Ecology of the Mule Deer, *Odocoileus hemionus*, Along the East Front of the Rocky Mountains, Montana

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Mule Deer, *Odocoileus hemionus*, wintering along the east slope of the Rocky Mountains from Sun River to Birch Creek in north-central Montana were found to represent seven herd units. Distribution and movement patterns of deer in each herd unit were influenced by the topography and vegetation on winter ranges and in the mountains west of winter ranges. Each herd unit consisted of deer that were yearlong residents on or near winter ranges, deer that summered in valleys near the winter range, and deer that moved 20 or more km to mountain summer ranges. Movement patterns and apparent vulnerability to hunting varied among segments. Degradation of mountain front winter ranges through intensive oil and gas development could significantly reduce Mule Deer numbers in large areas of the Rocky Mountains.

Key Words: Mule Deer, *Odocoileus hemionus*, population ecology, Montana.

Mule Deer, *Odocoileus hemionus*, populations along the East Front of the Rocky Mountains represent a valuable resource that could be detrimentally affected by hydrocarbon exploration and development in the overthrust formations that underlie the mountain front in the United States and Canada. Management of Mule Deer in the face of oil and gas development requires knowledge of the distribution, seasonal movements, and other ecological attributes of populations dependent on the mountain-prairie ecotone along the East Front. This information is broadly lacking for Mule Deer in the northern Rocky Mountains, where intensive studies involving marked and radio-collared animals and close population monitoring have been conducted in only a few areas.

Our study, conducted primarily between 1979 and 1983, provides some of the needed information for Mule Deer populations along a 64-km segment of the Rocky Mountain Front in north-central Montana. The results should be relevant to management of Mule Deer populations along the front range from central Montana northward into Canada.

Study Area

The 2725-km² study area was located in, and adjacent to, the Sawtooth Range in north-central Montana (48° N, 113° W). Southerly and northerly extensions of this range follow the Continental Divide from about Helena, Montana, to Jasper, Alberta.

Terrain on the Sawtooth Range is characterized by a series of parallel north-south faults with moderate west-facing slopes and precipitous east faces. Elevations range from 1311 to 2863 m. A narrow (1 to 3 km) band of foothills marks the transition between plains and mountains and provides most of the wintering areas for native ungulates. Major vegetation types in the study area included fescue — wheatgrass (*Festuca* spp. — *Agropyron spicatum*) grasslands, Limber Pine (*Pinus flexilis*) savannah, and forest dominated by Douglas-fir (*Psuedotsuga menziesii*), Alpine Fir (*Abies lasiocarpa*), or Lodgepole Pine (*Pinus contorta*). Annual precipitation recorded at weather stations near the study area averages 35 to 56 cm. Average annual temperature is about 5° C (U.S. Department of Commerce 1985). Winter snow cover is variable along the mountain front and is influenced by strong southwesterly chinook winds.

Over 90% of the total study area was administered by the United States Forest Service (USFS), U.S. Bureau of Land Management (BLM), and the Montana Department of Fish, Wildlife and Parks (MDFWP). However, more than 80% of the surface and 44% of the subsurface mineral (oil and gas) rights on Mule Deer wintering areas were privately owned or administered.

Methods

Mule Deer were divided into three groups according to range: the East of Divide, EOD, population segment; the West of Divide, WOD, population segment; and the Resident, RES, segment.

Mule Deer were captured using baited panel traps (Lightfoot and Maw 1963) and a helicopter drive-net (Beasom et al. 1980) on wintering areas during 1976 through 1982. Twenty-six were radio-collared and 124 were marked with individually recognizable neckbands. Radio-collared deer were relocated from fixed-wing aircraft one to three times per month from March 1979 through October 1981 and approximately once every other month from November 1981 to December 1982. Relocations during the first period were used to calculate seasonal home ranges using a minimum convex polygon approach (Lonner and Burkhalter 1986). Additional relocations of radio-collared and marked deer, used in the delineation of seasonal distributions and movements, were obtained by aerial and ground observations in the course of population surveys and other activities, and occasionally from returns of marked animals shot by hunters.

