04-194-be

Influence of Age of Males and Nutritional Condition on Short- and Long-term Reproductive Success of Elk

James H. Noyes
Oregon Department of Fish and Wildlife
La Grande

Bruce K. Johnson
Oregon Department of Fish and Wildlife
La Grande

Brian L. Dick
U. S. Department of Agriculture, Forest Service,
Pacific Northwest Research Station
La Grande, Oregon

John G. Kie
U. S. Department of Agriculture, Forest Service,
Pacific Northwest Research Station
La Grande, Oregon

Introduction

Rocky Mountain elk (*Cervus elaphus*) populations in some areas of northeastern Oregon have experienced declines in spring calf to cow ratios of nearly 80 percent over the last 40 years. Among the potential causes of these declines, the effects of age of male sires and the nutritional condition of females on conception dates and pregnancy rates have received the most attention from biologists and wildlife managers. Reliance on younger males as primary breeders can result in later conceptions and a prolonged rut period (Follis 1972; Hines and Lemos 1979; Noyes et al. 1996, 2002). Mechanisms involved with delayed conception due to male age have included late maturity of young males (Hines et al. 1985), female preference for older males (Gibson and Guinness 1980, Squibb 1985) and delayed timing of estrus in the absence of older males (Komers et al. 1999). The rate of conception (pregnancy), rather than the timing, does not appear to be dependent on the presence of older male sires (Follis 1972; Noyes et al. 1996, 2002).

Female nutritional condition during breeding influences date of conception (Trainer 1971, Mitchell and Lincoln 1973) and pregnancy rate (Trainer 1971, Albon et al. 1986). The importance of nutritional condition applies to males as well as females. It has been shown that age at puberty (Hines et al. 1985) and annual or long-term reproductive success of males depends on body size and dominance, both of which are influenced by birth date and nutritional condition (Green and Rothstein 1993, Komers et al. 1999). Although age of male sires, nutritional condition of females (and males to a lesser extent), predation and other determinants of ungulate productivity have been examined in many studies, interactions in Rocky Mountain elk have only recently been addressed (see Cook et al. 2004).

We conducted a study in two trials, from 1989 to 1993 and from 1995 to 1999, to assess the effects of male age and female nutritional condition on conception dates and pregnancy rates of female elk in northeastern Oregon (Noyes et al. 1996, 2002). Results of both trials showed a significant influence of male age on conception dates but not on pregnancy rates. Results from the interaction of male age and female nutritional condition pooled across trials likewise verified the importance of male age in affecting conception dates across a range of nutritional conditions.

The most commonly referenced manifestations of skewed sex ratios and nutritional limitations on elk reproduction are short-term (annual) differences in conception dates, pregnancy rates and calf survival. Beyond their short-term effects on calf survival, early conceptions and birth dates may be of greater significance in affecting long-term reproductive success and herd demographics. Benefits of early births may include higher lifetime reproductive success in female red deer (*C. e. elaphus* [Clutton-Brock et al. 1987]), bison (*Bison bison* [Green and Rothstein 1993]), and moose (*Alces alces* [Saether et al. 2003]). Understanding the importance of maintaining older males in elk populations, in conjunction with knowledge of nutritional condition and their interactions should assist wildlife managers in making informed, effective decisions about harvest management.

Study Area

We conducted our study within a 30 square mile (78 km^2) study area at the U. S. Forest Service's Starkey Experimental Forest and Range (Starkey) in northeastern Oregon, about 21 miles (35 km) southwest of La Grande. Elevation ranged from 3,680 feet (1,116 m) to 4,960 feet (1,502 m). Vegetation was a mixture of grassland, regenerating forests and older forest stands. Grand fir (*Abies grandis*), Douglas fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*) dominated the north aspects and higher elevations; ponderosa pine (*P. ponderosa*) was the dominant forest vegetation at lower elevations. Bluebunch wheatgrass (*Agropyron spicatum*) and Idaho fescue (*Festuca idahoensis*) typically dominated grassland vegetation. Mean annual precipitation was 20 inches (50.8 cm), and average mean temperatures were 24.8° Fahrenheit (-4° C) in January and 64° Fahrenheit (18° C) in July. Starkey was enclosed by an 8-feet (2.6-m) tall, game-proof fence that allowed us to adjust the population size and structure of a free-ranging elk herd. Further descriptions of the study area can be found in Noyes et al. (1996) and in Rowland et al. (1997).

