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ADAPTIVE SEX RATIOS: ANOTHER EXAMPLE?

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We investigated sex bias at birth among 165 young elk (*Cervus elaphus*) born to free-ranging, supplementally fed females in northwestern Wyoming during 1990–1992. Sex ratios of an additional 86 young born to females confined and supplementally fed in pastures during 1978–1982 also were recorded. Sex ratios for cohorts of neonates were not sex-biased. Likewise, sex ratios of neonates were not sex-biased in Grand Teton National Park, Wyoming, but they were male-biased on calving areas of lower densities of elk outside Grand Teton National Park. The proportion of males born in seven cohorts increased with earlier initiation of supplemental feeding and with digestibility of feed. Our findings appear to support the Trivers and Willard hypothesis of adaptive sex ratios.

Key words: *Cervus elaphus*, elk, nutrition, sex ratios, Wyoming

Observations of sex bias of both males and females among neonates of several species of cervids has prompted conflicting theories explaining this phenomenon (Clutton-Brock and Iason, 1986; McCullough, 1979). Fisher (1930) first proposed a theory of adaptive variation to explain distorted sex ratios of offspring. Trivers and Willard (1973) more thoroughly articulated this theory, which states that among polygamous mammals in which males exhibit greater variance in reproductive success than females, maternal investment should be greater in sons than in daughters. Furthermore, mothers should produce more sons than daughters when their body condition is superior during pregnancy. Selective resorption or abortion of male fetuses is the predicted functional mechanism (Maynard Smith, 1980; Rivers and Crawford, 1974; Trivers and Willard, 1973). Stressful environments or food shortage can increase the male-biased mortality both in utero and after birth (Clutton-Brock et al., 1985, 1986; Rivers and Crawford, 1974; Robinette et al., 1957). Studies of caribou (*Rangifer tarandus*; Thomas et al., 1989) and mule deer (*Odocoileus hemionus*; Kucera, 1991) support the hypothesis of Trivers and Willard

(1973). With increasing dominance rank of females (which correlated with body weight), progeny of red deer became significantly male-biased (Clutton-Brock et al., 1986).

Alternatively, in several populations of *Odocoileus* (Pederson and Harper, 1984; Verme, 1983), and reindeer (*R. tarandus*; Skogland, 1986) the sex ratio of embryos or young is male-biased when deer are subjected to nutritional stress, poor quality of habitat, or high population density. Hoefs and Nowlan (1994) reported on sex ratios at birth of supplementally fed, captive elk (*Cervus elaphus*), reindeer, caribou, mountain goats (*Oreamnos americanus*), Dall's sheep (*Ovis dalli dalli*), and Stone's sheep (*Ovis dalli stonei*). All six taxa showed a distorted sex ratio of neonates favoring females, which they attributed to food supplementation of those animals.

Clutton-Brock and Iason (1986) concluded that several different mechanisms might influence sex ratios at birth. They recommended additional research into the extent and consistency of variation in sex ratios, and the effects of parental environment or phenotype on the relative fitness of sons and daughters.

In northwestern Wyoming, ca. 23,000 elk are supplementally fed during winter, ca. 7,500 at the National Elk Refuge (Smith and Wilbrecht, 1990) and the remainder on 22 feeding grounds operated by the state of Wyoming (Thorne et al., 1991). The influence of winter feeding on weight dynamics and reproduction has been studied in confined elk (Oldemeyer et al., 1993; Thorne et al., 1976), but variation in sex ratios at birth of supplementally fed, free-ranging elk has not been reported.

Neonatal elk were captured and radiocollared in northwestern Wyoming to investigate survival, dispersal, and other aspects of population regulation (Smith, 1994). We recorded the sex of this sample of 165 young born to free-ranging females that were supplementally fed in winter at the National Elk Refuge. Newborns were captured in Grand Teton National Park, where densities of elk averaged 5.9/km², and in similar habitats of the Bridger-Teton National Forest (Cole, 1969), where densities of elk averaged 2.4/km² (Smith, 1994). We predicted that more males than females would be born outside Grand Teton National Park than in the Park based on previous research on ungulates by Clutton-Brock et al. (1986) and theoretical arguments of Trivers and Willard (1973).