Winter distribution, movements, and habitat use were further defined, and population characteristics determined, through ground and aerial surveys. The latter included nine helicopter surveys, two each in mid- and/or late winter 1979 through 1982 and one in January 1983, which provided complete or near-complete coverage of wintering areas. Ground classifications (age/sex ratios) during 1960 through 1978 and helicopter surveys in 1975 and 1978 by MDFWP management personnel provided supplementary data.

Population size estimates for 1980 through 1982 were derived as Lincoln Indices (Overton and Davis 1969) based on observations of marked and unmarked deer during complete-coverage helicopter surveys of winter ranges in March (Mackie et al. 1981). Population estimates could not be made for 1979, when few marked animals were available, and for 1983, when the helicopter survey was flown in mid-January and did not include one major winter range. Trapping operations during 1976 through 1981 provided known marked samples of 92, 107, and 50 at the time of March surveys in 1980, 1981, and 1982, respectively.

Ages of animals captured during helicopter drive-netting were estimated on the basis of tooth replacement and wear by Dave Pac, MDFWP. In known-age deer, 2½ to 6½ years old from the Bridger Mountains of southwestern Montana, approximately 90% of age estimates obtained using tooth wear were within 1 year of actual ages (D. Pac, personal communication). Harvest data were obtained from the MDFWP (Federal Aid Job Progress Reports, unpublished).

Results

Seasonal Distribution and Movements

Seven Mule Deer winter ranges were identified in the study area (Figure 1). These varied in size during the 1980 and 1981 winters from 10 km^2 to 24 km^2 for primary range and from 26 km^2 to 81 km^2 for total winter range. One, Swanson Ridges, apparently had been little used by deer during the mid 1970s but received consistent use during 1979 through 1983 as populations increased along the Front.

Primary winter range (Figure 2) supported deer concentrations in all winters, although the extent and period of concentration on primary winter range varied with winter severity. For example, in 1979, one of the harshest winters of this century (U.S. Department of Commerce 1979–80), deer on the Blackleaf-Teton winter range moved 3 km south of their concentration areas in other winters.

Total winter range included secondary ranges used in early and late winter or under abnormal conditions. Use of secondary winter range varied extensively between years and was apparently linked to snow cover.

Marked deer showed a high degree of fidelity to specific winter ranges as well as to individual home ranges within winter ranges. All radio-collared deer returned annually to the winter ranges on which they were trapped. Only one, an adult doe, significantly changed her activity center within a winter range between years. Among neck-banded deer, only four males (three yearlings and a 3½ year old) were known to have changed winter ranges. Annual winter range size for individuals varied from 0.4 to 13.0 km^2 for 19 females and from 0.7 to 6.0 km^2 for two males. Female winter home ranges averaged 3.4, 4.6, and 6.0 km^2 in 1979 (March to mid-May only), 1980, and 1981, respectively (Table 1). Cumulative winter ranges for 10 females followed through three winters averaged 15.9 km^2.

Secondary winter range overlapped or included some transitional range (areas on which deer concentrated during spring and/or fall). Transition ranges were generally adjacent to winter range but at higher elevations (Figure 2). Radio-collared deer with summer ranges west of the Continental Divide (the WOD population segment) tended to use transitional range for two to three months in autumn before moving on to winter range. Movements of this segment to transition range coincided with late October or early November