Methods

Herd Management

We managed the elk population during both trials to allow a single cohort of males to function as principal herd sires as they matured from 1 to 5 years of age. We estimated our elk population size with a model described in greater detail in Noyes et al. (1996).

We maintained a bull:cow ratio of the study cohort between 16:100 and 21:100 during both trials to minimize the effects of numbers of males. We conducted hunts for yearling male elk in early August (except 1989 and 1995) to reduce the number of yearling males prior to the breeding season. Males that were younger than the study cohort were trapped annually and released outside of Starkey.

We fed a maintenance ration of alfalfa hay to those elk that moved to the winter feed ground. Elk were returned to the study area in similar nutritional condition each year to minimize the influence of variable winter severity on elk reproduction. Noyes et al. (1996, 2002) provide further descriptions of herd management. Our research was conducted under approved animal welfare protocols (Wisdom et al. 1993).

Reproductive Data

We collected reproductive tracts (uteri and ovaries), udders, lower incisors and kidneys with associated fat from female elk killed by hunters in early

December. We determined conception dates, pregnancy status, lactation status and female age and nutritional condition (KFI), as described by Trainer (1971). We conducted blood tests for leptospirosis (*Leptospira* spp.) and for brucellosis (*Brucella abortus*) to identify presence of diseases that may have affected elk reproduction.

Statistical Analysis

Conception Date

We compared conception dates of females among male ages (years) in each trial with analysis of variance and accounted for female nutritional condition with analysis of covariance. We compared conception dates of lactating and nonlactating females older than or equal to 3 years old with *t*-tests. We used stepwise multiple regressions to predict conception date.

Pregnancy Rate

We excluded females younger than age 3 or older than age 13 when summarizing pregnancy rates pooled by male age across trials because of age and lactation status effects.

Female Nutritional Condition

We used analysis of variance to compare KFI among years for females greater than or equal to 2 years old and compared KFI of lactating and nonlactating females greater than or equal to 3 years old with *t*-tests. We also used *t*-tests to evaluate nutritional condition of lactating and nonlactating females between the two trials. We tested for correlation between KFI for all females and May to August precipitation.

Results

Conception Date

Conception dates varied with age of male sires in both trials and also when conception dates were pooled among trials and adjusted for female nutritional condition. The largest differences in mean breeding dates were between 5-year-old sires and yearling or 2-year-old sires. Females bred by males older than or equal to 3 years of age conceived earlier than females bred by younger males in both trials, and they had similar conception dates. Median dates of conception for females bred by yearling males were approximately 2 weeks later than when 5-year-old males were sires. Lactating females conceived about 9 days later than nonlactating females.

Conception dates became more synchronous as male age increased (See Figure 1 in Noyes et al. 1996 for the chronology of conceptions, which applies to both trials). The duration of the rut differed by an average of 31 days between years with yearling and 5-year-old male sires (Noyes et al. 1996, 2002). We discarded the latest 10 percent of conceptions in each year to reflect that portion of the annual reproduction with the most management relevance. The date by which 90 percent of pregnant females were bred by yearling males was approximately 3 weeks later than when 5-year-old males were the sires. The cumulative percent of conceptions moved toward earlier dates as male age increased (Figure 1).

