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Source: *Journal of Mammalogy*, Vol. 79, No. 3 (Aug., 1998), pp. 1038-1044

Published by: American Society of Mammalogists

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ANTLER SIZE AND WINTER MORTALITY OF ELK: EFFECTS OF ENVIRONMENT, BIRTH YEAR, AND PARASITES

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Correlates with antler size of 215 male elk (*Cervus elaphus*) that died during 5 winters on the National Elk Refuge, Wyoming, were investigated. The elk were 1.5–14.5 ($\bar{X} = 6.5$, $SE = 0.19$) years old. Males with clinical infestations of scab mites (*Psoroptes*) had antlers with more points, greater beam circumference, and greater mass than males not afflicted with mites. Development of antlers and infestation with scabies were correlated positively with age. Controlling for age, antler size was correlated with March and April temperatures during the year that they grew (nutritional effect) and weather conditions while the males were in utero. Population size, adult sex ratio, and supplemental winter feeding of elk at the National Elk Refuge exhibited no apparent influences on antler size.

Key words: *Cervus elaphus*, elk, antlers, nutrition, mortality, parasites, scabies, supplemental feeding, weather, Wyoming

Antlers function primarily as weapons in male-male competition for breeding opportunities (Bubenik, 1968; Clutton-Brock et al., 1979; Clutton-Brock, 1982) and possibly as symbols of male vigor that females may use to select mates (Geist, 1966, 1991). Antler size and complexity tend to increase with age (Flook, 1970; Goss, 1983; McCullough, 1982; Solberg and Saether, 1994; Wolfe, 1983), and both are correlated with male dominance and fighting ability (Bartos et al., 1988; Topinski, 1974) and consequently potential lifetime reproductive success (Clutton-Brock et al., 1988).

Although relationships between antler characteristics and age have been reported for harvested and culled elk (*Cervus elaphus*—Flook, 1970; Freddy, 1987; Frisina and Douglass, 1993; McCorquodale, 1989; Wolfe, 1983), little is known about elk that die of natural causes. In addition to age, other factors that affect antler size are nutrition (Goss, 1983; Nelson and Leege, 1982; Solberg and Saether, 1994), population density (Clutton-Brock et al., 1982;

McCorquodale, 1989), adult sex ratio (Solberg and Saether, 1994), and mass at birth, the latter through its affect on adult body size (Clutton-Brock et al., 1979, 1988; Geist, 1991; Hyvärinen et al., 1977; Mech et al., 1991). Supplemental winter feeding also may be expected to improve antler growth by retarding loss of body mass (Kozak et al., 1994; Taber, 1959). Finally, parasites and infectious disease can impair quality of secondary sexual traits (Hamilton and Zuk, 1982; Moller, 1991) and impose survivorship costs (Festa-Bianchet, 1989). Each autumn some males of the Jackson elk herd that are heavily parasitized with scab mites (*Psoroptes*) develop clinical scabies (Samuel et al., 1991; Smith, 1985). It is unknown how antler size of these parasitized and often emaciated animals compares to unafflicted elk.

My objectives were to: 1) profile antler characteristics of elk that die during winter; 2) investigate relationships of age, population density, adult sex ratio, previous growing season's weather, and supplemental feeding to antler size; 3) evaluate the rela-

tionship of antler size to parasitism by scab mites; and 4) evaluate if antler size attained in adult elk was a reflection of early development.

STUDY AREA

The National Elk Refuge (NER) (43°45'N, 110°45'W) encompasses 98 km² adjacent to the town of Jackson, Wyoming. Refuge habitats are 81% grasslands, shrub-grasslands, and cultivated fields and 19% woodlands. The southern half of the Refuge, where elk are primarily distributed and fed in winter, is <1% forested. The reporting station at Jackson, Wyoming, at 1,899 m above mean sea level, received 420 mm of precipitation annually. Monthly temperatures during January and July averaged -9.3 and 16.2°C, respectively (National Oceanic and Atmospheric Administration, 1977–1993, in litt.).

Elk were fed pelleted alfalfa hay for 35–91 days (\bar{X} = 63.8, SE = 9.1) during winters 1989–1990 to 1993–1994. Annual feeding rates averaged 3.4 kg/elk/day (SE = 0.2), and the number of elk on the NER ranged from 8,131 to 8,800 (\bar{X} = 8,408, SE = 114) during classification counts in February 1990–1994. The number of males ≥ 2 years old averaged 1,119 (SE = 36), or 13.3% (SE = 0.4) of the herd.

MATERIALS AND METHODS

The NER staff have endeavored to locate and document every elk mortality on the NER each winter since 1968 (Smith, 1985). Carcasses were located from snow cats, horseback, and on foot during November–May. Scavenging coyotes (*Canis latrans*), ravens (*Corvus corvax*), bald eagles (*Haliaeetus leucocephalus*), and golden eagles (*Aquila chrysaetos*) signaled locations of carcasses. Carcasses were documented in outlying areas during routine wildlife censuses, habitat surveys, and systematic searches for shed antlers each spring.

