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The Michigan elk herd: Ecology of a heavily exploited population

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Michigan State University, 1992

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THE MICHIGAN ELK HERD:
ECOLOGY OF A HEAVILY EXPLOITED POPULATION

By

Louis Charles Bender

A DISSERTATION

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ABSTRACT

THE MICHIGAN ELK HERD: ECOLOGY OF A HEAVILY EXPLOITED POPULATION

by

Louis Charles Bender

This study evaluated the impacts of hunting and viewing exploitation on elk behavior, social dynamics, and morphology. Additionally, an elk population model used by the Michigan Department of Natural Resources (MDNR) for population management was evaluated and modified. Elk behaviors were documented by social group observations, determination of elk flight distances, standardized elk-vehicle counts, and radio-telemetry. Morphological and population characteristics were determined by harvest analysis, radio-telemetry, and ground/air herd composition counts.

Elk flight distances were found to have increased 25% since the onset of hunting in 1984. Significant negative relationships were also found between the intensity of viewing use and elk viewability. Increased elk wariness is likely a product of both hunting and viewing exploitation, and is likely to continue to increase. Elk in Michigan showed no directional changes in either body weights nor antler development in response to the MDNR harvesting strategy.

Most social grouping patterns seen in Michigan are typical of Western elk populations. Despite being non-

migratory, elk in Michigan showed little constancy in social group composition. Elk also did not show an inverse group size-degree of cover relationship. Elk breeding behavior in Michigan was characterized by numerous small (4-6 elk) harems in which juvenile bulls were tolerated by harem bulls. Yearling bull dispersal was not seen in Michigan.

The 1987 MDNR elk population model was altered to better reflect observed herd parameters. Subsequent simulation modelling indicated that the current MDNR harvesting strategy, emphasizing cow harvest to regulate population size, with a more limited any-bull harvest, effectively accomplished MDNR population management goals (limiting herd size and distribution, and maintaining current sex- and age-composition). However, the MDNR strategy was very sensitive to changes in hunter behavior and decreases in bull:cow ratios. If Michigan elk hunters were more selective for older age-class, larger antlered bulls, or if bull:cow ratios declined below 60:100, the current MDNR harvesting strategy resulted in over-exploitation of the older bull age-classes. Decreases in this herd segment, the most popular for viewing purposes, would significantly impact the overall recreational opportunities associated with Michigan's elk herd.

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Finally, my deepest appreciations go to my family, without whose support none of this would have been possible. I dedicate this dissertation to my mother and father, who always provided support and guidance when I needed it. To Dad, a special word; given the same opportunities, you could have done so much more than this. And, yes, this really means that I'm finished with school.

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INTRODUCTION

Michigan's elk (*Cervus elaphus nelsoni*) herd is an extremely valuable and unique resource. Consisting of ~1200 individuals, it is the only wild harvested elk population east of the Mississippi River. The ecological uniqueness of the Michigan herd stems from its high levels of exploitation (both consumptive and non-consumptive), the nature of its habitat, and the sociological and political pressures present in both the elk range and on the elk population. These combinations of factors contribute to ecological adaptations in the Michigan herd unlike those present in other North American elk populations.

Eastern North American elk (*C. e. canadensis*) were historically present in lower Michigan during pre-settlement periods. However, the last known populations were extirpated in the late 1800's (Murie 1951). Several attempts were made to reintroduce elk into Michigan in the early 1900's. The records and results of these reintroductions are incomplete and confused. Most attempts likely failed, until 7 Rocky Mountain elk (*C. e. nelsoni*) were successfully reintroduced into Cheboygan County in 1918 (Moran 1973). This reintroduction likely formed the base of the present northern Michigan elk herd, although contributions from the numerous other reintroduction attempts are likely. Additionally, European red deer (C. elaphus) may also have been released into the elk range during this period (MPDC 1919), perhaps also contributing to the base of the present herd.

The reintroduced elk herd gradually increased in size until a peak population of an estimated 2000 individuals was reached in 1964 (Moran 1973). During this period the elk herd became a significant tourist attraction (MDNR 1984). The large numbers of elk, however, resulted in agricultural and forestry depredation problems. Additionally, pressure was applied by sportsmen to utilize the elk resource. In response to these factors, the Michigan Department of Natural Resources (MDNR) conducted a controlled elk hunt in 1964 and again in 1965 (Moran 1973). A total of 477 elk were harvested in the 2 years combined. Increased poaching during this period combined with the hunts to drop elk numbers to 300-700 by the mid- to late-1960's (C. Bennett, MDNR, pers. commun.). While relieving depredation problems, the elk hunts had the negative impact of decreasing elk visibility, creating unsatisfactory elk viewing opportunities.

The elk herd remained at low numbers throughout the duration of the late 1960's and early 1970's, a result of poaching and successional advancement of the elk range. In

1975, the MDNR began censusing elk via a combined air and ground search in late winter. The initial 1975 census resulted in the counting of 159 animals and an estimated population size of 200.

Concern over this low number prompted the MDNR to adopt measures to increase the elk herd size and re-establish the elk herd as a tourist attraction and harvestable resource. Efforts were made to increase law enforcement to curtail poaching, and also to improve elk habitat quality through increased forest cuttings and establishment of wildlife openings (Beyer 1987).

Subsequent winter censuses indicated that the elk herd responded favorably to the increased management efforts. Censuses of 1977, 1980, and 1983 produced population estimates of 300, 500, and 750, respectively. The herd again became a significant tourist attraction, but depredation problems similar to those of the 1960's again arose.

In 1984, the MDNR re-initiated a controlled annual elk hunting season in December. Aimed at regulating the growth of the herd by placing the emphasis of the harvest on cows, the December elk season has been held annually since 1984 with harvests of 39, 119, 93, and 129 animals for 1984-1987, respectively. To specifically target elk causing agricultural depredations, an additional localized October hunt was held from 1988-1990. Harvests during this period were 215 (72 in October, 143 in December), 169 (66 in October, 103 in December), and 204 (71 in October, 133 in December) for 1988-1990, respectively. Despite these harvests, however, the herd continued to increase. Annual censuses from 1984-1988 were 850, 940, 950, 1000, and 1020, respectively. Due to bad weather conditions, no census was performed in 1989. The 1990 count of 980 seemed to indicate that the population growth of the herd had finally been stemmed. However, the January 1992 count of 1121 elk, for an estimated population size of 1200, suggested either that growth of the elk herd had not been leveled by harvesting, or that previous population censuses were negatively biased.

The goal of the current MDNR elk management plan is "a viable elk population, in harmony with the environment, affording optimal recreational opportunities" (MDNR 1984). Specific objectives of this plan include an overwinter population of 800-900 elk (although these population goals may be revised in light of the 1992 census, indicating historic underestimation of elk numbers) and the maintenance of a large number of older age-class bulls for optimal viewing opportunities. To assist in population management aimed at achieving the goals of this plan, a computer simulation model has been employed to mimic the dynamics of the elk population, determine annual harvest quotas, and predict the impacts of hunting on herd composition and distribution.

Concerns exist over the accuracy of the elk population model, as it was developed on very limited biological data. Additionally, visibility of the elk has apparently decreased since the onset of the annual hunts in 1984. During this same period, viewing use of the elk herd has increased dramatically (T. Carlson, MDNR, pers. commun.). The ecological responses of the elk to this high level of combined consumptive and non-consumptive exploitation are unknown. Elk viewer dissatisfaction, however, appears to be increasing as a result of fewer animals being visible.

Michigan's elk herd is an extremely valuable recreational resource of high public interest. Proper and precise management of this herd is critical not only for the welfare of the population, but also as an example of modern wildlife management. It is thus necessary that the effectiveness of, and elk responses to, the current MDNR population management strategies be determined. To insure proper management of elk in the future, the MDNR population model should be refined and its accuracy maximized. Additionally, the impact of overall exploitation on elk visibility, social structure, and population dynamics and demographics needs to be documented, and possible new management alternatives evaluated. These steps are necessary for optimal management of this unique resource.

OBJECTIVES

The overall goals of this study are to (1) evaluate and refine the current Michigan elk population management model, (2) assess the demographic, dynamic, morphological, social, and behavioral dynamics of the elk, especially the responses to the annual hunt, and (3) develop alternative population management options for the Michigan elk.

Specific objectives will be addressed in each Chapter.

STUDY AREA

The elk range in Michigan covers approximately 1500 km^2 in the northern lower peninsula and includes portions of Otsego, Cheboygan, Montmorency, and Presque Isle counties (Moran 1973). It is centered on the 340 km^2 Pigeon River Country State Forest (PRCSF), Vanderbilt, MI, and the adjacent Camp 30 Hills area of Black River State Forest, Atlanta, MI (Fig. 1). Adjacent private forested and agricultural lands comprise the remainder of the elk range.

Vegetative cover in the primary elk range is mostly forested, with scattered agricultural land and wildlife openings (Moran 1973). Approximately 79% of the primary elk range is in forest cover-types (Moran 1973). Forest coverage is very diverse due to diversity in soil types, drainage, and exposure (Beyer 1987). Morainic uplands support sugar maple (*Acer saccharum*), basswood (*Tilia americana*), hemlock (*Tsuga canadensis*), northern red oak (*Quercus borealis*), red maple (*A. rubrum*), white pine (*Pinus strobus*), and red pine (*P. resinosa*). Steep morainic slopes support aspen (*Populus tremuloides*), various oaks, and red and white pine. The outwash plain-morainic ecotone is typified by red maple, aspen, and white birch (*Betula papyrifera*). Sandy outwash plains support jack pine (*P.*

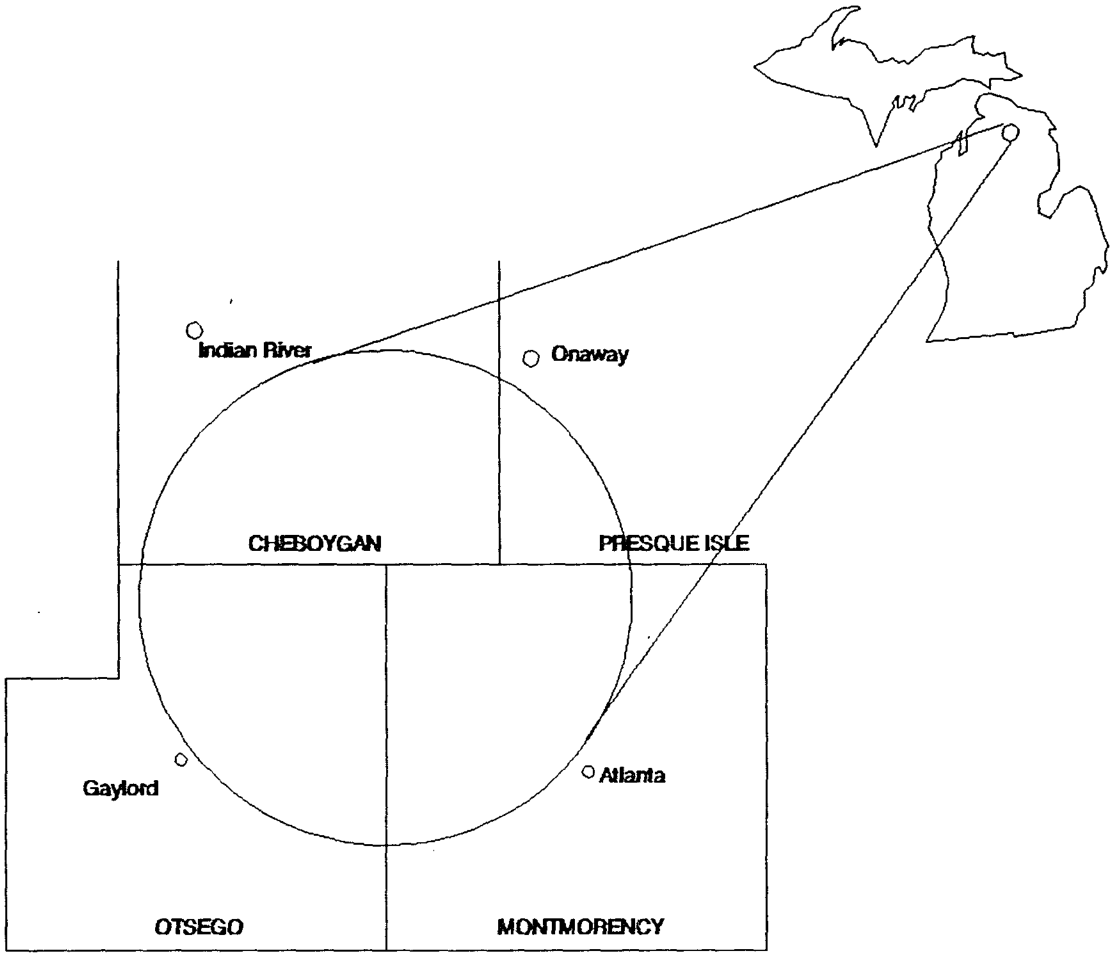

Figure 1. Location of the Michigan elk range, northern Lower Peninsula, Michigan.

banksiana), cherry (Prunus spp), and willow (Salix spp). Coniferous swamps are dominated by northern white-cedar (Thuja occidentalis), balsam fir (Abies balsamea), black spruce (Picea mariana), and balsam poplar (P. balsamifera).