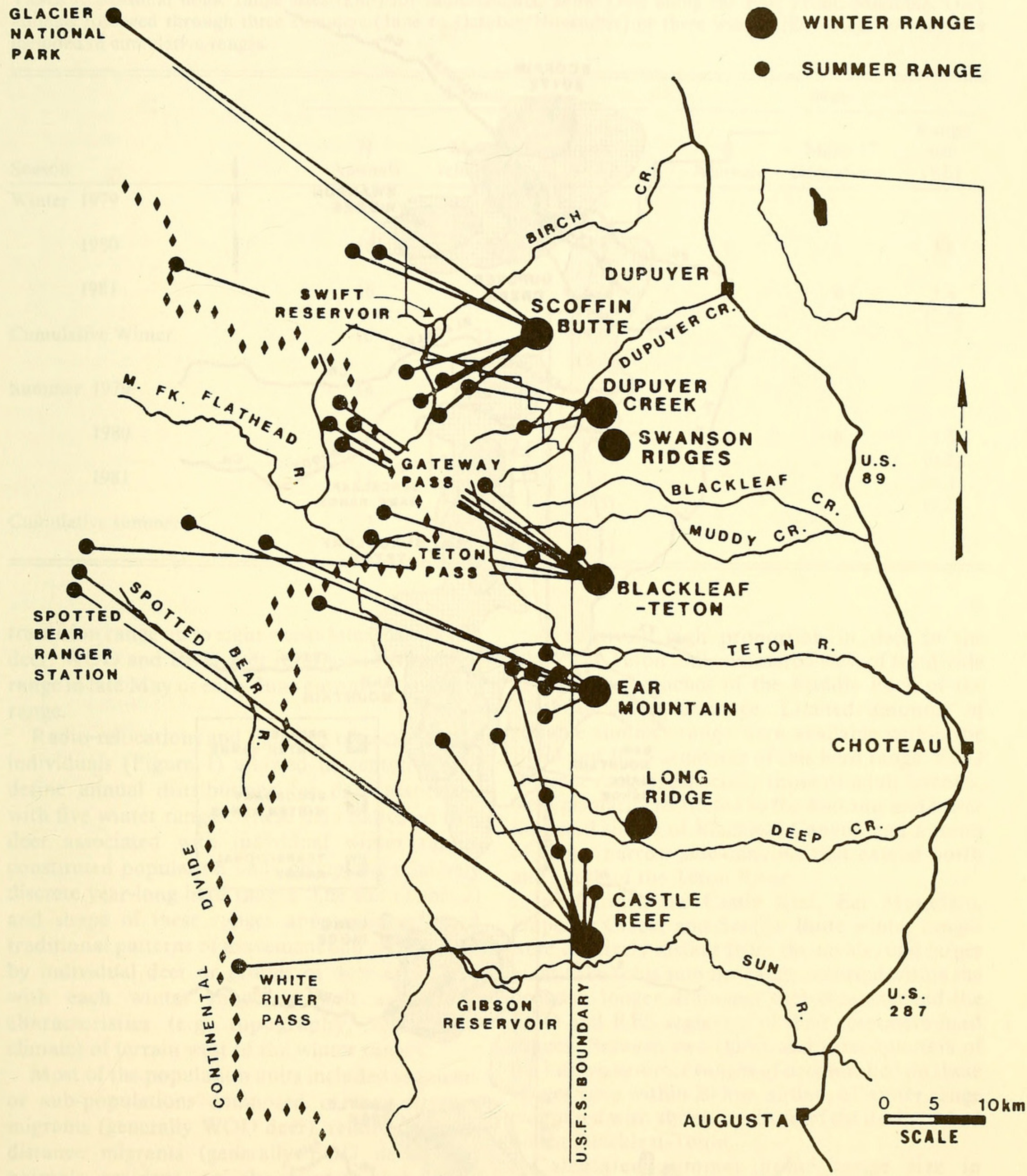

FIGURE 1. The East Front study area showing locations of winter and associated summer ranges used by marked Mule Deer.

snowstorms during the period 1979 through 1981. Deer summering in mountain valleys east of the Divide (the EOD population segment) and along the lower mountain front (the RES segment) either moved directly to winter range between late November and late December or moved on to

