VARIABILITY IN LIFETIME REPRODUCTIVE SUCCESS OF BIGHORN EWES

MARCO FESTA-BIANCHET, Département de biologie, Université de Sherbrooke, Sherbrooke, PQ J1K 2R1, Canada

JON T. JORGENSON, Alberta Department of Environmental Protection, Natural Resources Service, Suite 201, 800 Railway Ave., Canmore, AB T1P 1W1, Canada

Abstract: Variability in lifetime reproductive success was investigated in two marked populations of bighorn sheep (*Ovis canadensis*) in Alberta. Our analysis included only ewes that survived to at least 2 years of age. In both populations we found that average lifetime reproductive success decreased and interindividual variability increased as reproductive success was measured further from lamb birth. Almost all ewes produced a lamb every year, but individuals appeared to differ in their ability to raise lambs to weaning and to 1 year of age. Our results suggest that lamb:ewe ratios soon after parturition are of limited use in predicting population trends. When possible, counting yearlings is more useful than counting lambs.

The number of offspring produced by individuals over their lifetime represents probably the closest measure of fitness that can be obtained for wild animals, and is therefore of great theoretical interest (Oring et al. 1991, Pemberton et al. 1992, Alberts and Altmann 1995, Wauters and Dhondt 1995), even though reproductive success and fitness are not equivalent (McGraw and Caswell 1996). For wildlife management and conservation it is useful to know how individuals vary in their reproductive capacity because average reproductive success and individual variability in reproductive success have a direct effect on population dynamics, extinction probability and harvesting potential of wildlife populations (Clutton-Brock 1988).

The study of individual lifetime reproductive success in large mammals such as bighorn sheep (*Ovis canadensis*) requires the availability of marked individuals and accessible study sites where marked sheep can be readily found and their reproductive status assessed accurately. In addition, given that some bighorn ewes can live more than 15 years (Jorgenson et al. 1997), the documentation of lifetime reproductive success requires a long-term personal and financial commitment to a research program.

MATERIALS AND METHODS

Our study areas and methods to capture, mark and monitor sheep have already been described (Festa-Bianchet 1986, Jorgenson et al. 1993, Festa-Bianchet et al. 1995). We collected data from two marked populations in Alberta, Ram Mountain (data from 1975 to 1994) and Sheep River (data from 1981 to 1994). We calculated lifetime reproductive success for individually marked ewes that were monitored from 2 years of age onward. We limited our analyses to cohorts whose members had either all died or were older than 10 years by 1994. We excluded ewes that had been artificially removed, collected, or shot by hunters. At Sheep River, for each ewe we measured the number of lambs produced, weaned, and that survived to 1 year of age. At Ram Mountain we only measured the number of lambs produced and weaned, because in the earlier years of the study we did not have information on survival to 1 year for all lambs produced by individual ewes. Some lambs were not marked by the end of the field season in early October, others were marked but their mother was not identified, and a few lost their tags overwinter.

RESULTS

Because the Sheep River study started later than the Ram Mountain study, the average age at death of ewes in that population was less (Table 1) than for Ram Mountain ewes. Consequently, the sample for

Ram Mountain includes many old ewes that had a higher lifetime reproductive success than most Sheep River ewes. These differences, however, do not necessarily reflect differences in reproductive performance in the two populations.

As the measure of reproductive success that was used to compare individual ewes moved further from birth, variability in reproductive success increased in both study populations. The coefficient of variation increased markedly at Sheep River, but only slightly at Ram Mountain (Table 1; Figs. 1 and 2).