Approximately 450 ha in the primary elk range are maintained in managed wildlife openings of alfalfa, buckwheat, clover, or cool season grasses (T. Carlson, MDNR, pers. commun.). Permanent openings account for approximately 15% of the primary elk range (Moran 1973). Agricultural lands are limited in the primary elk range, but are dominant in many peripheral areas. Principal crops include corn, sugar beets, and various pasture grasses.

Soil types in the elk range include swampy highly fertile soils, medium-high fertility soils on till plains and moraines, and dry sandy soils on outwash plains (Moran 1973).

Climate alternates between continental-type and semi-marine (Moran 1973). Large daily, monthly, and seasonal temperature changes are typical. Fall and winter temperatures are moderated by lake-effect cloud cover and prevailing westerly winds.

The entire elk range typically has been open for the December hunts, including both primary and peripheral areas. Open areas for the October hunts have been limited to the peripheral, predominately agricultural areas surrounding the primary range.

Chapter 1: Behavioral Responses to Exploitation and Vulnerability of Elk in Michigan

Elk in Michigan have been hunted annually since 1984. Prior to this, except for 2 hunts in 1964 and 1965, the herd had been subject to no legal harvest. In response to damage complaints and potential impacts on timber regeneration, the MDNR established an annual December hunt in 1984. Additionally, to specifically target animals causing agricultural depredations, a localized October hunt was held from 1988-1990. The objective of these hunts has been to control the size and distribution of the herd to numbers and locations which minimize agricultural and forestry conflicts, while maintaining quality viewing opportunities for recreationists (MDNR 1984).

Although total levels have not been quantified, viewing use of the elk has also increased substantially since the onset of the hunts in 1984. The majority of this "non-consumptive" exploitation occurs during September-November, when rutting elk are highly visible and bulls are highly vocal. This same period is also the period of greatest behavioral stress on the population (Geist 1982).

Michigan elk have been extremely vulnerable to the annual hunts. Viewability of the herd has decreased since 1984, and wariness of individual elk has increased. This Chapter addresses the behavioral responses of elk in Michigan to exploitation, both hunting and viewing. It also addresses implications of elk vulnerability and trends for future management.

Specific objectives of the Chapter include:

(1) Determine changes in flight distances of elk since 1984-1986.

(2) Determine the relationship between levels of elk viewing and elk visibility.

(3) Determine the impact of hunting on the social group dynamics of elk.

(4) Determine trends in elk wariness and vulnerability in response to exploitation.

METHODS

Flight Distances

Flight distances, the average distance at which elk flee from an approaching person (Altmann 1958), were evaluated as an index of elk wariness. Flight distances were measured during Fall in 1984-1986 (Beyer 1987), and again in 1990-1991. Flight distances were determined by slowly approaching an elk until it fled. The distance from the observer to the place the elk was standing immediately before fleeing was measured using a range finder (Ranging, Inc., East Rochester, NY). Flight distance measurements were standardized by adhering to a set procedure: all animals were initially located with a vehicle; only animals in the open were sampled; if a group of animals was approached, flight distance measurement was taken on the closest animal; flight distances were recorded only during early morning or late evening; and flight distances were not recorded during periods of inclement weather (Beyer 1987). Flight distances collected in 1990-1991 were broken down into sex- and age-groups to see if differences in wariness existed between age- or sex-classes.

Social Group Behavior

Social group sizes before and after the December hunts were analyzed in 1990-1991 to determine if social groups were fragmenting or merging in response to hunting pressure. Social group sizes were determined for 5 consecutive days immediately prior to and immediately after the December hunts. Pre- and post-hunt social group sizes were determined for 3 and 5 randomly selected previously radio-collared elk in 1990 and 1991, respectively. Due to the short interval (1 day) between successive relocations, relocations were tested for autocorrelation (independence) using the Durbin-Watson statistic (Durbin and Watson 1951).

Behavioral Responses to Viewing

Two permanent 20-mile transects were established and driven on alternate nights September-October, 1991. Each transect consisted of 15 miles of primary (county-maintained) roads and 5 miles of secondary (non-maintained) roads. One transect was located in the PRCSF; the other in the Camp 30 Hills area. Transects were driven from 1 hr prior to sunset to sunset, and the following variables recorded: (1) total vehicles encountered, (2) total elk seen, and (3) total groups of elk seen. Data were analyzed to assess any relationship between numbers and/or groups of elk seen and vehicular traffic.

Effort and Kill Data

Data collected during the October and December hunts at MDNR check stations were used to assess trends in hunter effort, number of elk seen by hunters, and geographic distribution of the harvest with respect to land ownership (E. Carlson, MDNR, pers. commun.; Schmitt et al. 1985, 1986; Moran et al. 1987, Moran and Schmitt 1988, 1989; Carlson et al. 1990). These data were used to assess differences in parameters between the October and December hunts.

Data Analysis

Flight distance, social group, and hunter kill and effort data were analyzed using the non-parametric Mann-Whitney U and Kruskal-Wallis ANOVA tests (Siegel 1956). A Scheffe-type non-parametric test was used for multiple comparisons (Miller 1981). Elk-vehicle interaction data were analyzed using Pearson correlations (Sokal and Rohlf 1981). Comparisons of land-ownership with harvest distribution were made using Chi-square analysis (Siegel 1956). The acceptable level of statistical significance for all tests was set at $\underline{a} = 0.10$.

RESULTS

Flight Distances

Flight distances differed significantly between 1990-1991 and 1984-1986 (Table 1). Flight distance of elk increased approximately 25% from 1986 to 1990-1991, indicating that elk are getting increasingly wary. Bull elk were significantly more wary than cows in 1990; sexes did not differ in 1991 (Table 1). Large mature bulls (five or more antler points per antler beam, i.e. 5X5 or better) were the most wary age group in both 1990 and 1991. Younger bulls (four antler points per beam -- 4X4 -- or fewer) were significantly less wary than older bulls, and did not differ from cows.

Social Group Responses

Sizes of elk social groups did not differ pre- and post-hunt in 1990 or 1991 (Table 2). Group sizes associated with one radio-collared elk in 1991 were found to be

Table 1. Mean (SE) fall flight distances (in meters) for elk in 1990-1991 and 1984-1986 hunted regions.

YEAR	COMPONENT	FLIGHT DISTANCE (M)		
1991	Combined	60.9(3.1)^{a}		
	Cows		61.4(4.5)^{a}	61.4(4.5)^{a}
	Bulls		60.6(4.2)^{a}	
	Bulls--≥5X5			71.9(5.7)^{b}
	Bulls--≤4X4			54.6(7.5)^{a}
	Bulls--Yearlings			52.0(4.4)^{a}
1990	Combined	63.2(4.3)^{a}		
	Cows		59.5(3.4)^{a}	59.5(3.4)^{a}
	Bulls		66.3(7.3)^{b}	
	Bulls--≥5X5			77.0(11.3)^{b}
	Bulls--≤4X4			54.1(7.8)^{a}
	Bulls--Yearlings			68.0(15.1)^{ab}
1986	Combined	50.3(2.6)^{b}		
1985	Combined	44.7(2.9)^{b}		
1984	Combined	47.0(3.0)^{b}		

^{abc}Values sharing a superscript do not differ within a column for combined and within a column and year for sex- and age-classes ($\underline{a}$=0.10).

Table 2. Mean (SE) pre- and post-hunt social group sizes for elk monitored during the December 1990 and 1991 elk hunts.

YEAR	ELK	PRE-HUNT	POST-HUNT
1991[1]	1700	15.33(2.96)	10.00(2.52)
	1900	12.67(4.18)	16.33(1.33)
	1560	13.67(3.67)	14.00(3.21)
	0462	7.00(2.00)	8.67(0.89)
1990	0100	38.67(5.81)	35.33(2.60)
	0560	20.00(7.21)	37.67(7.13)
	0540	3.00(0.58)	2.00(0.58)

[1] Group sizes associated with one radio-collared elk in 1991 were dropped from analysis due to autocorrelation.

autocorrelated, and dropped from further analysis. No obvious trends were present in the data; in 1990, 2 of 3 groups decreased in size following the hunt, while 3 of the 4 remaining groups increased in size following the 1991 December hunt.

Elk-Vehicle Relationships

Total numbers of elk seen and total numbers of elk groups were negatively correlated with vehicle numbers for both the PRCSF and Camp 30 Hills (Table 3). Relationships were significant for both elk numbers and groups in the Camp 30 Hills. For the PRCSF, only elk numbers were significantly negatively correlated with vehicles.

Hunter Success and Kill Data

Hunter success has averaged 97.1% for the 8 December hunts, and 80.7% for the 3 October hunts (Table 4). While harvest rates have been high for elk hunting in Michigan, a downward trend is evident for at least the December hunts (Table 4).

Total hunter kill relative to land ownership was proportional to the amount of public and private land contained in the open area for both the October and December hunts, although data were incomplete, particularly for the October hunts (Table 4).

Table 3. Correlations between number of elk seen, number of elk groups seen, and number of vehicles counted on primary and secondary (two-tracks) roads on standardized transects in the PRCSF and Camp 30 Hills.

	PRCSF		Camp 30	
	r	PROB	*r*	PROB
Primary vs. Elk	-0.496	0.010*	-0.502	0.081*
Primary vs. Groups	0.317	0.317	-0.471	0.104
Secondary vs. Elk	-0.459	0.018*	-0.360	0.227
Secondary vs. Group	-0.094	0.650	-0.628	0.022*
Total vs. Elk	-0.573	0.002*	-0.539	0.057*
Total vs. Group	-0.199	0.330	-0.565	0.044*

*Significant correlations (*a*=0.10).

Table 4. Hunter success rates and harvest distribution with respect to land ownership for the annual elk hunts, 1984-1990.

		HARVEST		%	% OWNERSHIP		% HARVEST	
YEAR	HUNT	C&C[1]	BULL	SUCCESS	PUBLIC	PRIVATE	PUBLIC	PRIVATE
1991	DEC	91	57	95	48	52	41	59
1990	DEC	83	50	95	--	--	49	51
	OCT	44	27	79	--	--	45	55
1989	DEC	68	35	94	39	61	35	65
	OCT	36	30	83	28	72	33	67
1988	DEC	84	59	99	41	59	48	52
	OCT	49	23	80	--	--	--	--
1987	DEC	81	48	99	45	55	50	50
1986	DEC	54	39	98	--	--	--	--
1985	DEC	90	29	99	--	--	--	--
1984	DEC	39	10	98	--	--	--	--

MEAN (SE) SUCCESS DEC 97.1(0.7)
OCT 80.7(1.0)

MEAN (SE) OWNERSHIP AND HARVEST 40(3) 60(3) 43(3) 57(3)

---

[1] Cows and calves.