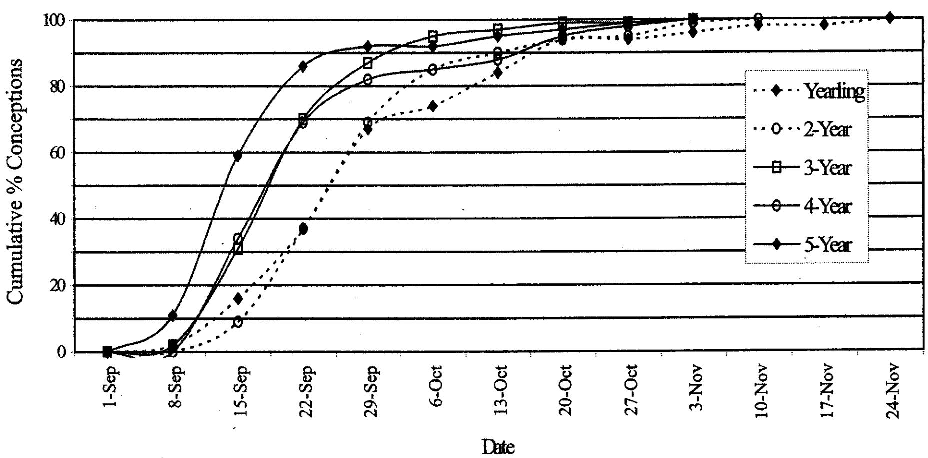

Figure 1. Cumulative percent conceptions for adult female elk (2 years or older) bred by males of five different ages at Starkey Experimental Range, Oregon, 1989 to 1999. Data were pooled from two identical 5-year trials. Age of sires increased each year from yearlings to 5-year-olds.

Pregnancy Rate

Pregnancy rates of females greater than or equal to 2 years old did not differ by male age in either trial. Pregnancy rates of females between 3 and 13 years of age pooled across trials, ranged between 89 percent and 94 percent (from Noyes et al. 1996, 2002). Pregnancy was related to KFI but not male age in pooled trials.

Female Nutritional Condition

The KFI of adult females differed among years and was significantly greater in 1989 and 1995, when yearling males were the primary herd sires. The KFI for all adult females during the second trial was less than KFI during the first trial. Pregnant, lactating adult females were in especially low nutritional condition in both trials when breeding was by 4-year-old males. KFI was lower in lactating females than in nonlactating females. KFI was correlated with May to August precipitation, and precipitation during those months was lower in the second trial than recorded in the first trial.

Discussion

We acknowledge the complex interactions among variables affecting reproduction in elk, but, for the purposes of this paper, we will emphasize the contribution of the age of male sires to differences in calf survival and long-term reproductive success.

We demonstrated the importance of mature males as sires in order to achieve early and synchronous conception in elk, but we found no relationship between age of males and pregnancy rates. In our study, female nutritional condition was significantly higher during the 2 years that immature males were sires than during the other years. Because of this, we were not able to determine if pregnancy rates of females bred by immature males might be lower if nutritional conditions were comparable to the other years. Holand et al. (2003) assessed the effects of skewed sex ratios and male age structure on calving rates of female reindeer (*Rangifer tarandus*) in excellent condition, and he questioned how the results might vary if females were in poor condition.

Early breeding by older male sires has been documented for elk (Follis 1972, Hines and Lemos 1979), moose (Saether et al. 2003), fallow deer (Komers et al. 1999) and reindeer (Holand et al. 2003). Conception dates for females in both of our trials were strongly influenced by the age of male sires across a range of nutritional conditions. After adjusting conception dates for differences in female nutritional condition, conception dates became increasingly early as male sires matured from yearlings to 5-year-olds.

Another influence of male age results from conception synchrony and its effect on female reproductive success and neonate survival. The significance of synchronous births on survival of neonates likely depends on the strategy for optimizing neonate survival employed by different species (Geist 1982, Clutton-Brock et al. 1987, Kiltie 1988).