Sex of 86 young born to adult female elk that were captured, held in pastures, and supplementally fed at the National Elk Refuge during winters of 1978, 1979, 1980, and 1982 (Oldemeyer et al., 1993) provided a comparative sample from confined elk supplemented with the same feed at the same location. We predicted no relationship between severity of winter and sex ratio at birth because level of ration and duration of feeding has varied annually to compensate for severity of winter and availability of standing forage.

MATERIALS AND METHODS

Boyce (1989) and Smith and Robbins (1994) described the boundaries, topography, and vegetative communities of the Jackson elk herd,

with a range that encompassed 5,490 km² in the Snake River watershed of northwestern Wyoming where this investigation took place (43°45'N, 110°45'W). Elevations ranged from 1,950 to >3,650 m. Summer ranges included sagebrush (*Artemisia*) grasslands, tall-forb meadows, and subalpine coniferous forests. Over 80% of the elk herd was supplementally fed for ca. 3 months each winter at either the National Elk Refuge or one of three state of Wyoming feeding grounds in the Gros Ventre drainage (Fig. 1).

The National Elk Refuge encompassed 98 km² of irrigated grasslands, shrublands, and mixed conifer-aspen (*Populus tremuloides*) forest near the southern end of the Jackson Hole Valley. About 125 elk/km² wintered on the southern 6,000 ha of the Refuge during the winters of this investigation. Mean annual temperatures decreased, and precipitation and snowfall increased from the National Elk Refuge northward to Yellowstone National Park (Smith and Robbins, 1994). The reporting station at Jackson, at 1,899 m elevation, is adjacent to the Refuge and receives 420 mm of precipitation annually. Monthly temperatures in Jackson during January and July averaged -9.3 and 16.2°C, respectively (National Oceanic and Atmospheric Administration, 1977-1993, Climatological Data, Wyoming; Fig. 1).

During 1990-1992, six newborns were captured by investigators on foot, eight from horseback, and 151 from a Hillar 12-E helicopter contracted from Hawkins and Powers Aviation in Greybull, Wyoming. We captured two groups of 25 neonates each year, one group that would summer inside Grand Teton National Park and another group that would summer outside the Park (Smith, 1994).

Captures were allocated among eight distinct calving areas based upon the proportion of adult females that used each calving area and the probability that animals born in each area would summer inside or outside Grand Teton National Park (Fig. 1). These criteria were developed in a 7-year study of radiocollared adult elk of the Jackson elk herd (Smith and Robbins, 1994). Capture efforts from the helicopter were rotated among the eight calving areas throughout 27 May-8 June 1990, 26 May-9 June 1991, and 27 May-6 June 1992. With the exception of one young captured on 21 May 1991, all efforts to capture young elk from horseback and on foot