Elk Visibility and Hunter Effort

The number of elk sighted per hunter was significantly greater for the December hunts as opposed to the October hunts in 1989 and 1990 (Table 5). October and December hunts did not differ significantly in numbers of elk seen per hunter in 1988. Numbers of elk seen per hunter were significantly lower in the 1989 and 1990 October hunts as compared to the October 1988 hunt (Table 5). In general, October hunts showed a declining trend in numbers of elk seen per hunter, while the December hunts remained fairly constant.

Hunter effort, measured as the number of days required to harvest an elk, was significantly greater in the October hunts than the December hunts for 1988-1990 (Table 5), with approximately 60%, 28%, and 30% more time required in October for 1990, 1989, and 1988 respectively. October hunts showed increasing effort required to bag an elk from 1988-1990, with significantly more time (approximately 1 day) required to harvest an elk in 1990 as compared to 1988-1989. Although the same trends were present in the December hunt effort data, the differences were significant only for 1991 compared to previous years (Table 5).

The number of elk seen per hunter day was significantly lower in the October hunts for all 3 years (Table 5), with December hunters seeing approximately twice the number of elk per day by 1990. The number of elk seen/hunter day

Table 5. Mean (SE) number of elk seen per hunter, days required to harvest an elk, and number of elk seen per hunter per day for the October and December hunts, 1988-1990, and December 1991 hunt.

	ELK SEEN		DAYS/ELK		ELK SEEN/DAY	
YEAR	OCT	DEC	OCT	DEC	OCT	DEC
1991		23.7(2.0)		2.7(0.1)^{1}		10.2(0.8)^{1}
1990	14.3(1.9)^{a1}	23.2(1.9)^{b}	3.4(0.2)^{a1}	2.1(0.1)^{b2}	4.2(0.4)^{a1}	10.8(0.2)^{b1}
1989	17.3(2.8)^{a1}	21.7(2.4)^{b}	2.6(0.2)^{a2}	2.0(0.1)^{b2}	6.7(0.5)^{a2}	10.7(0.3)^{b1}
1988	22.4(2.7)^{2}	23.8(1.8)	2.5(0.2)^{a2}	1.9(0.1)^{b2}	8.8(0.6)^{a3}	12.2(0.2)^{b2}

^{abc}Values sharing a superscript do not differ within a row for each category (a=0.10).

^{123}Values sharing a superscript do not differ within a column (a=0.10).

showed a significant decline from 1988-1990 for the October hunts; in 1990, hunters saw only 47% of the mean number of elk seen per day in 1988. The same trend was present for the December hunt from 1988 to 1989, but the number of elk seen/hunter day did not differ significantly from 1989-1991.

DISCUSSION

Elk in Michigan have been highly vulnerable to the annual October and December hunts. Hunter success rates typically have been greater than 90%, compared to a mean success rate of 15.5% for Western USA and Canadian elk hunting states/provinces for the decade of the 1970's (Potter 1982). Effort required to harvest an elk has been low, typically requiring only 1-3 days of hunting, with a large proportion taken during the first day of the season. The high vulnerability of elk in Michigan is principally due to their approachability (Table 1), as the forested nature of the elk range makes security cover abundant (Moran 1973, Beyer 1987).

Flight distances of Michigan elk are short, but have increased 25% since the onset of hunting (Table 1). Numerous examples are available in the literature documenting increased flight distances in response to hunting or other human disturbance (e.g., Behrend and Lubeck 1968, Schultz and Bailey 1978, Sage et al. 1983). Behrend and Lubeck (1968) found flight distances to be greater for hunted white-tailed deer (Odocoileus virginianus) than for non-hunted, and that the most heavily exploited class showed the greatest flight distances. In Michigan, no differences in flight distances were observed following the first 3 years of hunting (Beyer 1987), likely attributable to a lack of sufficient time for the elk to adapt to exploitation, and the relatively short hunting seasons for a restricted number of hunters. The 1990-1991 flight distance results show that after 6-7 years of hunting pressure, flight distances for elk in Michigan have significantly increased. This trend is likely to continue with additional years of hunting.

The emphasis of the elk harvest in Michigan has been directed at cows to limit the population to a desired number of 800-900 animals (MDNR 1984). If increased flight distances are solely the result of harvest pressure, the largest flight distances should be seen in the most heavily exploited class, as shown by Behrend and Lubeck (1968). Antlerless elk, predominately cows, are harvested in the greatest numbers in Michigan (Table 4), and at a similar percent of their population as mature bulls (E. Carlson, MDNR, pers. commun.). Flight distances of cows, however, were significantly less than for bulls in 1990, and did not differ in 1991 (Table 1). The most wary class of Michigan elk are the mature bulls ($\geq$5X5). Beyer (1987) found that mature bulls in Michigan were being harvested at an estimated effort rate 5X that of yearling bulls, and 1.67X that of 3X3 and 4X4 bulls. Thus, mature bulls having significantly greater flight distances than younger bulls ($\leq$4X4) (Table 1) is consistent with hunting-driven increases in flight distances (Behrend and Lubeck 1968), while the equal or lower flight distance of cows is inconsistent with such a response. Thus, legal harvest alone is unlikely to be the sole contributor to increased flight distances. It should be noted, however, that poaching losses are higher for bulls than cows. As poaching occurs over most of the year, bulls, and particularly larger bulls, may have flight distances increased by this disturbance.

Michigan elk are in great demand for viewing and photography. These uses have also increased considerably since the start of the annual hunts (T. Carlson, MDNR, pers. commun.). Large mature bulls are the most prized class for viewing and photographic purposes, and consequently are harassed more than cows by viewers and photographers. This can be very stressful to bulls during the fall due to concurrent reproductive activities (Geist 1982). This increased stress due to heavy non-consumptive use may play a major role in the increasing wariness being shown by elk in general, and prime bulls in particular, especially as elk increasingly associate humans with danger (consumptive exploitation). The impacts of viewing use on elk were evaluated using vehicle counts during prime viewing periods as an index of viewing utilization. Numbers of elk seen during prime viewing hours were negatively related to the numbers of viewers (Table 3). Additionally, the number of elk groups seen was also negatively related to the level of viewing, but less strongly. Thus, elk seem to be reacting to viewing pressure by becoming less visible; they are staying out of wildlife openings which are easily accessible by roads, and apparently avoiding roads in general during periods of heavy vehicle use. This pattern of adverse responses to both vehicles and roads is very common in exploited elk populations (Lyon et al. 1985, Edge and Marcum 1991). The increased flight distances exhibited by elk in Michigan are likely then a result of increased total exploitation levels, both consumptive and non-consumptive, not driven solely by hunting.

Observational evidence for non-consumptive impacts on elk wariness involves behavioral patterns seen in elk, particularly during radio-collaring activities. In areas of the elk range with poorer road access (Camp 30 Hills), elk have tended to come into wildlife openings to feed earlier in the evening, are more difficult to frighten out of the openings, and are more likely to return before dark if frightened off. In these areas in the morning, elk are quick to leave if disturbed. Conversely, in heavily roaded (high disturbance) areas (PRCSF), elk come into openings at a similar time in the evening (the period of high harassment), quickly leave if disturbed, and seldom return before nightfall. In these same areas elk tend to stay out longer in the mornings (the period of low harassment), and are more reluctant to leave if disturbed. Such observational evidence suggests that elk are altering their behavior to avoid being disturbed, and that in heavily disturbed areas increased foraging time in the mornings is necessary to compensate for time lost in the evenings due to disturbance.

Big game species often try to decrease individual vulnerability by altering movement patterns (Douglas 1971, Geist 1970, Schultz and Bailey 1978) and/or social group sizes (Hirth 1977, Geist 1982). Elk in Michigan show increased mean daily movements during hunting periods (Beyer 1987). Although this pattern may be a behavioral attempt to avoid hunters by movement, it more likely represents elk being disturbed by hunters and attempting to flee. The limited size of the Michigan elk range (1500 km^2), combined with concentrations of hunters in areas where elk have been located, make increased mean daily movements more likely to increase elk vulnerability than decrease it. Thus, elk are likely not altering local movement patterns to decrease individual vulnerability during the annual hunts.

Similarly, elk are not altering social group sizes in response to hunting pressure (Table 2). Theoretically, either increases or decreases in social group size could be attempts to limit individual vulnerability. An increase in group size could be an attempt to limit individual vulnerability by decreasing the probability that a given individual will be killed if the group is discovered--the "selfish herd" hypothesis (Hamilton 1971, Hirth 1977, Geist 1982). Conversely, by decreasing social group size the probability of being initially located is decreased, thereby decreasing individual vulnerability--the "hider" strategy (Hirth 1977, Geist 1982). Elk, evolutionarily, are a colonizer species, with a high inherent tendency to herd (Geist 1982). This would make the "selfish herd" strategy the more likely scenario to decrease individual vulnerability by altering social group size. Additionally, the "hider" strategy works best if the animals limit movements (hide). Elk in Michigan, however, show increased mean daily movements during the hunts (Beyer 1987), which would limit the utility of a "hider" strategy. Thus, if elk were to show a social group numerical response to hunting, it would likely be an increase in social group size. The absence of any changes in social group sizes during the hunts suggests that elk in Michigan are not utilizing this means of behavioral adaptation to limit vulnerability.

The increase in flight distance of elk indicates that vulnerability of elk may be decreasing, or may decrease in the future. Although not large declines, hunter success in the December hunts has declined over the past 2-3 years (from 98-99% in 1984-88 to 94-95% in 1989-91), while hunter effort has significantly increased and numbers of elk seen by hunters has significantly declined (Table 5) in at least one of the two hunts. Public comments also indicate that the hunt is getting more challenging; hunters now indicate that they have to 'work to get an elk', where in the first years of the hunt bagging an elk was thought to be simply a matter of 'walking out and shooting one as they stood contentedly by' (T. Carlson, MDNR, pers. commun.).

Factors other than elk wariness may also contribute to the overall high vulnerability of elk in both the October and December hunts. Beyer (1987) found that mean daily movements of elk increased during the hunt. Increased movements, likely the result of elk being disturbed by hunters, can increase vulnerability by allowing elk to be more easily sighted by hunters. Similarly, an elk or a group of elk fleeing a hunter is more vulnerable than hiding elk or stealthily moving elk. Easy road access throughout the elk range is another factor contributing to high vulnerability in both October and December hunts (T. Carlson, MDNR, pers. commun.). Cooperative MDNR personnel, in terms of directing hunters towards areas likely holding elk and connecting hunters with private landowners seeking hunters to hunt on their property, also contribute to high overall elk hunting success in Michigan.

Elk appeared to be more vulnerable during the December hunts than the October hunts (Table 4). Effort required to harvest an elk was significantly greater in October, while total numbers of elk seen and elk seen per day were significantly lower, again suggesting that elk are less vulnerable in the October hunts. The October hunts were established to try to eliminate elk in peripheral areas of the elk range where agricultural depredation problems were consistently high (D. Whitcomb, MDNR, pers. commun.). As these peripheral areas are primarily privately-owned, it was initially felt that hunter success was lower in the October hunts due to a lack of accessibility to hunting areas. A preliminary geographic analysis of land ownership and elk harvest distribution indicates that the differences in vulnerability between the December and October hunts were not due to differences in land ownership patterns, as public and private land percentages and elk harvest percentages were similar in the hunt areas (Table 4). Data on land ownership are lacking for two of the three October hunts, however, so this conclusion may change as information increases.