For a discussion on the effects of male age on calf survival and long-term reproductive success, we will assume a constant gestation length and, consequently, will consider the phrases birth date and conception date to be interchangeable. Results of previous research on the length of the gestation period in ungulates and the ability of females to adjust the length vary, depending on the species, the nutritional condition of females, supplemental feeding, the effects on calf weight and survival, and perhaps a host of other unknown factors. No consistent patterns between nutritional condition and gestation length appear to be available. Guinness et al. (1978) stated that differences in calving time are likely due to factors affecting the time of conception, and we will assume that early and late conceptions are reflected in early and late births.

Birth date has been closely linked to the probability of offspring survival. Late calving and reduced survival has been associated with lower body weight in autumn in reindeer (Holand et al. 2003) and in winter in moose (Saether et al. 2003). Delays in breeding as a result of highly skewed sex ratios and the subsequent delays in birthing may reduce survival of offspring. Winter survival of red deer was related to birth date and population density (Guinness et al. 1978, Loison and Langvatn 1998). Cook et al. (2004) suggested that winter survival of captive-reared calves under varied nutritional condition was not related to birth date but indicated that other potential causes of mortality (e. g. predation) were not present. Clutton-Brock et al. (1987) reported mortality of red deer calves increased by 1 percent for each day the calf was born after the median birth date. Captive red deer hinds that bred much later than normal did not lactate normally following the late births, and Guinness et al. (1978) suggested that their calves in the wild would quickly die.

The ability of young ungulates to exhibit compensatory growth is an important variable that should be considered in assessing the relationship between birth date and survival. Research has shown conflicting patterns of compensatory growth in ungulates. Late-born captive calf elk on low or medium quality diets reached weights in winter similar to early-born calves, while late-born calves on a high quality diet had significantly lower weights than early-born calves during the first year of a study (Cook et al. 2004). Compensation in the low and medium nutrition groups may have been influenced by growth rate differences between sexes; late-born calves were composed of 62 percent males, compared to 31 percent in early-born calves. This pattern of compensatory growth was reversed during the second year, however, and the advantage of early birth was present in the low and medium nutrition groups but not in calves in the high nutrition group. Guinness et al. (1978) observed a relationship between winter weights and birth dates of red deer under high nutritional conditions. Late-born calves had lower weights, further illustrating the difficulty in assessing the presence of compensatory growth under sometimes widely different conditions. Holand et al (2003) reported that late calving in reindeer was associated with lower body weight in autumn but suggested caution when applying results from enclosure experiments to wild, free-ranging populations.

The relative importance of birth date differences resulting from age of male sires and their interaction with nutritional condition varies among studies and whether they involve wild or penned ungulates. Ginsberg and Milner-Gulland (1994) reported that breeding delays of one estrous cycle (18 days) in red deer can result in a 36-percent decline in reproductive success of females. Cook et al. (2004) suggested that birth date differences of 3 weeks (the effect of male age differences in our study) were insuffìcent to influence winter survival of calves under captive conditions. Mean differences of 1 week or less may be biologically significant for reindeer in environments with short seasons (Holand et al. 2003).

Perhaps more important than the effects of birth date and nutrition on survival of young are the long-term cumulative effects on herd productivity. Most studies that have failed to identify cumulative effects are short-term studies and, thus, are not able to determine these effects beyond 1 or 2 years. Green and Rothstein (1993) conducted a 9-year study to evaluate the relationship between birth date, long-term growth and reproductive success in bison. They documented beneficial effects of early birth that endured for the length of the study. Early-born females had significant fitness advantages and were more fecund during their first 9 years (Green and Rothstein 1993). Body weight differences related to birth date persisted throughout the study in females, suggesting that adult body size is enhanced by early birth. Links between birth date and body mass of moose calves in winter have been reported by Saether et al. (2003), who suggested that there may be long-term consequences of skewed sex ratios. Early births enhanced the probability that females would give birth in the succeeding year; late births increased the likelihood of subsequent reproductive failure.