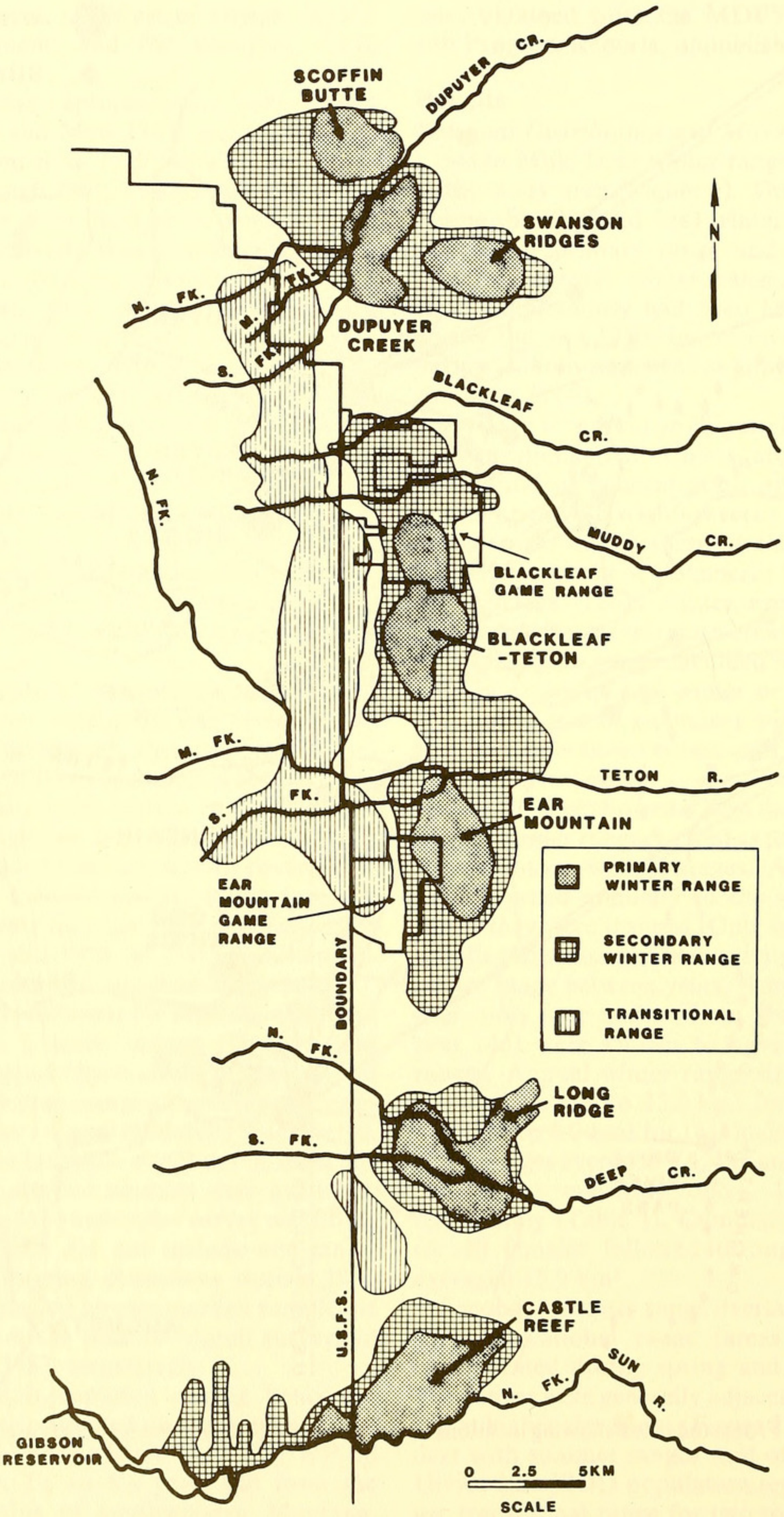

FIGURE 2. Primary, secondary, and identified transitional ranges used by Mule Deer wintering in the East Front study area.

TABLE 1. Seasonal home range sizes (km^2) for radio-collared Mule Deer along the East Front, Montana. Only animals followed through three summers (June to October/November) or three winters (December to May) are included in cumulative ranges.