DISCUSSION

In our study areas, it is rare for a ewe 3 years of age or older not to produce a lamb in a given year (Festa-Bianchet 1988a, Jorgenson et al. 1993), therefore it is not surprising that variability in lamb production was less than variability in the number of lambs weaned or that survived to one year. At Ram Mountain, some adult ewes did not produce lambs at high population density (unpublished data), but those were mostly from cohorts born after 1985 and not included in this analysis.
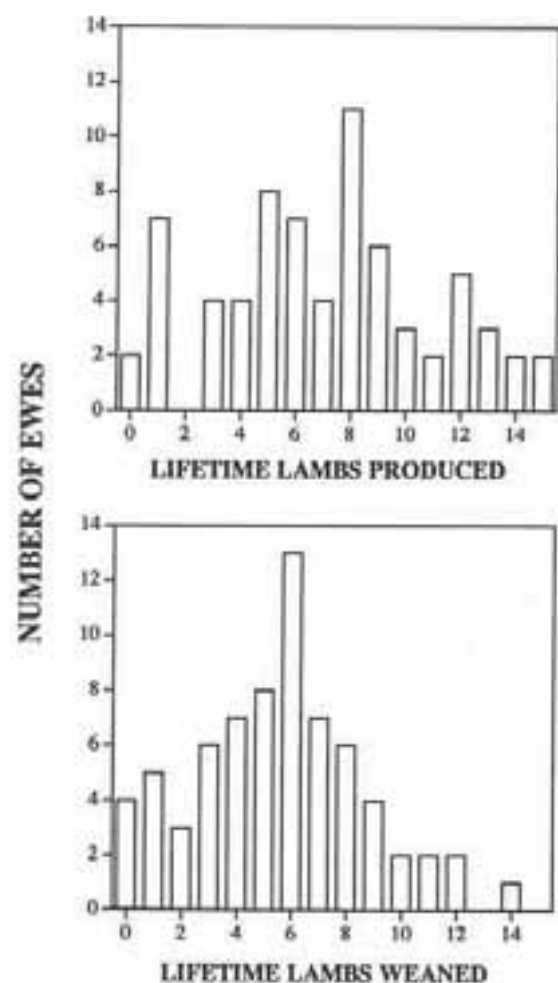

Figure 1. Lifetime reproductive success of female bighorn sheep at Ram Mountain, Alberta. a) number of lambs produced. b) number of lambs produced that survived to weaning (October).
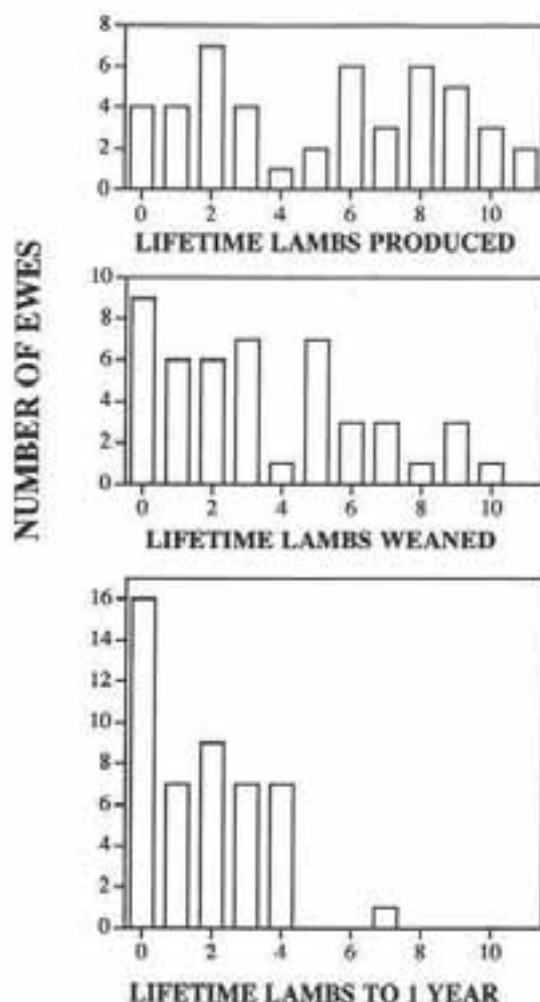

Figure 2. Lifetime reproductive success of female bighorn sheep at Sheep River, Alberta. a) number of lambs produced. b) number of lambs produced that survived to weaning (October). c) number of lambs produced that survived to one year of age.

An increase in variance in individual reproductive success as that success is measured further from birth is to be expected even if offspring mortality is random with respect to maternal characteristics (Cabana and Kramer 1991), therefore a further analysis is necessary to identify factors that may affect the ability of individual ewes to ensure survival of their lambs. The important implication of our results for bighorn sheep management is that the usefulness of lamb:ewe ratios or of lamb counts in predicting population trends is limited, as we have previously suggested (Festa-Bianchet 1992, Jorgenson 1992). Once lambs survive to one year of age they are independent of their mother, except in rare cases of very high population density (Festa-Bianchet 1991, L'Heureux et al. 1995). Therefore, the number of lambs surviving to one year is probably a better measure of individual reproductive success than the number of lambs produced, and counts of yearling sheep will provide managers with a better idea of future population trends than counts of lambs. Obviously, yearling sheep are more difficult to identify than lambs, especially during helicopter surveys. Our results suggest that in some cases, ground surveys may be better than aerial surveys of sheep populations. From the ground, trained observers could identify most yearling sheep. In addition, the risks to personnel involved in the survey will be decreased (Heimer 1994).