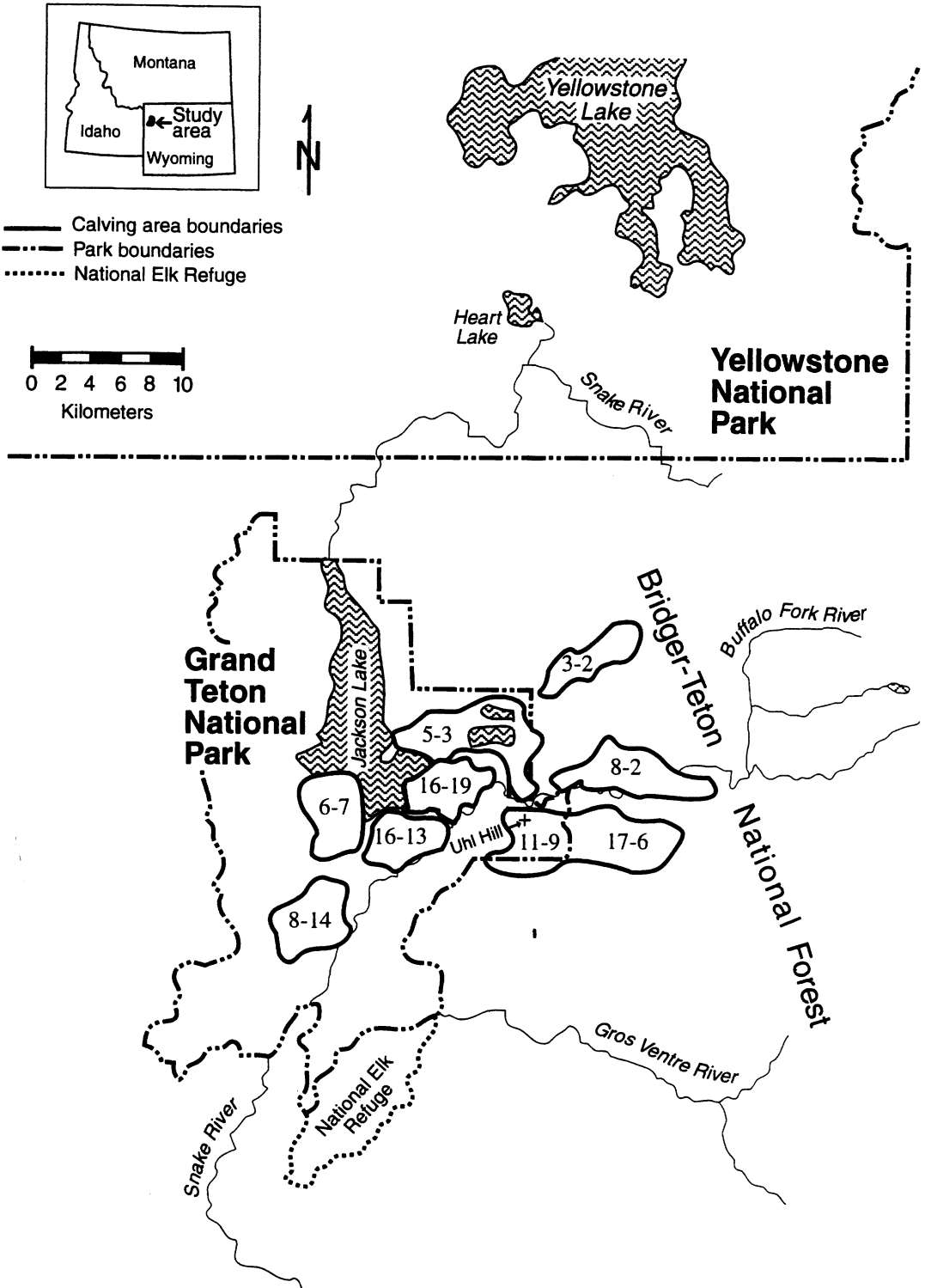


FIG. 1.—Number of neonatal elk (males—females) captured and radiocollared during 1990–1992 in the Jackson elk herd of northwestern Wyoming.

were apportioned to those calving areas in which collars had been cast by young previously captured from the helicopter. No young were captured after 30 June.

Captured young were manually restrained, blindfolded, hobbled, sexed, weighed to the nearest 0.25 kg, and aged. To age neonates, we measured eruption of incisor one and diameter of the umbilicus with a caliper, and categorized the degree of healing of the umbilicus, hardening of the hooves, and stature and coordination of the animal according to Johnson (1951).

Nearly all elk that frequented the areas where young were captured wintered on or adjacent to the National Elk Refuge (Boyce, 1989; Smith and Robbins, 1994; Smith et al., in press). To increase the number of years of data, we performed additional analyses of studies conducted at the National Elk Refuge in 1978, 1979, 1980, and 1982. Oldemeyer et al. (1993) described the experimental design of those studies that evaluated weight dynamics and reproductive success of adult female elk supplementally fed in pastures during winter. Nine to 10 females were held in each of three 4-ha pastures on the Refuge through birthing and released with their young ca. 1 August each year. The elk were fed 2.3 kg per animal per day of pelleted alfalfa hay, averaging 58.5% ($SE = 1.8\%$) digestibility and 16.4% ($SE = 0.4\%$) crude-protein content. The same type of feed also has been provided to the free-ranging herd on the refuge since 1975 for an average of 79 days annually (Smith and Wilbrecht, 1990).

Cessation of the 1978–1982 feeding trials each winter coincided with termination of supplemental feeding of the free-ranging herds of elk wintering on the National Elk Refuge. Thereafter, the elk foraged on vegetation growing in the pastures. During the period of parturition, pastures were walked daily to locate newborn young. A total of 86 young were captured, marked, sexed, and weighed within 24 h of birth. These confined elk provided study groups not subjected to varying densities of elk during the last trimester of gestation.