Elk distribution appears to be a more important factor than land ownership in affecting elk vulnerability during the October hunt. As the October hunts were conducted on peripheral range, fewer elk were present in the units open to hunting than in the December hunts, conducted over the entire elk range (both core and peripheral areas). Hence, hunting would be expected to be more difficult in October, simply because fewer animals are available. Elk vulnerability was further decreased in the October hunts due to a number of landowners not allowing hunting on their property (D. Whitcomb, MDNR, pers. commun.). Many of these landowners feed elk on their property as well. Elk quickly discover these refugia and remain on them during shooting hours, leaving after nightfall to feed on adjacent agricultural lands. A third factor limiting vulnerability during the October hunts involved the timing of the hunt. By late October, many of the elk responsible for the high depredation problems of summer and early fall have already left these peripheral areas and returned to the primary range (outside of the hunt unit(s)), further decreasing the number of elk available to hunters and thus the success rates of the October hunts (D. Whitcomb, MDNR, pers. commun.).

The lower success rates associated with the October hunts were thus not the result of decreased vulnerability due to behavioral or other intrinsic characteristics of elk during this period, but rather an artifact of distributional factors. Certain factors do make elk in the December hunts significantly more vulnerable, however. The usual presence of snow cover for locating and tracking increases vulnerability, as do the policies of certain large privately-owned hunt clubs (ranches) (G. Matthews, MDNR, pers. commun.). Several large hunt clubs, comprising over 25% of the primary elk range (Moran 1973), are included within the boundaries of the December hunt. These clubs encourage harvest on their lands and produce a significant portion of the elk harvest each December. Elk are especially vulnerable on these hunt clubs due to significant road access, the presence of guides very familiar with the club land, the distribution of elk on these lands, and less disturbance of elk on these protected lands by the public (G. Matthews, MDNR, pers. commun.). These factors all combine to increase the vulnerability of elk in the December hunt.

SUMMARY AND CONCLUSIONS

Elk in Michigan have been highly vulnerable to the annual hunts, principally due to their approachability. Other factors also contribute to this vulnerability, including easy road access, cooperative resource management personnel, the policies of private hunt clubs, and increased elk movements during the hunt. Both flight distances and hunter effort required to harvest an elk are increasing in Michigan, while numbers of elk seen by hunters and viewers are decreasing. Additionally, elk visibility is negatively correlated to the level of viewing activity. This suggests that elk are getting increasingly wary, likely as a result of both annual hunting and increasing non-consumptive demands on the herd.

Differences in elk vulnerability between the October and December hunts appeared to be primarily due to problems with elk distribution during the October hunts. Certain factors do increase December vulnerability, the most important being the presence of tracking snow and the inclusion of large privately-owned hunt clubs in the open hunt areas.

As exploitation levels, both consumptive and non-consumptive, are unlikely to decline in Michigan, the wariness of elk in Michigan is likely to increase, resulting in decreased elk vulnerability during the annual hunts. The numbers of elk permits issued in the future may have to be increased in anticipation of declining hunter success. Increased wariness is also likely to negatively impact viewing opportunities, a principal objective of the MDNR elk management plan (MDNR 1984). If the trend of increasing elk wariness continues, large 'protected' viewing areas may be needed to maintain quality elk viewing opportunities in Michigan. These wildlife openings should have a highly palatable forage for elk, easy public access, and be situated far enough from roads to minimize elk disturbance. Additionally, the elk should be protected from approach by the public, to allow more people the opportunity to view the elk.

Chapter 2: Morphological Responses to Exploitation

The MDNR elk population management strategy entails limiting overall population size and maintaining desired herd structure via a carefully controlled annual harvest. The emphasis of this harvest is aimed at cows to control the growth of the herd, with only a limited any-bull harvest. As a result, the characteristically high bull:cow ratios present in the Michigan herd have been maintained, allowing a large number of bulls to survive into the older age-classes. Combined with the population management goals of the elk management plan, an overall population size of less than 1000 (representing a density of <0.7 elk/km^2 using the size of the current elk range), this harvesting strategy is in effect a "trophy management" strategy, producing a large number of prime-aged bulls with high per capita resource availability. Such a strategy, in theory, should result in increased antler sizes in bulls, as well as increased body weights of both bulls and cows.

The goal of this Chapter is to assess the morphological responses of elk to the current MDNR harvesting strategy, as well as to evaluate changes in morphological patterns that have occurred since the 1964-1965 elk hunts. Specific objectives include:

(1) Assess any directional changes in elk weights from 1984-1991.

(2) Evaluate elk antler characteristics for any directional changes in selected measurements from 1984-1991.

(3) Compare weights and antler characteristics from elk harvested in 1964-1965 with elk harvested in 1984-1991 to determine the extent of changes attributable to significant changes in population size rather than to hunting-driven directional changes.

(4) Develop a linear discriminant function (LDF) to assess the ability of antler characteristics to accurately discriminate bull age-classes.

METHODS

Morphological data collected at MDNR elk check stations for the 1984-1991 hunts were analyzed to assess any changes in physical characters of the elk herd in response to harvesting. Data analyzed included cow weights, bull weights, and bull antler development. Morphological data were also compared with similar data from the 1964-1965 elk hunts (Moran 1973) to assess any changes in the parameters following the decline and subsequent recovery of elk numbers in the late 1960's-1980's.

Dressed weights of both bull and cow elk were compared within sex- and age-class over time. Data on antler characteristics collected included number of points, beam lengths, beam circumferences, and maximum inside spread. Antler data were compared within age-classes over years to assess any changes in antler quality in response to the current harvesting system. Antler data were also pooled and used to construct a Linear Discriminant Function (LDF) (Morrison 1990) to assess the ability of antler characteristics to predict ages of harvested bull elk. To achieve adequate sample sizes in the construction of the LDF, bull elk 8.5-9.5 years-old were combined, as were 10.5 years-old and older bulls; all other age-classes were unique.

Analysis of weight and antler development data was done using the Kruskal-Wallis one-way ANOVA (Siegel 1956). A generalized Scheffe-type test was used for multiple comparisons (Miller 1981). Level of significance was set at $\underline{a}=0.10$. The ability of the LDF to accurately determine bull age was assessed via misclassification rates utilizing the data used to construct the model. A correct overall and within age-class classification percentage of $\geq 90\%$ was considered adequate for model performance.

RESULTS

Weights of harvested bulls did not differ from 1984-1991 (Table 6). Several significant differences were present within cow weights among years within age-classes (Table 7). However, these differences constituted no noticeable trends of either cow weights increasing or decreasing through time.

Table 6. Mean (SE) field-dressed weights (in pounds) of bull elk harvested during the annual Michigan elk hunts, 1984-1991.

AGE	YEAR 84	 85	 86	 87	 88	 89	 90	 91
0.5	180[1]	245	218	208(19)	201	199(5)	167(10)	205(12)
1.5	285	327(15)	321(14)	273(6)	347(15)	350(20)	302(18)	X
2.5	335	418(9)	403(10)	401(13)	403(18)	412(11)	434(15)	415(18)
3.5	484(59)	453(50)	475(23)	490(37)	486(17)	474(19)	447(50)	408(19)
4.5	468	528(28)	528(35)	569(31)	505(18)	544(26)	537(22)	533(15)
5.5	X	492(2)	556(34)	576(24)	603(17)	603(26)	553(15)	592(17)
6.5	615(10)	630(22)	608(26)	556(16)	581(31)	608(37)	576(46)	641(16)
7.5	632	538(50)	597(22)	629(30)	693(78)	X	611(25)	576(31)
8.5-9.5	553	X	598(57)	516	625	642(20)	588(17)	660(17)
≥10.5	X	616	X	574(29)	620(35)	608(8)	584(32)	553(7)

X=No elk in age-class.

[1] Weights without SE indicate only 1 elk in age-class.

Table 7. Mean (SE) field-dressed weights (in pounds) of cow elk harvested during the annual Michigan elk hunts, 1984-1991.

AGE	YEAR 84	85	86	87	88	89	90	91
0.5	198(13)	185(5)	172(6)	178(12)	162(7)	172(18)	180(5)	171(18)
1.5	274(21)	278(11)	268(9)	289(10)	263(12)	258(6)	269(11)	244(15)
2.5	338(18)^{abc}	352(10)^{a}	343(9)^{ab}	307(13)^{c}	323(7)^{bc}	325(24)^{abc}	316(7)^{c}	317(18)^{bc}
3.5	378(19)^{a}	351(7)^{a}	337(10)^{b}	363(7)^{a}	368(6)^{a}	354(13)^{a}	339(9)^{b}	370(9)^{a}
4.5	361(15)	367(5)	364(11)	374(13)	378(15)	361(20)	359(10)	380(13)
5.5	369(28)	373(9)	370[1]	369(11)	377(10)	375(16)	353(12)	360(18)
6.5	397(16)	381(10)	372(21)	350(20)	395(17)	345(30)	395(13)	340(30)
7.5	391(26)	389(23)	389(9)	348(10)	378(21)	401(18)	376(7)	371(11)
8.5	376(12)	413(32)	377(24)	380	397(1)	365(41)	393(22)	391
9.5-11.5	350(0)^{bc}	340(8)^{c}	351(9)^{bc}	371(10)^{abc}	386(10)^{ab}	381(17)^{abc}	402(11)^{ab}	359(17)^{abc}
12.5-14.5	374(33)	X	353(1)	359(10)	412(26)	375(18)	342(14)	378(9)
≥15.5	360^{ab}	X	314(0)^{b}	413(13)^{a}	325^{ab}	322(21)^{b}	373(33)^{ab}	X

X=No elk in age-class.

[1] Weights without SE indicate only 1 elk in age-class.

^{abc}Weights within an age-class sharing a letter do not differ (*a*=0.10).

Due to small sample sizes with older age-class bulls, only harvested bulls 7.5 years-old or younger were analyzed for antler development. Numerous significant differences in antler characteristics were present within age-classes over time (Tables 8-14). However, these differences also appeared not to indicate any trends of increasing or decreasing antler quality over time.

The classification ability of the LDF developed from the antler data was poor (Table 15). Successful classification percentages ranged from 100% for 1.5 year-old elk to only 25% for 5.5 year-old elk. Yearling bulls were the only age-class successfully classified ≥90% of the time. Among other age-classes, no general patterns of misclassifications were present (Table 15). The overall successful classification rate was 59.8% (Table 15).

DISCUSSION

Relative to other populations of Rocky Mountain elk, the Michigan herd is comprised of large robust individuals. Elk in Michigan, especially those in the adult (3.5+) age-classes, are typically 10-20% heavier than the weights reported for other populations of Rocky Mountain elk (Greer and Howe 1964, Greer 1965 <u>in</u> Moran 1973, Houston 1982). The heavy-bodied characteristic of elk in Michigan is likely a result of superior range quality, possible hybridization, and/or the expression of a colonizer phenotype (Geist 1982)

Table 8. Mean (SE) antler characteristics (in inches) in 1.5-year-old bulls harvested in Michigan, 1984-1991.

	ANTLER CHARACTERISTIC						
	Left			Right			
YEAR	Points	Circum	Beam	Points	Circum	Beam	Spread
84	1.0	2.5[c]	12.0[b]	1.0	2.5	14.9	11.9
85	1.9(0.3)	3.6(0.1)[b]	18.1(1.1)[a]	2.0(0.4)	4.0(0.4)	17.3(1.2)	14.0(1.6)
86	1.8(0.3)	4.2(0.2)[a]	21.9(2.4)[a]	1.5(0.3)	4.0(0.3)	21.7(3.7)	14.5(0.5)
87	1.0(0.0)	2.5(0.3)[c]	12.2(1.7)[b]	1.0(0.0)	2.7(0.2)	11.9(2.0)	11.9(0.0)
88	1.3(0.2)	3.1[bc]	17.0(2.5)[ab]	1.4(0.2)	3.6(0.2)	14.8	14.7
89	1.6(0.3)	---	---	1.8(0.3)	---	---	---
90	1.4(0.2)	---	---	1.6(0.3)	---	---	---
91	1.3(0.3)			1.0(0.0)			

[abc] Means sharing a letter within a column do not differ (a=0.10).

