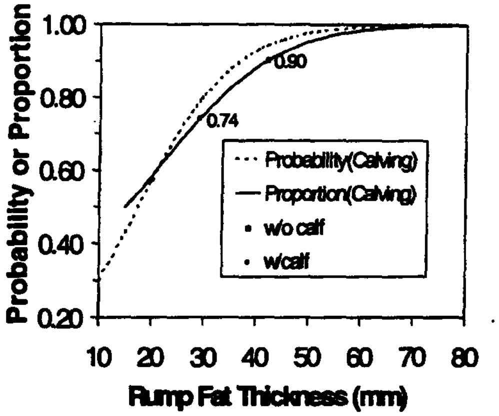

Fig. 1. Statistical relationship between rump fat thickness of individuals and their probability of calving estimated by Testa and Adams (*in press*), and resulting population relationship between mean rump fat thickness and proportion of females expected to bear calves. Predicted calving proportions are shown for females with and without an accompanying calf in the fall.

Additional data were incorporated into an estimate of reproductive cost by assuming that the reproductive status (presence or absence of a calf) of females first captured in March of 1994 had not changed since the previous November (Table 3). Calf mortality from November to March is low in the study area, and usually has been accompanied by mortality of the mother, so that reproductive status of surviving females in 1995 and 1996 rarely changed from the previous November (Testa, *unpubl. data*). Using loglinear categorical models, the calving rate was significantly less among females with a calf at heel in March ($P<0.001$), and the calving rate in 1994 was significantly less than in 1995 and 1996 ($P=0.05$), but no significant interaction was found ($P=0.75$). The cost of reproduction, as measured by the difference in reproductive rates between females with and those without an earlier calf at heel, was a 44% (28-62% C.I.) reduction in calving probability.

Table 3. Subsequent calving performance of female moose with and without a calf at heel in the autumn of 1994 and 1995. Data used to derive the logistic relationship with rump fat thickness (Fig. 1) were excluded. Calving rates are shown with 95% bootstrap Confidence Intervals.

Calf At Heel	No Spring Calf	Spring Calf	Calving Rate
No	6	56	0.90(0.82-0.97)
Yes	4	11	0.73(0.53-0.93)
Total	10	67	0.87(0.79-0.94)

Management Consequences of Reproductive Costs

The stage structured population model was run for 20 years under each of the conditions detailed in the methods. Output parameters are reported for the final year of the simulation, but they changed little after 4-5 years, even though starting stage structure was chosen to match the stable structure with baseline parameters given in Table 1. Under conditions of no harvest and no cost of reproduction, increasing summer calf survival from 0.33 to 0.65 increased calves:100 cows from 25 to 44 and rate of population growth from 1.00 to 1.07 (Fig. 2). Incorporating cost of reproduction (20, 40 and 60%) lowered both values, and the average calving rate in the manner expected (Fig 2a-c). By imposing a 40% cost of reproduction comparable to that estimated in the NSA, the potential harvest was reduced 10-13% from that expected without reproductive costs. With a 60% cost of reproduction harvests were reduced 15-19%. Where harvest was applied to control population growth, the calf:cow ratios in fall (Fig. 2f) were greater than in the simulations without harvest (Fig. 2a), while the effect of reproductive costs on measurable calving rates were approximately the same.