	Female			Male		
Season	N Animals	Mean N relocations	Range size (SE)	N Animals	Mean N relocations	Range size (SE)
Winter 1979	12	6	3.4 (0.8)			
1980	18	7	4.6 (0.7)	1	6	3.6
1981	16	8	6.0 (1.0)	2	6	3.4 (2.6)
Cumulative Winter	10	22	15.9 (3.3)			
Summer 1979	14	12	6.4 (1.1)			
1980	17	8	3.5 (0.7)	2	6	4.5 (0.8)
1981	11	7	1.4 (0.5)	2	6	18.3 (9.1)
Cumulative summer	7	27	11.1 (2.5)			

transition range up to eight weeks later than WOD deer. WOD and EOD deer returned to transition range in late May or early June enroute to summer range.

Radio-relocations and sightings of neck-banded individuals (Figure 1) allowed us tentatively to define annual distributions for deer associated with five winter ranges. These data indicated that deer associated with individual winter ranges constituted population units occupying relatively discrete year-long herd ranges. The size (Table 2) and shape of these ranges apparently reflected traditional patterns of movement and range usage by individual deer or groups of deer associated with each winter range as well as habitat characteristics (e.g. topography, vegetation, climate) of terrain west of the winter ranges.

Most of the population units included segments or sub-populations composed of long-distance migrants (generally WOD deer), relatively short-distance migrants (generally EOD deer), and animals resident on the winter range and immediately adjacent areas (RES deer). The proportion of deer in each segment varied among units, apparently in relation to the amount of suitable habitat, ease of access, and distance to areas west of the Continental Divide, and possibly as a function of traditional movement patterns.

A relatively high proportion of deer in the Blackleaf-Teton unit summered west of the divide in the upper reaches of the Middle Fork of the Flathead River drainage. Limited amounts of suitable summer range were available within the EOD and RES segments of this herd range. EOD summer ranges, especially those of adult females, were primarily restricted to the bottoms and lower timbered slopes of Blackleaf Canyon and a series of short, narrow side canyons that extend north and south of the Teton River.

In contrast, the Castle Reef, Ear Mountain, Dupuyer Creek, and Scoffin Butte winter ranges were relatively distant from the divide, and larger areas of suitable summer range occurred within the broader, longer drainages that characterized the EOD and RES segments of their respective herd ranges. Between two-thirds and three-quarters of the known summer ranges of deer marked on these ranges were within 20 km, airline, of winter range compared with about one-third of the deer marked on the Blackleaf-Teton.

Calculated summer home range size in individual years varied from 0.2 to 13.5 km^2 for 19 females and from 2.6 to 34.0 km^2 for three males. Mean summer home range size for females was 6.4, 3.5, and 1.4 km^2 in 1979, 1980, and 1981, respectively (Table 1). Cumulative home range size for seven females followed through three summers averaged 11.1 km^2.

TABLE 2. Population unit ranges (primary winter, total winter, transition range, and minimum yearly range) and mean estimated population numbers (counts divided by the proportion of marked animals seen in four helicopter surveys, March and April 1980 and March and April 1981) for Mule Deer on winter ranges along the East Front, Montana.

Location	Range (km^2)				Mean estimated population[a] (SE)
	Primary winter	Total winter	Transition	Minimum yearly	
Hunting District 441 (North of Teton River)					
Scoffin Butte	10.2	26.6		575	905 (42)
Dupuyer Creek	13.4	31.6	24.9	359	1073 (50)
Swanson Ridges	10.6	29.2			
Blackleaf-Teton	20.9	80.8	53.5	328	546 (86)
Hunting District 442 (South of Teton River)					
Ear Mountain	16.6	44.0	47.1	375	594 (105)
Long Ridge	23.9	37.6			1104 (245)[b]
Castle Reef	18.1	38.9	12.3	1056	1224 (211)

[a]Means are based on counts in March 1980, April 1980, March 1981, and April 1981 divided by 0.62, 0.65, 0.56, and 0.48, respectively.
[b]Mean based on three counts (January 1980, January 1981, and March 1981).

Population Characteristics and Trends

Population Size and Density — Counts in seven helicopter surveys which approached complete coverage of all winter ranges ranged from 2282 (April 1979) to 5093 (January 1982). Our best estimates of minimum total Mule Deer numbers on winter range were 5653 in March 1980, 6016 in March 1981, and 5956 in March 1982. During those surveys, we sighted 62%, 56%, and 56% of the known marked deer available. Sightability ranged from 48% to 65% for four other helicopter surveys (two in January and two in April) during 1980–1983.