Table 9. Mean (SE) antler characteristics (in inches) in 2.5-year-old bulls harvested in Michigan, 1984-1991.

	ANTLER CHARACTERISTIC						
	Left			Right			
YEAR	Points	Circum	Beam	Points	Circum	Beam	Spread
84	2.0	4.8^{ab}	28.3	3.0	4.0^{b}	26.5	21.8
85	4.2(0.4)	4.3(0.2)^{b}	29.2(0.9)	4.3(0.3)	4.4(0.2)^{ab}	29.3(1.0)	24.8(1.9)
86	4.5(0.3)	4.5(0.1)^{ab}	28.7(0.6)	4.8(0.3)	4.5(0.1)^{ab}	28.6(0.6)	24.3(0.8)
87	4.4(0.2)	4.3(0.1)^{b}	29.3(0.6)	4.0(0.2)	4.3(0.1)^{b}	29.4(0.6)	24.5(0.6)
88	4.5(0.2)	4.9(0.1)^{a}	28.7(1.1)	4.3(0.2)	4.8(0.1)^{a}	29.1(1.6)	25.4(1.7)
89	4.0(0.5)	---	---	4.2(0.2)	---	---	---
90	4.5(0.2)	---	---	4.6(0.3)	---	---	---
91	4.7(0.4)			5.0(0.3)			

^{ab}Means sharing a letter within a column do not differ (a=0.10).

Table 10. Mean (SE) antler characteristics (in inches) in 3.5-year-old bulls harvested in Michigan, 1984-1991.

	ANTLER CHARACTERISTIC						
	Left			Right			
YEAR	Points	Circum	Beam	Points	Circum	Beam	Spread
84	5.5(0.5)	5.0(0.1)	34.8(1.0)	5.5(0.5)	5.0(0.2)	34.8(0.1)	27.2(1.2)
85	4.3(0.3)	4.9(0.5)	30.3(3.6)	4.0(1.5)	4.8(0.8)	33.5(3.5)	28.4(3.4)
86	5.5(0.5)	5.2(0.1)	33.7(0.3)	5.8(0.3)	5.3(0.1)	34.2(0.6)	32.2(1.5)
87	5.3(0.3)	4.9(0.1)	32.7(0.4)	5.3(0.3)	5.0(0.1)	33.3(1.2)	28.1(2.8)
88	5.0(0.2)	5.7(0.3)	33.7(0.7)	5.1(0.3)	5.6(0.3)	33.0(1.0)	29.4(1.6)
89	4.9(0.4)	---	---	5.0(0.2)	---	---	---
90	5.0(0.4)	---	---	5.0(0.5)	---	---	---
91	4.3(0.3)				4.3(0.3)		

Table 11. Mean (SE) antler characteristics (in inches) in 4.5-year-old bulls harvested in Michigan, 1984-1991.

	ANTLER CHARACTERISTIC						
	Left			Right			
YEAR	Points	Circum	Beam	Points	Circum	Beam	Spread
84	5.0	5.0	36.9	6.0	4.9[b]	---	36.0
85	5.3(0.3)	5.2(0.1)	33.9(1.6)	5.0(0.4)	5.3(0.2)[b]	36.1(0.6)	28.1(1.0)
86	6.0(0.2)	5.7(0.1)	36.6(0.9)	6.1(0.1)	5.6(0.1)[b]	37.7(0.9)	31.5(1.5)
87	6.0(0.3)	5.6(0.2)	39.0(1.1)	5.4(0.3)	5.6(0.2)[b]	39.5(1.1)	32.6(1.1)
88	5.4(0.2)	6.3(0.5)	37.3(1.9)	5.5(0.2)	6.3(0.3)[a]	38.1(3.0)	31.0(2.0)
89	5.6(0.2)	---	---	5.7(0.2)	---	---	---
90	5.6(0.2)	---	---	5.4(0.2)	---	---	---
91	5.5(0.2)			5.5(0.2)			

[ab] Means sharing a letter within a column do not differ (a=0.10).

Table 12. Mean (SE) antler characteristics (in inches) in 5.5-year-old bulls harvested in Michigan, 1984-1991.

	ANTLER CHARACTERISTIC						
	Left			Right			
YEAR	Points	Circum	Beam	Points	Circum	Beam	Spread
84	---	---	---	---	---	---	---
85	5.0	5.8	40.5	5.0	6.1	44.8	35.3
86	5.8(0.4)	5.5(0.2)	38.1(2.5)	5.5(0.9)	5.8(0.2)	41.7(1.9)	30.8(2.1)
87	5.8(0.3)	5.7(0.2)	41.3(1.4)	6.2(0.5)	5.9(0.2)	40.5(0.9)	35.1(1.5)
88	6.2(0.1)	6.4(0.3)	39.5(3.4)	6.1(0.3)	6.5(0.5)	39.6(2.1)	34.0(1.5)
89	6.3(0.2)	---	---	6.3(0.2)	---	---	---
90	6.0(0.2)	---	---	5.6(0.2)	---	---	---
91	6.1(0.1)			6.3(0.2)			

Table 13. Mean (SE) antler characteristics (in inches) in 6.5-year-old bulls harvested in Michigan, 1984-1991.

	ANTLER CHARACTERISTIC						
	Left			Right			
YEAR	Points	Circum	Beam	Points	Circum	Beam	Spread
84	6.0	6.4	47.8	6.0	6.0	43.9	33.8
85	5.5(0.5)	6.5(0.2)	45.0(4.5)	6.5(1.5)	6.3(0.3)	45.5(4.1)	34.4(0.9)
86	6.0(0.0)	6.2(0.4)	40.9(6.4)	5.0(0.0)	6.7(0.2)	43.2(6.2)	39.4(1.6)
87	7.0(1.0)	6.3(0.3)	45.3(1.0)	6.5(0.5)	6.4(0.1)	45.0(1.0)	31.0(0.1)
88	6.4(0.2)	6.5(0.5)	38.5(3.6)	6.4(0.6)	6.3(0.3)	40.5(4.8)	31.5(5.4)
89	5.8(0.3)	---	---	6.3(0.5)	---	---	---
90	5.8(0.3)	---	---	5.8(0.3)	---	---	---
91	6.0(0.6)			6.7(0.3)			

Table 14. Mean (SE) antler characteristics (in inches) in 7.5-year-old bulls harvested in Michigan, 1984-1991.

	ANTLER CHARACTERISTIC						
	Left			Right			
YEAR	Points	Circum	Beam	Points	Circum	Beam	Spread
84	7.0	6.3	46.1	8.0	6.3	45.0	33.6
85	6.6(0.5)	6.2(0.2)	43.1(1.4)	6.6(0.5)	6.2(0.2)	42.4(1.6)	33.9(2.7)
86	5.7(0.3)	6.5(0.4)	43.0(2.5)	6.0(0.0)	6.5(0.4)	44.1(1.8)	37.4(3.6)
87	6.3(0.3)	6.6(0.4)	44.9(0.8)	6.7(0.3)	6.4(0.3)	45.1(2.5)	32.5(0.8)
88	6.0(0.0)	6.9(0.6)	43.8(1.6)	6.0(0.0)	6.8(0.5)	43.4(1.4)	37.4(0.9)
89	---	---	---	---	---	---	---
90	6.1(0.1)	---	---	5.7(0.2)	---	---	---
91	7.0(0.8)			7.0(0.8)			

Table 15. Successful classification rates and misclassified ages of the bull antler Linear Discriminant Function (LDF) developed for bull elk harvested in Michigan, 1984-1990.

AGE	Percent Successful Classification	Ages Misclassified as
1.5	100.0	---
2.5	89.7	3.5
3.5	66.7	2.5,4.5,5.5
4.5	45.5	3.5,5.5,6.5,7.5
5.5	25.0	4.5,6.5,7.5
6.5	44.4	7.5,8.5
7.5	33.3	4.5,5.5,6.5,8.5-9.5,≥10.5
8.5-9.5	66.7	6.5
≥10.5	66.7	7.5,8.5
OVERALL	59.8	

in the Michigan elk.

Weights of harvested elk showed no directional trends from 1984-1991 (Tables 6-7). During this period, the estimated size of the Michigan herd was relatively stable, likely in the 900-1200 range. Although statistical comparisons are not possible, the 1984-1991 weights are in general slightly heavier than those recorded by Moran (1973) for 454 elk harvested during the 1964-1965 hunts (Table 16), especially for the older (3.5+) age-classes. During 1964-1965, the elk population was estimated to be significantly larger than the 1984-1991 levels (approximately 2000 elk), and the quality of the elk range was thought to be poorer than at present. Thus, the generally lighter weights recorded for harvested elk in 1964-1965 relative to 1984-1991 may represent a density-dependent response in body size to decreased per-capita resource availability, although the greater numbers of elk permits issued in 1964 and 1965 (relative to 1984-1991) may have allowed less hunter selectivity for larger elk as well. However, the 1964-1965 weights still tended to be larger than those recorded for Western USA Rocky Mountain elk populations (Moran 1973).

As previously noted, the most likely factors responsible for the historically larger body sizes of elk in Michigan include higher quality habitat, possible hybridization with other _C_. _elaphus_ subspecies, and/or the expression of a colonizing phenotype in the Michigan elk.

Table 16. Mean (range) field-dressed weights (in pounds) of elk harvested during the 1964-1965 Michigan elk hunts (from Moran 1973).

AGE	BULLS	COWS
0.5	187 (130-233)	177 (105-234)
1.5	295 (219-362)	275 (210-345)
2.5	393 (293-471)	327 (242-378)
≥3.5	497 (360-656)	358 (256-459)

The Michigan elk range is far more productive than most Western elk ranges, and the further availability of MDNR wildlife plantings and peripheral row crops combine to make the forage plane of elk in Michigan superior to most, if not all, Western ranges. This abundance of high quality forage, combined with low elk densities (~1200 elk on ~1500 km^2, i.e $\leq$1 elk/km^2), result in high per capita availability of nutritionally superior forage. Elk populations that encounter large quantities of relatively unexploited food sources have been shown repeatedly to consist of large-bodied large-antlered individuals, while those on over-grazed nutritionally poorer ranges consist of smaller bodied individuals (Geist 1982, Clutton-Brock et al. 1985, McCorquodale et al. 1989). Thus, the heavy body weights associated with elk in Michigan relative to Western herds is likely at least partially attributable to the presence of abundant high-quality food sources historically characteristic of the Michigan elk range.

The current Michigan elk herd was commonly thought to have originated from the release of 7 Rocky Mountain elk in Cheboygan County in 1918 (Moran 1973). However, a more detailed look into the history of elk releases in Michigan (Glenn 1990) notes numerous releases that could have contributed to the present herd, including, potentially, red deer and Roosevelt elk. A preliminary analysis of the genetic makeup of the Michigan elk suggested that certain alleles more commonly associated with Roosevelt elk (or red deer) than Rocky Mountain elk are present in the current Michigan herd (Glenn 1990). This evidence suggests the possibility of a hybrid origin for the Michigan elk herd. Roosevelt elk are the largest bodied of the North American elk subspecies, being on average ~10-20% heavier than the Rocky Mountain subspecies (Boyd 1978). If the Michigan elk herd originated from hybrids of Rocky Mountain and Roosevelt elk, then the characteristically large body size of Michigan elk may have been one of the traits acquired from the Roosevelt elk component. However, the genetic makeup of the Michigan elk herd has not been thoroughly investigated, and any evidence of a hybrid origin is still largely speculative. Such an origin, however, could conceivably at least partially account for the large body sizes associated with elk in Michigan.