To illustrate the range of interpretation of research results, Cook et al. (2001) stated that marginally deficient nutrition was responsible for delayed breeding of prime-aged lactating females despite high pregnancy rates. In our study of 17 prime-aged lactating females in deficient nutritional condition (less than 9 percent body fat), pregnancy rate was 94 percent, and conception dates were not delayed. This is another indication that age of male sires is an important influence on pregnancy rates and conception dates and is implicated in herd demographics due to reduced survival of late-born calves.

A longer, slower trend toward lower productivity in ungulate populations may exist with late conceptions because hinds that conceived early or produced heavy calves had higher lifetime success (Clutton-Brock et al. 1983). Several mechanisms are plausible to explain reduced long-term reproductive success. Delayed births may not allow females to recover from the demands of lactation in order to ovulate early in the rut or at all (Laflamme and Connor 1992). Female red deer that have delayed conception by one estrous cycle (18 days) may experience a 36 percent decline in reproductive success. In bison (Green and Rothstein 1993) it has been shown that the effects of late birth and the resulting decreased body mass may have lasting consequences that are likely not evident from the results of annual reproductive performance.

Reproductive success of males is related to body mass. Early-born bison calves are socially dominant to late-born calves and may have increased reproductive success (Lott 1979, Green and Rothstein 1993). Many life history characteristics are closely related to body mass of young females (Saether et al. 2003), which in moose is related to their body mass as calves, which is related to birth date. Because of this same relationship in male calves, the effects of late births result in reduced body mass of yearling males, which again can result in lower reproductive success. We could speculate that this pattern might function as a mechanism by which a subtle cycle of later births, lower body mass and decreased reproductive success is repeated to the long-term detriment of elk productivity.

The age of male sires can also influence reproductive dynamics and survival by means other than dates of conception. Young males may be either socially (behavior) or physiologically immature during the rut period. Female fallow deer avoided subadult males more than mature males (Komers et al. 1999).

Females with subadult males lost more weight (4.2 percent) during the rut than females with mature males (1.9 percent), and reduced body reserves could compromise female survival. Male moose in Norway exhibited a long-term decline in mean body mass as the proportion of adult males decreased (Solberg and Saether 1994) . They also found that the oldest male age groups experienced the largest declines. The relationship between male body mass and reproductive success has been reported for red deer and bison. Early birth affects the social dominance status and breeding success in male bison.

Young females may be especially sensitive to skewed sex ratios (Solberg et al. 2002, in Saether et al. 2003). In our study the behavioral immaturity of yearling males might explain the reproductive performance of 2-year-old females. There were approximately equal numbers of 2-year-old females for each of the five age classes of male sires (60 females total). Pregnancy rates were similar, ranging from 82 percent to 100 percent, and nutrition was significantly higher when yearling males were sires; however, conception dates of 2-year-old females were again about 3 weeks different between immature and mature male sires.

Management Implications

Effective management of elk populations might involve providing mature males to obtain early and synchronous conceptions, and interact with nutritional condition to enhance the survival of calves and long-term productivity. The importance of dates of conception might also be to set the stage for the influences of female nutritional condition. Without early conception, high nutritional condition of females cannot solely determine the probability of calf survival. We have restricted our discussion to interactions among male age and the nutritional condition of females and males. The nutritional condition of elk herds can be reduced for reasons other than habitat quality. Preliminary results from ongoing studies evaluating the energetic effects of recreational use (Wisdom et al. 2004) and increased movements related to hunting seasons (Ager et al. 2004) indicate energetic costs that also may affect herd demographics. Preliminary results from 4 years of a 6-year study evaluating archery disturbance during the rut indicate lower pregnancy rates and asynchronous conceptions (J. H. Noyes, unpublished data 2003).