If deer sightability in our study area during the severe 1979 winter was intermediate to sightability during the same winter in the Bridger Mountains of southwestern Montana (64%) and the Missouri Breaks of central Montana (74%) (Mackie et al. 1981), the count obtained from the February 1979 MDWFP complete coverage survey, 3532, would suggest that approximately 5000 Mule Deer wintered on the study area in late winter 1979. Only 2753 deer were counted during the 1983 survey. However, weather conditions were exceptionally mild, deer were widely distributed in January when the survey was conducted, and a portion of one winter range was not covered.

The apparent 6% population increase from March 1980 to March 1981 was consistent with other observations which indicated growth in wintering populations on the Front from 1977/1978 through 1981. Our data suggested that the population stabilized in 1981–1982; the single, early winter 1983 count did not provide a valid estimate of trends to 1983.

Density estimates on individual winter ranges, based on mean counts from helicopter surveys in 1980–1981 adjusted for the proportion of marked animals seen in each survey, indicated an inverse relationship between deer density and both total population unit range and winter range size (Table 2). The Castle Reef Winter Range supported the highest average number of deer and Blackleaf-Teton the lowest, during 1980–81.

Population structure — Since no significant differences were noted between fawn to adult ratios obtained from ground and helicopter classification data in a sample of eight winter range by year combinations during 1981–1983 (paired t-test; mean ground ratio = 49, mean helicopter ratio = 46; $t = 0.275$; $p > 0.10$), the most comprehensive data sets available (ground surveys in 1980–1981 and helicopter surveys in 1982–1983) were used to examine trends in productivity. Fawn to adult ratios, based on early (January–February) and late (March–April) winter classifications, suggested that fawn production/survival was moderately high overall but may have declined from 1980 to 1982 (Table 3). The mean ratio for all winter ranges in 1980 was above the 1961–1979 mean of 52 fawns per 100 adults for winter ranges along the Front (Kasworm 1981), while those for

TABLE 3. Fawn to adult ratios (fawns/100 adults) recorded on six winter ranges between January and February and between March and April along the East Front of the Rocky Mountains, Montana. Ratios for 1980-81 were obtained from ground surveys and those from 1982-83 from helicopter surveys. Numbers of animals classified as adults or fawns are given in parentheses.

	Winter range					
Year	Scoffin Butte	Dupuyer Creek-Swanson Ridges	Blackleaf-Teton	Ear Mountain	Castle Reef	Long Ridge
1980						
January-February	69 (687)	66 (575)	76 (232)	64 (171)	70 (416)	
March-April	60 (48)	67 (275)	58 (331)	62 (202)	61 (148)	
1981						
January-February	54 (559)	35 (188)	55 (175)	57 (327)	42 (306)	
March-April	46 (291)	52 (449)	44 (286)	54 (356)	54 (159)	
1982						
January-February	28 (82)	51 (113)	58 (503)	31 (356)	36 (233)	64 (224)
March-April	38 (153)	45 (193)	56 (39)	48 (346)	47 (258)	55 (31)
1983						
January-February	53 (388)	48 (233)	39 (133)	52 (147)	58 (391)	56 (182)

1981, 1982, and early winter 1983 were similar to or only slightly below the mean. Overwinter mortality was apparently low in all years. Although ratios varied somewhat between individual winter ranges, the differences were not significant (Chi-square, $p > 0.05$).

Males constituted 16%, 17%, and 19% of 1445, 1516, and 1475 animals classified in helicopter surveys during January 1981, 1982, and 1983, respectively. Sex ratios determined from helicopter classifications in January 1982 and 1983 indicated 34 and 40 males per 100 females for all winter ranges combined. Small samples classified on some winter ranges precluded assessment of possible differences among individual ranges. Moderately high male to female ratios on the area were also indicated by sex ratios of deer handled in drive netting operations–35 males per 100 females in 1980 and 55 per 100 in 1981.