A third factor that may contribute to the large body sizes seen in elk in Michigan is the expression of a dispersal or colonizer body form (Geist 1982). As previously noted, colonizing ungulates often are large-antlered, large-bodied individuals (Geist 1982, McCorquodale et al. 1988, Leader-Williams 1988), since colonizing ungulates typically encounter an abundance of resources and grow large phenotypically. Under these colonizing conditions, the larger individuals usually out-compete the smaller, resulting in a genetic increase in body size in the colonizing population (Geist 1982). Elk in general are a colonizing form of their ancestral stock, red deer. The abundant high quality foods present in the Michigan elk range, along with the low elk densities, especially over the last 20 years, may thus have resulted in a genetic response of increased body size, as the habitat characteristics encountered by elk in Michigan are more similar to those encountered by colonizing elk populations rather than established populations under some degree of density-dependent regulation. This response, although similar to the body size response due to high per capita resource availability discussed earlier, differs in that the increase in body size is genetic, not simply phenotypic plasticity. Thus, the heavy body weights of elk in Michigan may also be a result of a genetic response to abundant resource availability in the Michigan elk range.

Ungulate populations with access to abundant high quality food resources typically consist of large-antlered individuals as well as large-bodied (Geist 1982, Clutton-Brock et al. 1985, McCorquodale et al. 1989). Various "trophy management" harvesting schemes have also been shown to increase the size and/or quality of antlers as well (Fleming 1983, Franklin et al. 1985, Ueckermann 1987, Weigand and Mackie 1987). Most of these involve holding the population well below the "carrying capacity" of the range, with the emphasis of the harvest being placed on females to allow increased male survivorship into the older age-classes. The increased number of older males, combined with increased per capita resource availability, theoretically results in more prime-aged males with larger better quality antlers, i.e. a population with a large number of trophy animals.

Since the re-initiation of elk hunting in 1984, the population management strategy employed by the MDNR has essentially been a trophy management scheme. The elk population is limited to ~1000 animals, the emphasis of the harvest is placed on the cows, and high numbers of bulls, especially older age-class bulls, are maintained (bull:cow ratios ≥60:100). Antler data from 1984-1991, however, show no tendencies of increasing antler quality in harvested Michigan bull elk (Tables 8-14). Moreover, the antler data from the 1984-1991 hunts does not differ greatly from that recorded for the 1964-1965 hunts, when the population level was approximately twice the 1984-1991 levels (Table 17; Moran 1973). Thus, the current harvesting scheme, while maintaining large numbers of prime-aged bulls in the Michigan herd (**Chapter 5**), has not resulted in increased antler quality in the bulls. Nor, apparently, has the increased habitat quality and increased per capita resource

Table 17. Mean antler characteristics (in inches) for elk harvested during the 1964-1965 Michigan elk hunts (from Moran 1973).

Age	Beam Circumference	Beam Length	Maximum Spread
1.5	3.5	17.0	13.3
2.5	4.3	28.3	24.3
3.5	5.0	32.0	28.0
4.5	6.0	40.5	34.5
5.5	6.5	44.0	38.0
6.5	6.5	46.3	37.8
≥7.5	6.5	46.0	41.3

availability in the 1970's-1990's resulted in increased antler sizes relative to the 1960's.

Antler development is generally considered to be a function of nutrition, genetics, and age (Clutton-Brock et al. 1979, 1985; Bubenik 1982, Fleming 1983, Gore et al. 1985, Ueckermann 1987, McCorquodale et al. 1989). Michigan elk have traditionally been thought to have small antlers relative to their body size; elk in Michigan are typically 10-20% heavier than other Rocky Mountain elk populations, but the herd has produced few Boone and Crockett Club record book bulls (bull elk with a total antler score of 325 points or better). Since the Michigan elk range provides abundant high quality food resources for the elk herd, this has been used to suggest that the genetics necessary for trophy antler development are lacking in the Michigan herd, i.e. that the founding individuals lacked the genetic basis for superior antler development.

Glenn (1990), comparing Boone and Crockett scores for elk harvested in the 1989 Michigan hunt with those harvested on Vermejo Park, New Mexico (Wolfe 1982), a ranch whose elk population is specifically managed for trophy production, found Michigan scores to be only slightly less than Vermejo scores. Glenn (1990) concluded that this similarity in antler size and development indicated that the genetic basis for antler development in the Michigan elk herd was not inferior to other populations. Two complications are present in Glenn's (1990) interpretation of these results, however. First, although he stressed that the Vermejo Park herd was specifically managed for trophy elk, Glenn (1990) apparently did not realize that the harvest management strategy used on the Michigan elk herd is also a trophy management strategy. Thus, his implicit assumption that the Vermejo Park herd should produce superior Boone and Crockett scores due to the harvest strategy alone was incorrect. Secondly, the nutritional aspects of the Michigan range are likely better than those present on Vermejo Park, as evidenced, for example, by the heavier weights of elk in Michigan relative to other populations of Rocky Mountain elk. Since antlers are a "luxury" tissue, of lower energetic priority than either body growth or maintenance (Clutton-Brock et al. 1979, Geist 1982), if 2 populations have approximately equal genetic potential for antler growth, superior antler development should be seen in the population with superior nutritional status. The importance of the nutritional aspect has been stressed much more than the genetic in the development of trophy antlers (Clutton-Brock et al. 1979, 1985; Gore et al. 1985, Ueckermann 1987). Thus, it could be argued that in the comparison of Boone and Crockett scores from bulls harvested in Michigan and in Vermejo Park (Glenn 1990), Michigan elk should have been superior to Vermejo Park bulls if the genetic potential for antler development was similar. Therefore, Glenn's

(1990) conclusion that the genetic basis of antler development is not inferior in the Michigan elk herd is premature, and more in-depth research needs to be done on this subject before any hard conclusions on the genetic potential for antler development in the Michigan elk herd are warranted.

Glenn (1990) also presented evidence to suggest that some of the genetic makeup of the Michigan elk herd was more common in Roosevelt elk or red deer than Rocky Mountain elk. Although much more extensive genetic work is necessary to determine the presence of any hybridization in the Michigan elk herd, this hypothesis is potentially helpful in explaining some of the morphological characteristics present in the herd (such as large body size). Roosevelt elk, as previously noted, are physically larger than Rocky Mountain elk, but possess antlers which tend to be more massively beamed but of shorter beam lengths and lesser spread (Bryant and Maser 1982). This combination of characteristics results in lower Boone and Crockett scores; hence, Roosevelt elk are given their own records category, separate from Rocky Mountain elk. If hybridization with Roosevelt elk or red deer did occur early in the history of the Michigan elk herd, it is conceivable that the characteristics for smaller antlers could have been assimilated from either Roosevelt elk or red deer. As previously noted, Roosevelt elk could also have contributed genetic material towards the heavier body weights seen in Michigan elk relative to other Rocky Mountain elk populations, although a phenotypical and later genetic response to resource availability could just as easily account for the large body sizes. Thus, early hybridization with either Roosevelt elk or red deer could potentially account for the smaller than expected antlers on Michigan elk. It should be emphasized, however, that the possibility of hybridization, while suggested by the preliminary work of Glenn (1990) and the reintroduction history of the Michigan elk, is only a hypothesis; significantly greater detailed genetic studies of the Michigan elk herd will be necessary to determine the presence of, or extent of, hybridization within the Michigan herd.

Age is the third factor necessary to produce large antlers. Little data are available on the developmental history of elk antlers with age. Flook (1970) found antler growth to be almost continuous throughout the life of elk, peaking at age 12. Flook (1970) also noted large variation in antler growth between the 7th and 11th sets. Similarly, Bubenik (1982) felt that peak antler size was attained in bull elk with their 11th or 12th sets of antlers. Wolfe (1982) also found elk in the Vermejo Park, NM, to reach peak antler development at age 10.5. Red deer have been variously reported to attain peak antler development at 8-14 years (Ueckermann 1987), 11-12 years (Foldes and Brull 1972), and 14-16 (Bubenik 1982). Since red deer are longer lived than elk (Clutton-Brock et al. 1982, Geist 1982), they likely develop their largest antlers at a later age.

Similarly, little information is available on when elk antler development ceases (Bubenik 1982). In red deer populations on poor quality range, peak antler development is typically attained with the 10th or 11th set; in contrast, peak development on good quality range may not occur until the 14th-16th set (Bubenik 1982). Deterioration in the antler sizes of red deer conversely begins at 10-11 or 16-18, depending upon the nutritional status of the individual. Thus, although little information is available on when peak antler development is attained in elk, the age is likely to be influenced greatly by the nutritional status of the individual/population.

Due to the superior nutritional status of elk in Michigan, it is likely that peak antler development will not be attained until age 9-10 or older (similar to those ages reported by Flook (1970) and Bubenik (1982)). Using the conservative value of age 9.5, of 403 bull elk $\geq$1.5 years old harvested in Michigan from 1984-1991, only 22 (5.5%) were $\geq$9.5 years-old (Table 18), with the oldest being 17. This sample has too few individuals in the age-classes beyond 7.5 to determine the actual peak of antler

Table 18. Numbers of known-age elk harvested in Michigan by age-class, 1984-1991.

	YEAR																	
	BULLS									COWS								
AGE	84	85	86	87	88	89	90	91	SUM	84	85	86	87	88	89	90	91	SUM
0.5	1	1	1	4	3	8	4	5	27	3	9	3	4	7	7	14	8	51
1.5	1	7	4	3	9	9	11	3	47	5	10	5	11	32	19	13	17	112
2.5	1	6	13	16	20	11	16	6	89	4	13	12	12	19	6	21	10	97
3.5	2	3	4	5	23	9	6	13	65	2	13	8	14	16	10	19	16	98
4.5	1	4	7	8	10	16	9	13	68	6	7	8	7	9	11	16	11	75
5.5	0	1	5	6	7	8	12	9	48	2	6	1	9	7	6	8	6	45
6.5	1	2	2	2	5	4	4	3	23	3	9	3	4	8	6	6	3	42
7.5	1	5	3	3	3	0	7	4	26	3	9	2	4	8	11	7	4	48
8.5	1	0	2	1	2	3	5	1	15	3	2	3	1	4	4	4	2	23
9.5	0	0	0	0	0	4	2	1	7	1	3	1	2	5	2	2	1	17
10.5	0	0	0	1	2	2	2	0	7	0	2	2	0	1	4	4	0	13
11.5	0	0	0	1	0	0	0	1	2	1	3	1	3	1	0	1	1	11
12.5	0	0	0	2	0	0	1	0	3	1	2	2	0	3	1	2	3	14
13.5	0	0	0	0	0	0	2	0	2	1	0	0	1	1	0	1	3	7
14.5	0	0	0	0	0	0	0	0	0	0	0	1	3	2	2	1	1	10
15.5	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	3
16.5	0	0	0	0	0	0	0	0	0	1	0	1	2	0	0	0	0	4
17.5	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	1	0	3
18.5	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	2
19.5	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
20.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
22.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2

development in Michigan, or, similarly, the age of antler regression. However, if peak development is not attained until age 9.5 or later, as is likely the case, the absence of many Boone and Crockett bulls being harvested in Michigan may be attributable to the low numbers of elk in the peak development age-classes that have been harvested. Combined with the rareness of producing a record book bull in any area, this low harvest in the trophy age-classes possibly contributes to the lack of record book bulls produced in Michigan.

The Michigan elk herd has been managed under a trophy management strategy since the initiation of the annual elk hunts in 1984. Through the 1991 harvest, however, there has been no noticeable improvement in antler quality in response to this strategy (Tables 8-14). Due to the low numbers of bulls harvested, however, such a trend would be difficult to document if present. For example, the largest number of bulls harvested in any single age-class in any one year was 23, and of 136 possible age-class X year combinations (17 age-classes of bulls X 8 years of hunting), the number of bulls in any one age-class within a year has been ≤ 2 89 times (65.4% of the total) (Table 18). Thus, the quantity of available data is insufficient to determine any changes in antler characteristics from 1984 to the present, especially as these changes are likely to be small.