During winters 1989–1990 to 1993–1994, I measured circumference of the right and left antler beams above the burr, and the total number of points on each antler beam of elk that died. Antlers of elk ≥ 2 years old were sawed from

the skull through the pedicel and weighed to the nearest 0.25 kg. Ages of yearlings were based on tooth eruption and replacement (Quimby and Gaab, 1957). The Wyoming Game and Fish Department Laboratory in Laramie, Wyoming determined ages of elk ≥ 2 years old from cementum annuli. Each carcass was examined for external maladies including exudative dermatitis and alopecia, lesions characteristic of animals afflicted with scab mites (Samuel et al., 1991; Smith, 1985). Skin samples were examined at the National Wildlife Health Research Center to confirm presence of scab mites. If mortalities were not found within several days of death, scavenging often precluded determining ectoparasite infestations.

I did not know birth weights of elk that died in winter. However, cohort birth weights varied annually with April and May temperatures in red deer in Scotland (Albon et al., 1983, 1987) and with March temperatures in elk in Jackson (Smith et al., 1997). Therefore, environmental conditions during their birth year were used as a proxy to evaluate influence of birth weight on antler size of mature elk.

Annual classification counts of the elk were conducted in February from feed trucks to estimate number of adult males (≥ 2 years old), yearling males, females (≥ 1 year old), and calves on the Refuge. To these counts, I added number of males ≥ 1 year old that had died earlier in winter to determine total number of males present.

I used analysis of covariance (ANCOVA) to test if the effect of disease status on antler mass was significant after adjusting for differences in age of male elk with and without clinical scabies (Sokal and Rohlf, 1981). For all statistical tests, $P < 0.05$ was considered significant.

RESULTS

Mean age (\bar{X} = 6.53, SE = 0.19) of 215 male elk ≥ 1 year old that died on the NER during winters 1989–90 through 1993–94 varied annually (F = 2.58, $d.f.$ = 4, 202, P = 0.04). Only 5% of mortalities exceeded 10.5 years of age, and they were combined into a ≥ 11.5 age class.

Antler measurements were obtained from 193 elk, and antler mass was obtained from 114 of the 215 male elk. Just 1 of 17 (6%) yearling males had more than one point on

TABLE 1.—Number of antler points observed on male elk that died during winters 1989–1990 through 1993–1994 at the National Elk Refuge, Wyoming.

Antler points ^a	Age (years)										Total
	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	≥11.5	
1 by 4	1 ^b										1
2 by 4		1 ^b		1 ^b	1 ^b						3
2 by 6								1 ^b			1
3 by 3	1	1									2
3 by 4		1 ^b									1
3 by 6					1 ^b					1 ^b	2
4 by 4	1	1									2
4 by 5		1	1		1	1 ^b					4
4 by 6			1 ^b	1 ^b							2
5 by 5		4	5	2	3			1	3	1	19
5 by 6		2	3	2	2	2	5 ^c			1	17
5 by 7									1 ^b		1
6 by 6		4	10	20	27	23	9	7	2	4	106
6 by 7			1	1	2	2		1	1		8
6 by 8							1				1
7 by 7					1	2		1		1	5
7 by 8									1		1
Total	3	15	21	27	38	30	15	11	8	8	176
Mean	6.3	9.7	11.2	11.5	11.6	12.0	11.8	11.7	11.8	11.5	
SE	0.9	0.6	0.2	0.3	0.2	0.2	0.2	0.5	0.6	0.5	
% broken ^d	33	13	5	7	5	3	13	18	13	13	

^a Indicates number of antler points on left and right antlers.

^b ≥1 point broken from the antlers.

^c One of the 5 elk had points broken from its antlers.

^d The % of animals in the age class with points broken from their antlers.

one of its antlers. In all characteristics measured, antler size declined after 10.5 years of age (Tables 1 and 2).

Among the 215 mortalities, 124 (58%)

TABLE 2.—Antler mass (kg) and basal circumference (cm) of male elk that died during winters 1989–1990 through 1993–1994 at the National Elk Refuge, Wyoming.