The SYSTAT (SYSTAT, Inc., Evanston, IL) for Windows statistical software package was used to test hypotheses. Frequencies of each gender of elk captured among years and between areas were compared with chi-square tests. We used two-way analysis of variance (ANOVA) to test differences in capture ages of young be-

TABLE 1.—Sex, Julian dates of birth, and age in days at capture of elk born during 1978–1982 in pastures at the National Elk Refuge and free-ranging young born 1990–1992 in Grand Teton National Park and the Bridger-Teton National Forest of northwestern Wyoming.

Year	Sex	n	Date of birth	Age at capture
			$\bar{X} \pm SE$	$\bar{X} \pm SE$
1978	M	8	161.6 \pm 2.4	
1978	F	10	160.2 \pm 2.5	
1979	M	11	161.2 \pm 2.1	
1979	F	6	161.2 \pm 3.3	
1980	M	12	159.4 \pm 2.0	
1980	F	17	158.5 \pm 1.9	
1982	M	9	156.4 \pm 2.3	
1982	F	13	159.1 \pm 2.2	
1990	M	27	150.5 \pm 1.3	3.9 \pm 0.34
1990	F	26	148.8 \pm 1.5	4.0 \pm 0.35
1991	M	35	151.9 \pm 1.2	3.1 \pm 0.30
1991	F	28	149.6 \pm 1.5	4.1 \pm 0.33
1992	M	28	151.9 \pm 1.3	3.4 \pm 0.33
1992	F	21	151.5 \pm 1.7	3.1 \pm 0.38

* All young captured 1978–1982 were ≤ 1 day-old.

tween sexes and among years. Linear relationships of sex ratios for cohorts with environmental and supplemental feeding variables were tested with least-squares simple and multiple regression. For all statistical tests, $\alpha \leq 0.05$ was considered significant.

RESULTS

The mean ($\pm SE$) ages of captured elk were 3.5 \pm 0.19 days for 90 males and 3.7 \pm 0.20 days for 75 females (range = 0–7 days; Table 1). Two-way ANOVA indicated no differences in the interaction term, or in the main effects of year ($F = 2.22$, $df = 2, 159$, $P = 0.11$) or sex ($F = 0.86$, $df = 1, 159$, $P = 0.36$) on age at capture.

There were no differences in the relative frequencies of each sex captured among years during 1978–1982 ($\chi^2 = 2.88$, $df = 3$, $P = 0.41$), or during 1990–1992 ($\chi^2 = 0.44$, $df = 2$, $P = 0.80$), or during all 7 winters ($\chi^2 = 4.76$, $df = 6$, $P = 0.57$). Sex ratios neither varied from 1:1 during 1978–1982 (46.5:53.5; $\chi^2 = 0.29$, $df = 1$, $P = 0.59$), nor during 1990–1992 (54.5:45.5; $\chi^2 = 1.02$, $df = 1$, $P = 0.31$; Table 1).

TABLE 2.—Variables associated with winter feeding and numbers of elk wintering on the National Elk Refuge during the winters preceding capture of young in this study. Mothers of young captured during 1978–1982 were confined to pastures on the National Elk Refuge. Mothers of young captured during 1990–1992 were free-ranging.

Variable	1978	1979	1980	1982	1990	1991	1992
Daily ration (kg/elk) ^a	5.0	5.1	5.0	5.0	7.9	7.5	6.6
Percentage of digestible dry matter	58.5	61.8	60.3	53.4	62.7	62.8	61.4
Percentage of crude protein	16.6	17.5	15.8	15.5	17.4	17.5	15.8
Number of days fed	75	106	67	82	67	69	57
Date feeding began (Julian date)	20	0	36	22	23	15	22
Date feeding ended (Julian date)	95	100	86	106	89	83	83
Depth (cm) of snow in December	38.1	83.8	10.2	63.5	22.9	40.6	22.9
Number of elk	8,413	7,828	7,749	6,530	8,323	8,314	8,800

^a During 1978–1982, free-ranging elk were fed 6.13 ± 0.67 kg per elk per day and the confined elk fed 5.0 ± 0.08 ($P = 0.14$).