We have identified several variables and their interactions that affect elk reproduction in slightly different ways. The challenge to wildlife managers is to provide the conditions that will allow the most opportunities for increased production over the greatest range of conditions. Managing for mature bulls through harvest regulations is much more straightforward than predicting precipitation and annual forage production. The presence of mature males in ungulate populations may be warranted for reasons other than their effects on short-term productivity. The significance of mature males in elk populations, regardless of the interpretations of research results, should not be ambiguous because of the evolutionary doctrine that states natural selection operates to provide conditions that enhance the survival of species. Mature bulls ordinarily function as principal sires of polygamous harems (Bubenik 1982). We seek to understand some of the complex interactions that are present today under conditions that have been greatly altered. Wildlife managers might consider all variables affecting the productivity of elk herds (male age, nutritional condition, predation, human disturbance and others). Challenges lay in adapting management options to the variety of social and environmental conditions that currently exist.

Reference List

Ager, A. A., B. K. Johnson, P. K. Coe, and M. J. Wisdom. 2004. Landscape simulation of foraging by elk, mule deer and cattle on summer range. *Transactions of the North American Wildlife and Natural Resources Conference.* 69:687–707.

Albon, S. D., B. Mitchell, B. J. Huby, and D. Brown. 1986. Fertility in female red deer (*Cervus elaphus*): The effects of body composition, age, and reproductive status. *Journal of Zoology (London).* 209:447–60.

Bubenik, A. D. 1982. Physiology. In *Elk of North America: Ecology and management*, eds. J. W. Thomas, and D. E. Toweill, 125–79. Harrisburg, Pennsylvania: Stackpole Books.

Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1983. The costs of reproduction to red deer hinds. *Journal of Animal Ecology.* 52:367–83.

Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1987. Early development and population dynamics in red deer:Density-dependent effects on juvenile survival. *Journal of Animal Ecology.* 56:53–67.

Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. DelCurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. *Wildlife Monograph.* 155:1–61.

Cook, R. C., D. L. Murray, J. G. Cook, P. Zager, and S. L. Monfort. 2001. Nutritional influences on breeding dynamics in elk. *Canadian Journal of Zoology.* 79:845–53.

Follis, T. B. 1972. *Reproduction and hematology of the Cache elk herd.*, 72–8. Salt Lake City, Utah: Utah Division of Wildlife Resources.

Geist, V. 1982. Adaptive behavioral strategies. In *Elk of North America: Ecology and management,* eds. J. W. Thomas, and D. E. Toweill, 219–78. Harrisburg, Pennsylvania: Stackpole Books.

Gibson, R. M., and F. E. Guinness. 1980. Differential reproduction among red deer (*Cervus elaphus*) stags on Rhum. *Journal of Animal Ecology.* 49:199–208.

Ginsberg, J. R., and E. J. Milner-Gulland. 1994. Sex-biased harvesting and population dynamics in ungulates: Implications for conservation and sustainable use. *Conservation Biology.* 8:157–66.

Green, W. C. H., and A. Rothstein. 1993. Persistent influences of birth date on dominance, growth and reproductive success in bison. *Journal of Zoology (London).* 230:177–86.

Guinness, F. E., T. H. Clutton-Brock, and S. D. Albon. 1978. Factors affecting calf mortality in red deer (*Cervus elaphus*). *Journal of Animal Ecology.* 47:817–32.

Hines, W. W., and J. C. Lemos. 1979. *Reproductive performance by two age-classes of male Roosevelt elk in southwestern Oregon, wildlife research report no. 8.* Portland, Oregon: Oregon Department of Fish and Wildlife.

Hines, W. W., J. C. Lemos, and N. A. Hartman. 1985. *Male breeding efficiency in Roosevelt elk of southwestern Oregon, wildlife research report no. 15.* Portland, Oregon: Oregon Department of Fish and Wildlife.

Holand, O., K. H. Roed, A. Mysterud, J. Kumpula, M. Nieminen, and M. E. Smith. 2003. The effect of sex ratio and male age structure on reindeer calving. *Journal of Wildlife Management.* 67:25–33.

Kiltie, R. A. 1988. Gestation as a constraint on the evolution of seasonal breeding in mammals. In *Evolution of life histories of mammals*, ed. M. S. Boyce, 257–89. New Haven, Connecticut: Yale University Press.