Additionally, the Michigan elk herd has always had an excellent nutritional plane, even prior to the re-initiation of hunting in 1984. During the 1970's the population was low (~200 elk in 1974), but grew rapidly and spread throughout the entire present range during the 1970's and early 1980's. Thus, the elk herd during this period could be classified as a "colonizing population", as described by Geist (1982). Such populations are typically characterized by large body sizes and peak antler development (Geist 1982, Clutton-Brock et al. 1985, McCorquodale et al. 1989). It is possible that the elk herd reached its maximum potential growth and antler sizes during this "colonization" period. The trophy management harvest strategy from 1984-1991 thus would merely have maintained these peak parameters for the elk herd, rather than increasing either antler or body sizes, as the nature of the harvesting strategy is to maintain low elk densities with maximum numbers of prime-aged bulls, rather than a selective culling scheme aimed at bulls considered to be inferior. This colonizing aspect of the Michigan herd, characterized by relatively low densities, high numbers of prime-aged bulls, and high per capita resource availability, could easily be applied to the entire history of elk in Michigan. This could help explain the lack of differences seen in antler characteristics between elk harvested in the 1964-1965 hunts and the 1984-1991 hunts; however, this explanation is clouded by the generally greater body weights for elk harvested in the 1984-1991 hunts.

Within localized populations, antler size and development is popularly considered a reliable indicator of age, although this relationship certainly does not hold true among disjunct populations. Considerable time and expense is involved in tooth sectioning to accurately determine the age-distribution of the Michigan elk harvest (S. Schmitt, MDNR, pers. commun.). Knowledge of the age-distribution is especially important for bull elk, both to evaluate how well the current harvest strategy is maintaining the desired prime-aged classes, as well as for future evaluation of trends in antler development in response to the current, or future alternate, harvest strategies. To evaluate the ability of antler characteristics to discriminate age-classes of the Michigan elk, both as a test of the local population hypothesis above and as a means of saving the considerable time and expense associated with tooth-sectioning aging, a linear discriminant function (LDF) model was developed utilizing 7 antler characteristics. This model proved to be a poor predictor of age in harvested bulls, having a successful classification rate of only ~60%. Thus, the recorded antler characteristics appear to be poor predictors of the ages of bull elk harvested from the Michigan herd.

Several factors likely contributed to the poor performance of the LDF model. Inherent in the development of any LDF model is the assumption that the variables measured are appropriate or useful discriminators (C. Ramm, MSU Dept. of For., pers. commun.). It is possible that the antler characteristics used to develop the LDF (points, beam lengths, beam circumferences, and maximum spread) were not the best possible measures of antler development. However, these characteristics are the most commonly used to assess antler quality and development (for example, Boone and Crockett scores are based on these measures) and, secondly, they were the only measures historically available for the Michigan elk herd. Thus, while it is possible that the measures used in the LDF development were inappropriate, no other measures have been suggested in the literature as being superior indicators of antler development.

The assignment of class-specific prior classification probabilities for membership in any discriminate class also effects the efficiency of LDF models (C. Ramm, MSU Dept. For., pers. commun.). The default in linear discriminant analysis (LDA) is to assign unknowns equal probability of belonging to any of the discriminant classes present in the LDF. In actuality, if the true priors diverge from equality, the likelihood of correct classification decreases. It is possible to calculate alternate prior probabilities from the sample used to construct the LDF;

this assumes, however, that all subsequent unknown samples will have the same probabilities of belonging to a specific age-class as did the sample used in building the LDF. Unfortunately, hunter-killed samples tend to vary greatly in numbers killed within specific age-classes. Additionally, the pooling of age-classes used in the development of this LDF (to generate larger sample sizes) further decreases the likelihood of calculating accurate prior probabilities. Thus, the prior probabilities of membership in any age-class were set as equal in this LDF. Since actual harvesting of bulls is unlikely to be equal across all age-classes, this assumption likely contributes to the poor performance of the LDF model. In the absence of being able to determine accurate priors, however, this bias appears to be unavoidable, or at least no worse than the bias associated with any other set of prior placement probabilities that could have been used.

A third mechanical problem that likely contributed to the poor performance of the LDF was the small sample sizes associated with each age-class, along with the pooling of 8.5-9.5 and ≥10.5 year-olds into single age-classes. These operations likely contributed to the poor performance of the LDF model; however, they were necessary to generate sample sizes deemed adequate ($n \geq 50$) for model development. The classification biases associated with these operations therefore appear to be unavoidable.

Despite the numerous mechanical assumptions, and their associated biases, present in the development of the LDF model, it is likely that most of the responsibility for the poor classification accuracy of the model is due to faulty biological reasoning. The assumption that local populations can be differentiated into age-classes by their antler development, although used in European hunting reserves (Ueckermann 1987) and commonly held among North American naturalists, is likely not valid, especially across any time frame. Numerous characteristics within a local population can affect antler development in cervids, including genetically superior sires (Williams et al. 1982, Harmel 1982, Ueckermann 1987), individual social status (Bartos and Hyanek 1982, Clutton-Brock et al. 1982), degree of individual genetic heterozygosity (Smith et al. 1982), and nutritional status (Clutton-Brock et al. 1982, Suttie and Kay 1982, Ullrey 1982, Ueckermann 1987). As all these factors can vary within local populations, it is unlikely that antler development can be predicted accurately within the population. This is especially true when temporal effects are added in; differences in annual resource availability, siring stock, gene frequencies for antler characteristics, etc., all tend to vary to a greater degree among years than within. Thus, the biological assumption behind the LDF antler model, that local populations display characteristic patterns of antler development, is likely invalid, especially when temporal variances are added in, as in the construction of this LDF model.

SUMMARY AND CONCLUSIONS

Michigan's elk are characterized by heavier body weights and relatively small antlers compared to Western Rocky Mountain elk populations. Several factors likely have contributed to this pattern, especially the excellent nutritional plane of the Michigan herd in conjunction with the colonizing aspect of elk in Michigan. Possible hybridization with other C. elaphus subspecies may also have contributed to these characteristics.

Although under a trophy management harvesting strategy since 1984, elk have shown no directional changes in either body size nor antler development in response to the MDNR population management strategy. Comparisons with weight and antler data from 1964-1965, when the elk population was estimated to be approximately twice the present level, also show little change. Additionally, since the re-initiation of elk hunting in 1984, the population size of the Michigan herd has actually been slightly increasing (**Chapter 5**), an extension of the continuous increase since the population low of ~200 elk in the early 1970's. Thus, it is likely that even subsequent to the implementation of population management via hunting in 1984, the Michigan herd was not experiencing any density-dependent regulation. Since the

MDNR harvesting strategy emphasizes maintaining high per capita resource availability by limiting total elk numbers, and is not a selective culling system aimed at "inferior" animals, no directional responses in either body sizes or antler development would necessarily be expected.

Elk in Michigan show comparatively poor antler development relative to body sizes. Since the nutritional plane of the herd is superior, this is most likely a problem of genetics and/or an artifact of the ages of harvested bulls. Antler sizes of Michigan bulls are slightly inferior to trophy-managed Western herds, while the nutritional status of Michigan bulls is likely equal to or better than these herds. This suggests that the genetics for superior antler development may be lacking in the Michigan herd. This is potentially attributable to either poor siring stock, or possible early hybridization with other elk subspecies and/or red deer. However, peak antler development in the Michigan herd is likely not achieved until ages 9.5-10.5 or even later. Very few elk in these older age-classes have been harvested in Michigan. This lack of an older age-class bull harvest may be due to high poaching levels, very high older bull mortality brought on by intense competition resulting from the high numbers of bulls present in the Michigan herd, or, perhaps, bull elk in Michigan age faster than in other elk populations and simply do not commonly survive into the ages of peak antler development. Thus, the lack of Boone and Crockett Club record book bulls from the Michigan herd, where conditions superficially appear ideal for their production, is likely due to some combination of poor genetic potential and a lack of older age-class harvest, suggesting poor survivorship in older age-class bulls.

Finally, linear discriminant analysis indicated that bull antler characteristics are poor indicators of age-class in Michigan bulls. Although numerous methodological biases were present in the linear discriminant function developed in this Chapter, the myriad of ecological factors affecting antler development--genetics, relative nutrition, weather, social status, etc--all likely combine to vary antler development significantly among individuals, locally, and temporally. The popularly held notion that antler development is an accurate indicator of age in elk is thus likely erroneous.

Chapter 3: Social Group Dynamics of Elk in Michigan

Many aspects of the social group dynamics of elk and red deer have been extensively studied. Most of the research on elk social dynamics, however, has involved only Western herds. These herds typically differ greatly from the Michigan herd in terms of sex- and age-structure, habitat availability, dispersal potential, and seasonal movements. These factors can all significantly impact the social dynamics of elk, particularly social group sizes and patterns. For example, Franklin and Lieb (1979) hypothesized that non-migratory elk herds, such as Michigan's, should exhibit relatively static social group sizes and compositions, while Hirth (1977) and others suggested that social group sizes should vary with habitat structure.

Moran (1973) evaluated many social group characteristics of the Michigan elk. Since Moran's (1973) work, however, the elk herd has been subject to increasingly heavy exploitation levels. Changes in population size and exploitation levels may have combined to alter the social group responses to their environment made by elk in Michigan. The goal of this Chapter is to evaluate the current social group dynamics of elk in Michigan, particularly in reference to the dynamics documented by Moran (1973). Specific objectives include:

(1) Determine the sizes, composition, and constancy of elk social groups.

(2) Determine how the above differ based on sex, time, and habitat.

(3) Determine the characteristics of elk harems in Michigan.

METHODS

Social Group Dynamics

The sizes of elk social groups were evaluated by group observations, both of groups containing radio-collared individuals and all other elk groups encountered. Observations on group sizes were made throughout the year on as many groups as possible per day. Observations were made from vehicles during daylight hours when an accurate count and compositional breakdown of observed groups was possible. All groups observed had the following minimum data recorded; group size, group composition, and habitat occupied.

Group sizes and membership were evaluated throughout the year to assess seasonal patterns in the social organization of the Michigan elk. Information on group sizes, composition, and individual specificity was compared with the same data from Moran (1973), which in effect represents a pre-heavy exploitation control.

Group observations were pooled to increase sample sizes based on habitat structure and an elk's biological year.

Elk habitat was segregated into 6 vegetative structural types which accounted for the diversity of vegetation-types present in the elk range: (1) dense coniferous forest (DCF), (2) dense hardwood forest (DHF), (3) open coniferous forest (OCF), (4) open hardwood forest (OHF), (5) opening (OPEN), (6) and shrub/regeneration (S/R). Group observations were also pooled based on the biological year of elk into the following periods: (1) WINTER (January-March), (2) Pre-CALF (April-May), (3) CALF (June), (4) Post-CALF (July-August 15), (5) Pre-RUT (August 15-September 15), (6) RUT (September 15-October), and (7) Post-RUT (November-December). These periods were based on known differences in elk behavioral and social patterns among the periods (Geist 1982).

Group Constancy

Social groups associated with 20 previously radio-collared elk were intensively monitored during June-September, 1990, to evaluate the constancy of social group membership within a season. Each radio-collared elk was observed at least weekly, and the sizes and compositions of their associated groups determined. These observations allowed the determination of whether the membership of elk social groups was constant within this season. A group changing in either number of individuals or in the composition of its membership would be indicative of a dynamic group membership. Similarly, if groups varied little in size and composition, a static group membership would be suggested. Longterm associations between radio-collared elk in the same social group could also be indicative of static membership, if size and composition of the groups remained similar.

Data Analysis

All comparisons were made utilizing the Kruskal-Wallis one-way ANOVA (Siegel 1956). A generalized Scheffe-type test was used for multiple comparisons (Miller 1981). Minimum level of significance was set at $\underline{a}$=0.10.

RESULTS

Social Group Dynamics

A total of 627 distinct group observations was made on elk from 1990-1991.