Annual variation in the percentage of males at birth was not correlated with supplemental feed ration ($P = 0.61$) or duration of feeding ($P = 0.27$), but in years when supplemental feeding began earlier, more males were born ($r^2 = -0.70$, $F = 11.8$, $d.f. = 1,5$, $P = 0.02$; $\hat{y} = 64.32 - 0.69x$). Winter feeding began earlier when depth of snow in December (x_1) was greater and numbers of elk wintering on the National Elk Refuge (x_2) were larger ($R^2 = 0.97$, $F = 54.4$, $d.f. = 2,4$, $P < 0.01$; $\hat{y} = 91.43 - 0.41x_1 - 0.01x_2$). The combined effects of starting date of feeding (x_1) and percentage of digestible dry matter (x_2) in supplemental feed explained 90% of the variation in percentage of males born in each cohort ($R^2 = 0.90$, $F = 17.1$, $d.f. = 2,4$, $P = 0.01$; $\hat{y} = -29.6 - 0.58x_1 + 1.52x_2$; Table 2 and Fig. 2).

No difference existed in the relative frequencies of young captured from Grand Teton National Park ($n = 127$) and Bridger-Teton National Forest ($n = 38$) among years ($\chi^2 = 3.67$, $d.f. = 2$, $P = 0.16$; Table 3). A significantly greater ratio of males: females were captured in the Forest (28:10) than in the Park (62:65; $\chi^2 = 6.33$, $d.f. = 1$, $P = 0.01$). The sex ratio of young captured annually did not vary in Bridger-Teton National Forest $\chi^2 = 0.87$, $d.f. = 2$, $P = 0.64$) or in Grand Teton National Park ($\chi^2 = 0.44$, $d.f. = 2$, $P = 0.80$; Table 3).

DISCUSSION

Male : female ratios of neither elk born in the Refuge pastures nor free-ranging neonates were significantly different from 50:50. The sex ratio of the free-ranging sample, however, may be biased because capture effort was minimal late in the calving season, after 15 June. Clutton-Brock et al. (1982) reported that male red deer tended to be born earlier than females. Young born in pastures on the National Elk Refuge, however, showed no tendency for either sex to be more common after 15 June. Among our larger sample of free-ranging young, males were born later than females (Smith et al., in press). This was not a function of age at capture because captured males were similar to females in age (Table 1). A better representation of late-born elk may have skewed the sex ratio toward males.

Many authors have reported in-utero sex ratios in elk of the northern Rocky Mountains that were statistically not different from 50:50 (W. G. Hepworth, in litt.; Kit-tams, 1953; Murie, 1951), but these are generally sex ratios from mid-pregnancy. Post-conception sex ratios favoring male cervids may be the general rule (Flook, 1970; Verme, 1983) with male-biased prenatal mortality reducing that sex ratio. For example, prenatal mortality of mule deer in Utah was heaviest during the first 2–3 months of gestation and relatively minor