The drive-netting operations also provided data on age structure. Yearlings and fawns constituted 39% of 68 animals trapped in 1980 and 43% of 42 handled in 1981. The oldest discernable age group, 6 1/2 years and older, made up 6% and 12% of the two samples (Figure 3).

Mortality — A minimum of 70% of 84 marked adult females survived for at least one year following capture; only four (5%) were known to have died, while fates of 21 were unknown. Among fawns, a minimum of 56% of 32 marked were known to survive at least one year, none were known to have died, and the fates of 14 were unknown. Of the 26 marked adult males, five (27%) survived, seven died, and the fates of 12 were undetermined.

Winter mortality appeared to be low in all years, as evidenced by little or no change in fawn to adult ratios from early to late winter. Deer harvests in the study area were generally light (200–300 animals/year) during 1979–1983. Regulations allowed harvest of one deer per hunter, and hunting was limited to bucks only except for a two-week, either-sex period. Mild autumn conditions during the study resulted in deer dispersing widely during the hunting season and low vulnerability of deer to hunters. None of our marked females were known to have been shot, at least in the first year following marking. Hunting was the major known cause of mortality among males, with six of the seven known deaths being hunter returns.

Discussion

Historically, all deer inhabiting the East Front and adjacent summer ranges have been considered a single population. Subunits have been arbitrarily defined to include animals occurring within hunting districts established primarily for administrative purposes. In contrast, our findings indicate Mule Deer associated with individual winter ranges along the East Front constitute discrete population units distributed within individual year-long ranges. This distributional

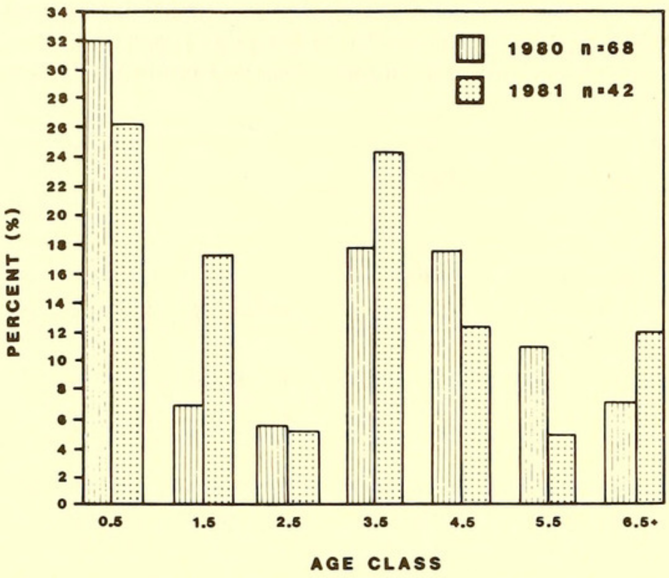

FIGURE 3. Age distribution of Mule Deer examined during trapping operations in the East Front study area during 1980 and 1981.

pattern is similar to that described for Mule Deer populations in the Bridger Mountains of southwestern Montana (Mackie and Pac 1980; Pac et al. 1984) and may represent the general pattern followed by Mule Deer on mountain-foothill habitat in the northern Rocky Mountains.

Summer and winter home range sizes were similar to those calculated for Mule Deer in the Bridger Mountains (Pac 1976; Steery 1979; Nyberg 1980; Rosgaard 1981) using similar data collection and analysis techniques. The large difference between cumulative and annual seasonal home range sizes was also noted in the Bridgers and may be either a function of small annual samples or an artifact of home range calculation using the minimum polygon approach (MacDonald et al. 1980).

The size and shape of the herd units apparently reflected traditional patterns of movement and range usage by deer from each winter range as well as habitat/environmental features of the area accessible to, or traditionally used by, those deer. The fact that numbers and density of deer varied between units suggested a possible functional relationship between environmental features and demographic characteristics of Mule Deer in each unit.