Age (years)	Mass			Circumference		
	<i>n</i>	\bar{X}	<i>SE</i>	<i>n</i>	\bar{X}	<i>SE</i>
2.5	2	1.6	0.2	2	111	6
3.5	5	4.8	0.6	6	156	22
4.5	11	5.8	0.4	11	213	6
5.5	15	7.5	0.5	15	204	1
6.5	23	7.1	0.4	23	210	3
7.5	24	7.6	0.5	24	217	7
8.5	10	8.4	0.6	10	223	7
9.5	7	9.1	0.9	7	237	13
10.5	7	9.2	1.1	7	230	15
≥11.5	7	7.3	1.0	8	227	12

males were afflicted with scabies, and another 39 (18%) may have had scabies but there was insufficient hide remaining to make that determination. Excluding the 39 mortalities of unknown status, carcasses with clinical scabies were significantly older than those without scabies ($t = 5.5$, $d.f. = 168$, $P < 0.01$), had more total antler points ($t = 7.42$, $d.f. = 166$, $P < 0.01$), had greater antler circumference ($t = 2.57$, $d.f. = 104$, $P = 0.01$), and had greater antler mass ($t = 3.23$, $d.f. = 102$, $P < 0.01$; Table 3). Controlling for the covariate age, antler mass of males with scabies exceeded ($F = 4.89$, $d.f. = 1, 96$, $P = 0.037$) antler mass of males without clinical scabies.

Antler mass varied among the 10 age classes ($F = 3.67$, $d.f. = 9, 100$, $P < 0.01$; Table 2). However, age classes 5.5–8.5 produced similar antler mass ($F = 0.8$, $d.f. = 3, 68$, $P = 0.48$) and were combined to

TABLE 3.—Age and antler measurements of winter mortalities of elk with and without clinical scabies from the National Elk Refuge, Wyoming, winters 1989–1990 through 1993–1994.

Measurement	Elk with scabies		Elk without scabies	
	\bar{X}	SE	\bar{X}	SE
Age (years)	7.5	2.2	5.1	3.5
Total antler points	11.6	1.3	8.2	4.6
Circumference of antlers (cm)	216.3	29.8	193.0	42.3
Mass of antlers (kg)	7.8	2.4	5.5	2.3

evaluate factors that influenced the size that antlers achieved. Log₁₀-transformed mean temperatures in March and April from the spring in which antler growth began accounted for 91% of variation in antler mass produced annually ($r^2 = 0.91$, $F = 30.2$, $d.f. = 1, 3$, $P = 0.01$). The antler mass that they produced was unaffected by number of days that those males were fed ($r^2 = 0.07$, $F = 0.23$, $d.f. = 1, 3$, $P = 0.70$), the starting date of feeding ($r^2 = 0.12$, $F = 0.40$, $d.f. = 1, 3$, $P = 0.60$), nor the ration that they received ($r^2 = 0.04$, $F = 0.09$, $d.f. = 1, 3$, $P = 0.80$) during the winter prior to their deaths.

Mean monthly temperatures in January and March of their birth year accounted for 90% of the variation in antler mass when animals died 5.5–8.5 years later ($R^2 = 0.90$, $F = 22.9$, $d.f. = 2, 5$, $P = 0.003$). However, both the number of days that their mothers were supplementally fed ($r^2 = 0.76$, $F = 18.9$, $d.f. = 1, 6$, $P = 0.005$) and the daily ration that their mothers received ($r^2 = 0.83$, $F = 30.0$, $d.f. = 1, 6$, $P = 0.002$) during their birth year varied inversely with mean antler mass that males produced during the year of their death. Those data suggest that the maintenance rations fed to elk had no positive effect on antler mass of males, whereas winter temperatures and duration of winter did.

DISCUSSION

Mean ages of male Rocky Mountain elk harvested in Colorado (Freddy, 1987),

Banff National Park (Flook, 1970), New Mexico (Wolfe, 1983), and Montana (Frisina and Douglass, 1993) were less than ages of winter mortalities on the NER. Likewise, mean ages of male elk ≥ 1 -year-old harvested during migration to the NER during 1991–1995 ranged from 3.6–4.2 years ($SE = 0.10$ – 0.20 , $n = 3,790$ —S. L. Cain, in litt.), compared with 6.5 years ($SE = 0.19$) for winter mortalities. These data suggest that male elk are harvested at an average age that is younger than elk that die of causes not associated with hunting.

Classifications of elk on the NER showed that 17.1% of 503 yearlings during winter 1990–1991 and 16.5% of 436 yearlings during winter 1991–1992 had at least one branched antler. Fifteen percent of Colorado's White River elk herd (Freddy, 1987) and 24% of yearlings harvested in southwest Montana (Frisina and Douglass, 1993) had at least one branched antler. Yearlings with as many as 4 points/antler were observed on the NER each winter. Only one of 17 yearlings that died on the NER carried antlers with at least one branched beam. This suggests that yearlings with less well-developed antlers, an indication of body weight and condition (Hyvärinen et al., 1977; Clutton-Brock et al., 1982; McCullough, 1982), were more likely to perish during winter.