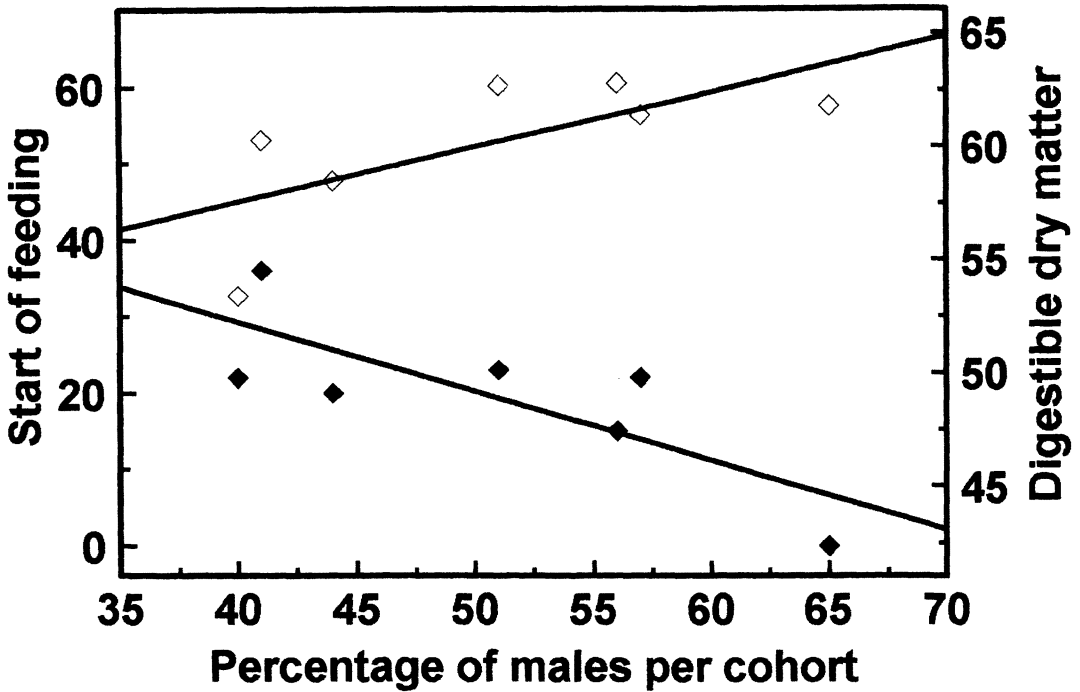


FIG. 2.—Percentage of males among captured neonates of seven cohorts of elk, the starting date (Julian) of supplemental feeding (solid diamonds) and percentage of digestible dry matter of pelleted alfalfa fed (open diamonds) to the Jackson elk herd the preceding winters on the National Elk Refuge, Wyoming.

thereafter (Robinette et al., 1957). Fetal loss or change in fetal sex ratio from conception to mid-pregnancy has not been measured in Jackson elk or in other elk herds. Moreover,

TABLE 3.—Sex of neonatal elk captured from the Jackson elk herd during May and June 1990–1992.

Location of capture	Year	Males	Females	Total
Grand Teton National Park	1990	13	21	34
Grand Teton National Park	1991	22	21	43
Grand Teton National Park	1992	17	17	34
Bridger-Teton National Forest	1990	13	3	16
Bridger-Teton National Forest	1991	7	4	11
Bridger-Teton National Forest	1992	5	2	7

sex bias has not been investigated in brucellosis-induced abortions during mid- and late-gestation, which reduce productivity of the Jackson elk herd by ca. 7% (Oldemeyer et al., 1993).

We therefore indirectly assessed whether annual variation in winter stress may be responsible for fetal deaths and resulting sex ratios at birth. We measured winter stress as a function of differences in environmental conditions during early winter, initiation date of supplemental feeding, quantity and quality of daily feed rations that females received, and number of days that elk were fed. Sex ratios at birth for cohorts were not related to feed ration in winter or number of days fed. Nonetheless, more males were born in years when supplemental feeding began earlier, which occurred when depth of snow in December and the number of elk on the Refuge were greater; factors influencing availability of forage, expendi-

tures of energy, and weight loss of females (Hobbs, 1989; Parker et al., 1984). Furthermore, the proportion of males born varied with the digestibility of the feed their mothers were provided in winter. In the context of the Trivers and Willard (1973) hypothesis, survival of male fetuses, which are energetically more costly to produce, is favored by nutritional supplementation early in gestation, when prenatal mortality becomes male-biased under stress of winter malnutrition (Maynard Smith, 1980; McMillen, 1979; Robinette et al., 1955, 1957).

Jackson elk leave the National Elk Refuge and arrive at calving areas during the last one-third of pregnancy (Smith and Robbins, 1994). A larger proportion of males were born in Bridger-Teton National Forest than in Grand Teton National Park. The smaller sample captured in the Forest (where fewer elk were born) is a potential source of bias. Yet any sampling bias should be equal in the Forest and Park because we followed the same strict sampling protocol and capture efforts were distributed similarly across the period of parturition in both areas.

Robinette et al. (1957) reported that mule deer and white-tailed deer produced more male than female offspring on summer habitats with low densities of deer and more abundant food resources. We assumed that densities of elk on calving areas outside Grand Teton National Park were lower than within the Park because densities of elk on summer ranges averaged 2.4/km² outside Grand Teton National Park and 5.9/km² inside the Park (Smith, 1994). Furthermore, 33% of radiocollared females that calved in Grand Teton National Park summered outside the park, whereas all females that calved outside Grand Teton National Park also summered outside the park (Smith and Robbins, 1994). Like Robinette et al. (1957), we suggest that females from summer ranges with lower densities of elk entered winter in superior condition, (al-

though we do not have data on this) and lost fewer fetuses.

Alternative explanations for the preponderance of males born outside Grand Teton National Park concern factors we did not measure. Dominance rank of females, which is influenced by body weight (Clutton-Brock et al., 1986), and date of conception of offspring (Verme and Ozoga, 1981) have been correlated with sex ratios at birth. The male bias reported here should be confirmed with replicate sampling that incorporates documentation of the phenotypes and dates of conception of females.

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