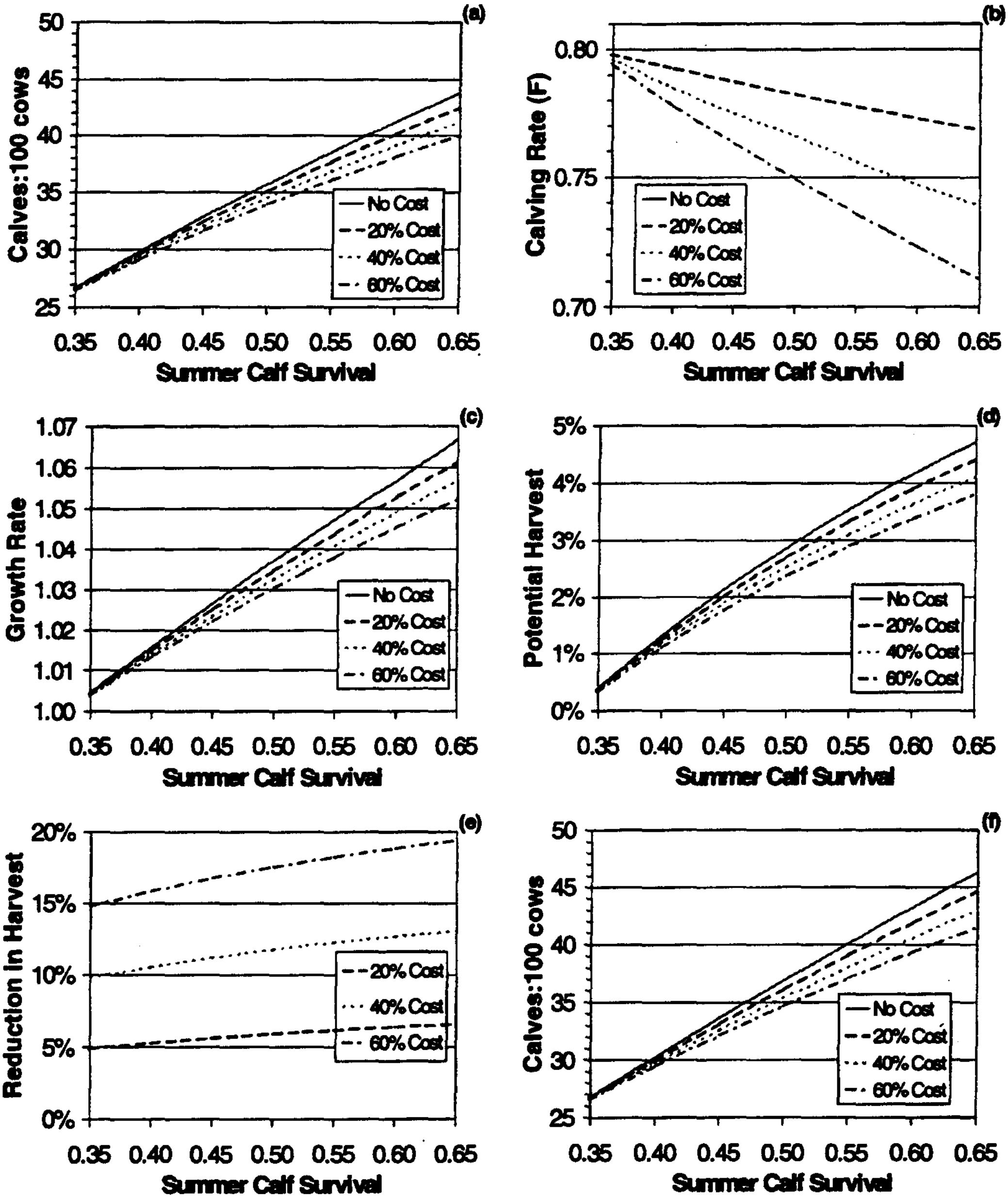

Fig. 2. Simulation results for female moose population as summer calf survival was varied from 0.33 (baseline) to 0.65. Results show 4 scenarios in which the cost of reproduction was varied from 0-60% to illustrate the effects of such costs on measurable population parameters: (a) calves:100 cows in fall without a harvest, (b) calving rate (F) of adult females, (c) population growth rate (λ), (d) potential fall harvest as a percentage of female population older than calves, (e) reduction in harvest expected due to 20%, 40% and 60% cost of reproduction, and (f) calves: 100 cows in fall when a sustainable harvest was imposed.

Table 4. Subsequent calving performance of female moose with and without a calf at heel in March of 1994-1996. Calving rates are shown with 95% bootstrap Confidence Intervals. Data are pooled according to results of association tests with loglinear models.