Komers, P. E., B. Birgersson, and K. Ekvall. 1999. Timing of estrus in fallow deer is adjusted to the age of available mates. *American Naturalist.* 153(4):431–6.

Laflamme, L. F., and M. L. Connor. 1992. Effect of postpartum nutrition and cow body condition at parturition on subsequent performance of beef cattle. *Canadian Journal of Animal Science.* 72:843–51.

Loison, A., and R. Langvatn. 1998. Short- and long-term effects of winter and spring weather on growth and survival of red deer in Norway. *Oecologia.* 116:489–500.

Lott, D. F. 1979. Dominance relations and breeding rate in mature male American bison. *Zeitschrift-Fuer-Tierpsychologie.* 49(4):418–32.

Mitchell, B., and G. A. Lincoln. 1973. Conception dates in relation to age and condition in two populations of red deer in Scotland. *Journal of Zoology (London).* 171:141–152.

Noyes, J. H., B. K. Johnson, L. D. Bryant, S. L. Findholt, and J. W. Thomas. 1996. Effects of bull age on conception dates and pregnancy rates of cow elk. *Journal of Wildlife Management* 60:508–517.

Noyes, J. H., B. K. Johnson, B. L. Dick, and J. G. Kie. 2002. Effects of male age and female nutritional condition on elk reproduction. *Journal of Wildlife Management.* 66 (4):1,301–7.

Rowland, M. M., L. D. Bryant, B. K. Johnson, J. H. Noyes, M. J. Wisdom, and J. W. Thomas. 1997. *The Starkey project: History, facilities, and data collection methods for ungulate research, general technical report PNW-GTR-396.* Portland, Oregon: U. S. Department of Agriculture, Forest Service.

Saether, B.-E., and M. Heim. 1993. Ecological correlates of individual variation in age at maturity in female moose (*Alces alces*): The effects of environmental variability. *Journal of Animal Ecology.* 62:482–9.

Saether, B.-E., E. J. Solberg, and M. Heim. 2003. Effects of altering sex ratio structure on the demography of an isolated moose population. *Journal of Wildlife Management.* 67:455–66.

Solberg, E. G., and B.-E. Saether. 1994. Male traits as life-history variables: Annual variation in body mass and antler size in moose (*Alces alces*). *Journal of Mammalogy.* 75:1,069–79.

Solberg, E. J., T. H. Ringsby, B.-E. Saether, and M. Heim. 2002. Biased adult sex ratio can affect fecundity in primipareous moose. *Wildlife Biology.* 8:117–28.

Squibb, R. C. 1985. Mating success of yearling and older bull elk. *Journal of Wildlife Management.* 49:744–50.

Trainer, C. E. 1971. *The relationship of physical condition and fertility of female Roosevelt elk (*Cervus canadensis roosevelti*) in Oregon.* M.S. thesis, Oregon State University, Corvallis.

Wisdom, M. J., J. G. Cook, M. M. Rowland, and J. H. Noyes. 1993. *Protocols for care and handling of deer and elk at the Starkey Experimental Forest and Range, general technical report PNW-GTR-311.* Portland, Oregon: U. S. Department of Agriculture, Forest Service.

Wisdom, M. J., A. A. Ager, H. K. Preisler, N. J. Cimon, and B. K. Johnson. 2004. Effects of off-road recreation on mule deer and elk. *Transactions of the North American Wildlife and Natural Resources Conference.* 69:531–50.

Transactions
of the
Sixty-ninth North American Wildlife and Natural Resources Conference

Conference Theme:
Resource Stewardship in the 21st Century:
A Voyage of Rediscovery

March 16 to 20, 2004
DoubleTree Hotel and Spokane City Center
Spokane, Washington

Edited by
Jennifer Rahm

Published by the
Wildlife Management Institute
Washington, DC
2004

Special Session Six. Policy Implications from Long-term Studies of Mule Deer and Elk: A Synthesis of the Starkey Project