Our population studies were not sufficiently intensive to detect differences in parameters such as sex and age structure, reproduction, mortality rates, etc.. Studies elsewhere in Montana (R. J. Mackie, D. F. Pac, and H. E. Jorgensen. 1978, 1980. Population ecology and habitat relationships of Mule Deer in the Bridger Mountains, Montana. *In* Montana Deer Studies Job Progress Report, MDFWP, Helena) have shown that deer-habitat interactions and population characteristics vary between individual population units: the broader the difference in habitat, the greater the difference in population parameters and dynamics. Similarly, Barlow and McCulloch (1984) suggested that the Kaibab Mule Deer herd, which has long been considered a single population, may comprise two sub-populations experiencing different environments and exhibiting different biological characteristics.

White-tailed Deer, *Odocoileus virginianus*, associated with individual winter yarding areas in the same winter range in Minnesota have been found to be separate sub-populations (Nelson and Mech, *in press*). Other studies of White-tailed Deer (Dapson et al. 1979; Ramsey et al. 1979) have defined differences in demographic characteristics between populations in different adjacent habitats which were associated with differences in genetic homogeneity between populations.

In the past, under existing administrative boundaries, deer inhabiting ranges east and west of the Continental Divide have constituted separate subunits, and East Front winter ranges were considered to support primarily EOD deer. Our findings indicate that most Mule Deer occupying the portions of the Bob Marshall Wilderness Area and the Flathead and Lewis and Clark national forests lying north of the Sun River, south of Glacier National Park, and east of the upper South Fork of the Flathead River must winter along the East Front within our study area. Deer management surveys (J. Cross, J. McCarthy, and G. Olson, personal communication) have indicated that very few Mule Deer winter west of the Continental Divide within that area. This would imply that maintenance of summering Mule Deer populations within that 3000 km^2 area is directly dependent upon the amount and quality of winter range available along the East Front. Conversely, maintenance of maximum Mule Deer populations on East Front winter ranges depends upon habitat and population management practices within that entire area of summer range.

The movement of WOD deer to transitional and winter ranges on the East Front with snowstorms in late October or early November, and movement of EOD deer later in November or in December, are consistent with findings from other studies (Pac 1976; Steery 1979; Nyberg 1980; Rosgaard 1981) involving Mule Deer populations with herd ranges split by a major mountain divide. This differential movement may be of special significance in harvest management along the East Front. Hunter access is typically highest in the vicinity of winter ranges. The earlier movement of WOD deer likely results in greater hunting pressure being applied on them compared to EOD deer, which remain more widely dispersed and at somewhat higher elevations during late October and November. Such differential harvest, if excessive, could lead to gradual reduction and eventual elimination of the WOD segment or prevent Mule Deer from completely "filling" (Mackie 1983) available summer habitat west of the Continental Divide.

During 1980–1985, population densities and structure on winter ranges in the study area fell within the range of values reported for healthy, productive Mule Deer populations in other mountain-foothills habitats in Montana (R. J. Mackie, D. F. Pac, and H. E. Jorgensen. 1978, 1980. Population ecology and habitat relationships of Mule Deer in the Bridger Mountains, Montana. *In* Montana Deer Studies Job Progress Report, MDFWP, Helena). The intermittent and widely scattered hydrocarbon development in the study area had no detectable impact on Mule Deer distribution, numbers, or productivity (Ihsle 1982; G. Olson and J. McCarthy, personal communication).

Should intensive, unplanned and unregulated development occur on winter concentration areas or should hunter pressure increase markedly as a result of increased road density or greater human populations, the recreational and esthetic benefits provided by Mule Deer in vast areas of the northern Rocky Mountains could be jeopardized. To avoid this possibility, herd units, seasonally important use areas, and characteristic herd structure for healthy populations should be identified along the entire Rocky Mountain Front prior to widespread development of oil and gas fields. Management plans could then be tailored to individual herd units rather than broad geographic areas, and general regulations could be replaced with specific management goals that would be more beneficial to Mule Deer populations and would include fewer unnecessary impediments to oil and gas development.

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