Year	Calf At Heel	No Spring Calf	Spring Calf	Calving Rate
1994	No	5	23	0.82 (0.68-0.96)
	Yes	10	2	0.16 (0.00-0.42)
1995-96	No	7	91	0.93 (0.88-0.97)
	Yes	10	18	0.64 (0.46-0.82)
1994		15	25	0.63 (0.48-0.78)
1995-96		17	109	0.87 (0.80-0.92)
1994-96	No	12	114	0.90 (0.85-0.95)
	Yes	20	20	0.50 (0.35-0.65)

DISCUSSION

The cost of successfully rearing a calf to fall, in terms of subsequent calving probability, was predicted well by the quantitative link with rump fat provided by Testa and Adams (*in press*). This was, however, only a weak test of the statistical model involving rump fat because the samples compared are from the same years, and have similar calf:cow ratios and calving rates. A stronger test may come when calf:cow ratios in fall differ markedly from the ones contributing to the statistical model derived here, and when other variables can be included that contribute to variations in autumn rump fat stores. In the context of managing moose calf predation losses, and using the calving histories in the NSA from 1994-96, plausible costs of reproduction produced moderate reductions in fecundity, calf recruitment and harvest potential that partially offset the gains expected from reducing neonatal calf predation. These compensatory effects were on the order of 10-13% of expected harvests with the average cost of reproduction estimated in this study, and 5-20% of expected harvests from the outside range of those cost estimates.

Costs of reproduction in ungulates are greater under more stressful conditions (Clutton-Brock *et al.* 1983, Festa-Bianchet 1989), with particularly good evidence of density dependent effects in red deer. Greater effects of such life history trade-offs would therefore be expected at higher moose densities, or during severe winters. In the present study, the intent was to anticipate how the most obvious life history trade-off, that between current calf survival and next year's calving probability, might affect the management strategy of reducing neonatal losses to predation in order to increase moose harvest. Other reproductive costs, particularly in adult survival, have been demonstrated in red deer (Clutton-Brock *et al.* 1983) and fur seals (Boyd *et al.* 1995). These were not explored in this case because they are likely to be confounded with predation, the factor being exploited in the attempted manipulation of summer calf mortality in GMU 13. For example, most adult fatalities in the NSA from 1994-1997 (7 of 10) have occurred to females with calves, and almost all (7 of 8) of the confirmed instances of predation on adults by bears and wolves involved females with a calf at heel (Testa, *unpubl. data*). Also, low rump fat measurements of moose, which were strongly correlated with present calf at heel, were correlated not only with subsequent calving success, but also with poor neonate survival (Testa and Adams, *in press*). It is not known whether this effect would remain when predation is lowered.

The simulations of harvest were primarily intended to assess how a simple cost of reproduction might affect harvest expectations. The modeled harvest rate was dependent only on calf survival, not any other life table parameter. If calf survival is increased by reducing the number of predators, other life table parameters may also change due to direct effects, as well as the indirect effects of reproductive costs. Also, the short period of study used here is not adequate to predict adult survival over a greater range of years and conditions. Therefore, estimates of calf recruitment and potential harvest reported here are not as reliable as the expected *relative* effect of the reproductive costs that were estimated.

ACKNOWLEDGEMENTS

Suzan Bowen, Jackie Kephart, Enid Keyes, Bill Taylor, Kris Hundertmark, Tom Stephenson, Dennis McAlliser, John Blake, Kimberly Beckman, Bill Collins, John Crouse, Howard Golden, and Jim Woolington assisted with field work at various times. G.R. Lee flew all of the spotting during captures and most of the radiotracking flights in a Piper PA/18 "supercub". Chris Soloy piloted a Hughes 500 helicopter for captures in 1994-95. Helicopter Wildlife Management caught 13 moose in November 1994. Invaluable library support was provided by Celia Rozen. S.D. Miller, D. Murray, T.R. Stephenson and an anonymous reviewer made constructive comments on the manuscript. This work was supported by Federal Aid in Wildlife Restoration, Project W-24-5.

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