As noted by Flook (1970) and Wolfe (1983), we found that measurements and mass of antlers declined after 10.5 years of age. Clutton-Brock et al. (1988) reported that fighting ability and breeding success in male red deer peaked between the ages of 7 and 10. Males >10 years of age were no longer able to successfully compete for mating privileges (Clutton-Brock et al., 1982).

Male elk with clinical scabies were older ($\bar{X} = 7.5$, $SE = 2.2$ years) than those in which scabies was absent ($\bar{X} = 5.1$, $SE = 3.5$ years), as previously reported for winter 1982–1983 on the NER (Smith, 1985). Elk achieve maximum body mass, scrotum circumference, and sperm production when 7

years of age (Flook, 1970; Haigh, 1984). Male elk with scabies, had on average, reached the age of maximum breeding potential (Clutton-Brock et al., 1988).

Clinical signs of scabies appear in male elk subsequent to the fall rut (Smith, 1985). The heavier age-adjusted antlers of males with scabies suggests that larger-antlered males may have been predisposed to mite infestations. Given the competitive advantage of large antlers (Clutton-Brock et al., 1982), males with scabies were likely dominant and were weakened by the rigors of the autumn rut. This hypothesis, first suggested by Murie (1951), remains to be tested.

Correlates with antler mass, the characteristic of antlers considered most indicative of breeding success (Clutton-Brock et al., 1988) and metabolic efficiency (Geist, 1991), were independent of population density and sex ratio. Liberal food supplementation of cervids can enhance antler size (Suttie and Hamilton, 1983; Suttie and Kay, 1983). However, the maintenance rations fed at the NER, which varied with severity and duration of winter conditions and numbers of elk on the NER (Oldemeyer et al., 1993; Smith et al., 1997), did not influence antler size that these wild elk produced during the summer prior to their deaths.

During their growth year, antler mass varied with combined mean monthly temperatures in March and April, the months during which new vegetation growth and antler growth began. Warm temperatures in March and April promote early abundance of new grasses and forbs. These foods are more highly digestible and nutritious than pelleted alfalfa fed to the elk and speed recovery of body condition lost during autumn and winter (Nelson and Leege, 1982; Smith et al., 1997). Timing of protein, energy, and other nutrient availability, in excess of somatic needs, influences growth of antlers, which are highly sensitive to nutrition (Goss, 1983; Ullrey, 1983).

Greater food supplementation of their mothers during their birth year did not re-

sult in larger, but rather smaller, antlers of male elk at 5–8 years of age. Instead, mass of antlers of males varied with weather conditions while in utero. Mean monthly temperatures during January, the coldest month of the year, and March, the month during which new plant growth generally first appears on the NER, accounted for 90% of the variation in antler mass of elk mortalities in winter. Smith et al. (1997) reported that combined mean monthly temperatures in December, January and March accounted for 98% of the variation in cohort birth weights of the Jackson elk herd. Review of those data shows that mean monthly temperatures in January and March account for 95% of the variation in cohort birth weights ($R^2 = 0.95$, $F = 39.6$, $d.f. = 2, 4$, $P = 0.002$). Temperate cervids lower activity and food intake in winter (Kozak et al., 1994; Mautz, 1978; Nelson and Leege, 1982) limiting potential benefits on reproduction of feeding alfalfa hay at the NER. Larger birth-weight cohorts, that experienced high survival, followed milder winters and earlier growth of nutritious forage in spring coincident with the final trimester of pregnancy (Smith et al., 1997). Larger birth-weight cohorts produced larger antlers, supporting Geist's (1991) contention that relative mass of antlers in males should be correlated with relative neonatal mass produced by females. Although Geist (1991) analyzed interspecific relationships of antler mass and neonatal mass, my data suggest that the relationship also applies to intercohort variations within a population.

Temperatures during the growing season preceding their deaths and ambient temperatures when male elk were in utero are presumed independent effects on antler mass. The former effect emphasizes the sensitivity of antler growth to prevailing foraging conditions during each year of cervid's lives (Bubenik, 1982; Taber, 1959; Vogt, 1948). The latter provides further evidence of the persistent effects throughout their lifetimes that environmental conditions during the year of birth manifests on growth,

reproductive success, and survival of cervids (Albon et al., 1987; Mech et al., 1991). Finally, supplemental winter feeding of free-ranging elk, at maintenance rations provided on the NER, cannot be justified as a means of producing larger young at birth or larger antlers.

ACKNOWLEDGMENTS

This research was funded by the United States Fish and Wildlife Service. J. A. Creasy, M. B. Hedrick, K. L. Painter, R. D. Pape, A. D. Ridgway, R. L. Rogers, T. A. Root, and R. R. Rowley collected data, teeth, and antlers from elk mortalities. R. L. Rogers measured and weighed antlers. J. Berger provided helpful comments on the manuscript.

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Submitted 1 July 1997. Accepted 29 November 1997.

Associate Editor was John A. Litvaitis.