As the measure of individual reproductive success changed from the number of lambs produced to the number of lambs weaned over the lifetime, the coefficient of variation increased substantially more in the Sheep River population than in the Ram Mountain population (Table 1), likely reflecting the differences in timing of lamb mortality in the two study areas. Mortality before weaning tends to be greater at Sheep River

than at Ram Mountain, possibly because of recurring problems with pneumonia in the Sheep River population (Festa-Bianchet 1988b). We suspect that individual variability in lifetime reproductive success at Ram Mountain would have greatly increased had we been able to measure the number of lambs produced by each ewe that survived to one year of age.

LITERATURE CITED

Alberts, S. C., and J. Altmann. 1995. Balancing costs and opportunities: dispersal in male baboons. American Naturalist 145:279-306.

Cabana, G., and D. L. Kramer. 1991. Random offspring mortality and variation in parental fitness. Evolution 45:228-234.

Clutton-Brock, T. H. 1988. Reproductive success. Chicago: University of Chicago Press.

Festa-Bianchet, M. 1986. Seasonal dispersion of overlapping mountain sheep ewe groups. Journal of Wildlife Management 50:325-330.

Festa-Bianchet, M. 1988a. Age-specific reproduction of bighorn ewes in Alberta, Canada. Journal of Mammalogy 69:157-160.

Festa-Bianchet, M. 1988b. A pneumonia epizootic in bighorn sheep, with comments on preventive management. Proceedings of the Northern Wild Sheep and Goat Council 6:66-76.

Festa-Bianchet, M. 1991. The social system of bighorn sheep: grouping patterns, kinship and female dominance rank. Animal Behaviour 42:71-82.

Festa-Bianchet, M. 1992. Use of age ratios to predict bighorn sheep population dynamics. Proceedings of the Northern Wild Sheep and Goat Council 8: 227-236.

Festa-Bianchet, M., J. T. Jorgenson, M. Lucherini, and W. D. Wishart. 1995. Life-history consequences of variation in age of primiparity in bighorn ewes. Ecology 76:871-881.

Heimer, W. E. 1994. Aerial survey and Dall sheep population size: comparative usefulness of external and internal population dynamics for management purposes. Proceedings of the Northern Wild Sheep and Goat Council 9:43-50.

Jorgenson, J. T. 1992. Seasonal changes in lamb: ewe ratios. Proceedings of the Northern Wild Sheep and Goat Council 8: 219-226

Jorgenson, J. T., M. Festa-Bianchet, J.-M. Gaillard, and W. D. Wishart. 1997. Effects of age, sex, disease, and density on survival of bighorn sheep. Ecology 78:1019-1032.

Table 1. Lifetime reproductive success and age at death for marked bighorn sheep ewes in two populations in Alberta.

	Average	SD	CV
Sheep River (N = 47 ewes)			
Lambs born	5.23	3.43	65.49
Lambs weaned	3.45	2.90	84.22
Lambs surviving to 1 year	1.72	1.86	96.57
Age at death	7.45	3.62	48.64
Ram Mountain (N =70 ewes)			
Lambs born	7.09	3.89	54.83
Lambs weaned	5.54	3.13	56.53
Age at death	9.34	4.01	42.89

Jorgenson, J. T., M. Festa-Bianchet, and W. D. Wishart. 1993. Harvesting bighorn ewes: consequences for population size and trophy ram production. Journal of Wildlife Management 57:429-435.

L'Heureux, N., M. Lucherini, M. Festa-Bianchet, and J. T. Jorgenson. 1995. Density-dependent mother-yearling association in bighorn sheep. Animal Behaviour 49:901-910.

McGraw, J. B., and H. Caswell. 1996. Estimation of individual fitness from life-history data. American Naturalist 147:47-64.

Oring, L. W., M. A. Colwell, and J. M. Reed. 1991. Lifetime reproductive success in the spotted sandpiper (Actitis macularia): sex differences and variance components. Behavioral Ecology and Sociobiology 28:425-432.

Pemberton, J. M., S. D. Albon, F. E. Guinness, T. H. Clutton-Brock, and G. A. Dover. 1992. Behavioral estimates of male mating success tested by fingerprinting in a polygynous mammal. Behavioral Ecology 3:66-75.

Wauters, L. A., and A. A. Dhondt. 1995. Lifetime reproductive success and its correlates in female Eurasian red squirrels. Oikos 72:402-410.