The probabilities of belonging to a mixed group or a bull-only/cow calf group differed between bulls and cows for each biological season (Table 19). Bulls were much more likely to be present in single sex groups during the fall and winter than were cows. Cows were much more likely to be present in single sex cow-calf groups during the Pre-CALF, CALF, and Post-CALF periods. During these same periods, bulls were more likely to be in mixed groups.

Table 19. Probability of group-type membership for any individual bull or cow elk by season in Michigan.

	SEASON						
Group Type	WINTER	Pre-Calf	CALF	Post-CALF	Pre-RUT	RUT	Post-RUT
No. Obs.	39	58	66	87	117	171	149
COWS							
Cow-calf	0.00	0.81	0.83	0.77	0.29	0.21	0.32
Mixed	1.00	0.19	0.17	0.23	0.71	0.79	0.68
BULLS							
Bull-only	0.31	0.37	0.30	0.58	0.59	0.44	0.27
Mixed	0.69	0.63	0.70	0.42	0.41	0.56	0.73

Group Sizes by Sex

Mixed groups were significantly larger than cow-calf or bull-only groups for each season (Table 20). Cow-calf groups and bull-only groups did not differ in mean group sizes during any season, except for WINTER, when no cow-calf groups were observed.

Cow-calf groups were significantly larger in the Pre-CALF periods relative to all other seasons (Table 20). Cow-calf groups were smallest during the CALF period.

Mixed groups were significantly larger during WINTER than any other period (Table 20). Pre-RUT mixed groups were smallest. Mixed groups during the other seasonal periods were intermediate, and differed little.

No significant differences were present in sizes of bull-only groups (Table 20). Bull-only groups tended to be largest during the winter and spring (WINTER and Pre-CALF) and smallest during the summer and fall.

Social Group Constancy

Membership in elk social groups was highly dynamic (Table 21). Social groups tended to vary considerably in both sizes and group composition throughout the study period. The only exceptions to this dynamic group membership pattern were groups composed solely of a lone individual or a cow and her calf (Table 21).

On 18 occasions, ≥ 2 radio-collared elk were present in

Table 20. Mean (SE) elk social group sizes by seasons for cow-calf, bull-only, and mixed groups in Michigan, 1990-1992.

				SEASON			
TYPE	WINTER	Pre-CALF	CALF	Post-CALF	Pre-RUT	RUT	Post-RUT
C-C	X	9.6(0.9)^{a12}	1.6(0.7)^{b1}	3.6(0.6)^{c1}	2.3(1.0)^{bc1}	3.1(0.9)^{bc1}	4.4(0.7)^{c1}
MIXED	35.1(3.1)^{a1}	16.6(4.6)^{bcd1}	8.6(3.9)^{bcd2}	10.0(2.6)^{bcd2}	5.2(1.6)^{cd2}	13.1(1.1)^{bcd2}	15.8(1.1)^{bc2}
BULL	2.6(0.7)^{2}	3.7(0.9)^{2}	1.3(0.9)^{1}	2.1(0.3)^{1}	1.5(0.2)^{1}	1.9(0.2)^{1}	2.6(0.3)^{1}

X=No observations.
^{abcd}Values sharing a letter within a row do not differ ($\underline{a}$=0.10).
^{12}Values sharing a number within a column do not differ ($\underline{a}$=0.10).

Table 21. Social group sizes for consecutive observations of radio-collared elk during June-August 1990.

		Observation Number														
ELK	SEX	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
0770	C	2	1	1	2	3	1	1	8	7						
0462	C	3	3	23	10	10										
0130	C	1	3	5	4	1	15	4	8	9						
0210	C	1	2	1	1	1	1	2	2	9						
0520	C	4	1	15	23	8										
0830	C	1	1	1	3	15	5	23	10							
0560	C	3	3	1	1	1	1	1	6	2	4	2	7	3	1	5
1761	C	1	1	3												
0710	C	1	1	1												
0540	C	6	3	3	2	1	9									
1641	C	3	2	6	31	31	2	7	9	2	2					
0910	C	7	1	1	4	2	10	8								
0750	C	1	1	1	1	23	4	1								
0340	C	1	7													
0080	B	1	1	4	3											
1780	B	3	1	1	1											
1121	B	3	2	1	9	1										
1110	B	2	1	1	2	3	1									
0290	B	1	3	1	1	4										
1522	B	1	2	1	1											

the same social group. Re-observations of these groups were always made within 3 days following the association of the radio-collared elk. Not once in the 18 occasions were the radio-collared elk still associated after the 2-3 days. Additionally, of the 18 instances of radio-collared elk associations, only on 5 subsequent occasions throughout the study period were the same elk ever associated again.

Group Sizes by Vegetative Structure

Cow-calf only groups did not differ in social group sizes among vegetation types in any season (Table 22). Bull groups also did not differ in group sizes among vegetation types (Table 23). Mixed groups differed in group sizes during the Post-CALF and RUT seasons. Mixed-group sizes were significantly larger in open vegetation types than in forested or shrubby types during the RUT; groups in dense cover were larger during the Post-CALF period (Table 24).

Harems

Twenty-seven distinct harems were located and observed in 1990, with a mean size of 6.11(0.75) elk. Sixteen distinct harems were observed in 1991, with a mean size of 5.75(0.66) elk. If bulls other than the harem-master in or on the periphery of the harem are excluded from the count, mean harem sizes decrease to 5.48(0.64) and 5.38(0.58) for

Table 22. Mean (SE) cow-calf social group sizes between different vegetative structure types by season.

SEASON	DCF	DHF	OCF	OHF	OPEN	S/R
				VEGETATION TYPE[1]		
WINTER	X	X	X	X	X	X
Pre-CALF	11.3(6.1)	9.3(4.0)	X	14.0(7.8)	8.0(3.6)	6.5(1.6)
Post-CALF	3.5(0.7)	3.6(0.9)	5.0(1.5)	5.3(3.0)	X	2.6(0.8)
Pre-RUT	X	X	X	X	2.3(0.5)	2.0(0.7)
RUT	X	3.7(0.3)	X	X	3.1(0.7)	X
Post-RUT	X	4.0(0.5)	X	X	2.5(0.5)	3.7(0.8)

X=No groups counted in this vegetation type.

[1] DCF=dense coniferous forest, DHF=dense hardwood forest, OCF=open coniferous forest, OHF=open hardwood forest, OPEN=opening, S/R=shrub/regeneration.

Table 23. Mean (SE) bull-only social group sizes between different vegetative structure types by season.

			VEGETATION TYPE[1]			
SEASON	DCF	DHF	OCF	OHF	OPEN	S/R
WINTER	X	X	X	X	X	X
Pre-CALF	X	X	X	X	X	X
Post-CALF	1.9(0.6)	2.0(1.0)	1.8(0.6)	X	X	X
Pre-RUT	X	X	1.3(0.3)	1.0(0.0)	1.6(0.2)	1.6(0.4)
RUT	X	1.0(0.0)	1.7(0.3)	1.0(0.0)	2.1(0.3)	1.8(0.5)
Post-RUT	3.3(1.9)	X	X	4.0(2.5)	1.9(0.4)	X

X=No groups counted in this vegetation type.

[1] DCF=dense coniferous forest, DHF=dense hardwood forest, OCF=open coniferous forest, OHF=open hardwood forest, OPEN=opening, S/R=shrub/regeneration.

Table 24. Mean (SE) mixed social group sizes between different vegetative structure types by season.

			VEGETATION TYPE[1]			
SEASON	DCF	DHF	OCF	OHF	OPEN	S/R
WINTER	34.0(5.4)	X	X	X	X	41.8(13.3)
Pre-CALF	X	X	X	X	X	X
Post-CALF	X	11.4(2.9)[a]	5.4(1.3)[b]	X	X	X
Pre-RUT	X	X	4.0(0.6)	X	5.6(0.8)	4.3(0.7)
RUT	X	X	3.5(0.5)[a]	9.0(1.5)[b]	14.0(1.5)[c]	8.0(1.0)[b]
Post-RUT	X	17.8(3.4)	22.0(7.3)	18.5(3.8)	12.4(1.6)	17.9(2.9)

X=No groups counted in this vegetation type.

[1] DCF=dense coniferous forest, DHF=dense hardwood forest, OCF=open coniferous forest, OHF=open hardwood forest, OPEN=opening, S/R=shrub/regeneration.

[ab] Means sharing a letter within a row do not differ (a=0.10).

1990 and 1991, respectively.

Seventy-six percent of observed 1990 harems and 69% of 1991 harems were established in grassy openings typically associated with elk; the remainder were in savannahs or thinned timber. Additionally, the openings used were small; 75% were ≤2ha.

Twenty-two percent of 1990 harems contained more than 1 bull elk; 19% of 1991 harems contained >1 bull. The additional bulls present in these harems were yearlings or other young bulls (≤4X4).

All harems observed were held by a 6X6 or larger bull, with the exception of 4 1990 harems, 3 of which were held by 5X5 bulls, and 1 by a 4X4. Additionally, 19 and 24 lone bull elk were observed during the rutting season in 1990 and 1991, respectively. Of these, 10 of 19 in 1990 and 11 of 24 in 1991 were 5X5 or larger (5 of 19 and 10 of 24 were ≥6X6 in 1990 and 1991, respectively).

DISCUSSION

Social Group Membership

The social organization of elk is believed to be composed of 2 basic social units; bull-only groups and cow-calf groups (Franklin and Lieb 1979, Clutton-Brock et al. 1982, Geist 1982). Bull-only groups tend to be smaller and less stable than cow-calf groups (Franklin and Lieb 1979, Clutton-Brock et al. 1982, Houston 1982). Younger bulls (less than 2-3 years old) are often associated with cow-calf groups, especially in winter, resulting in mixed groups (Moran 1973, Franklin and Lieb 1979).

In this study, bulls and cows differed in their probabilities of belonging to either a single-sex or a mixed group (Table 19). Cows were more likely to belong to cow-calf groups during the spring and summer (probability $\geq$77%), and to mixed groups during the fall and winter (probability $\geq$68%). Cows occurred exclusively in mixed groups during the winter. In contrast, bulls were more likely to belong to mixed groups in all seasons except late summer and early fall. This result, however, may be an artifact of the tendency of adult bulls to belong to smaller, more secretive groups than cows, which are by intent much more difficult to observe.

These grouping results were similar to those observed for elk in Michigan by Moran (1973). Moran (1973) also noted low association between bulls and cows during the summer months, with greatest mixing of bulls and cows during the spring and fall periods. Exclusive cow-calf groups were most common during the summer, and no exclusive cow-calf groups were noted by Moran (1973) during December. These same patterns were shown in this study.

Annual Variation in Group Patterns

Annual variation in elk social group sizes tends to be pronounced, particularly for herds that are migratory, heavily hunted, and/or subject to seasonal resource limitations (Franklin and Lieb 1979, Clutton-Brock et al. 1982, Houston 1982, Geist 1982). Shoesmith (1979) reported that group sizes in Yellowstone elk peaked during June through mid-August. Knight (1970), in contrast, found elk groups to be largest during the winter for the Sun River herd. Similarly, Houston (1982) reported the same pattern for the Northern Yellowstone herd; group sizes peaked in winter, then declined as elk dispersed into forests. Clutton-Brock et al. (1982) found that social group sizes in red deer were smaller in winter than in summer, regardless of habitat utilization.

In contrast to the above patterns showing annual variation in elk social group sizes, Roosevelt elk in Prairie Creek Redwoods State Park, California (Lieb 1973, Franklin et al. 1975, Franklin and Lieb 1979) and Roosevelt elk along the Hoh River in Olympic National Park (Jenkins 1980) showed relatively constant annual group sizes; the only exception being when cows left the groups to calve. These herds, however, were sedentary, unhunted, and suffered no pronounced seasonal effects on resource availability.

Moran (1973) found social group sizes to vary annually in Michigan elk, with largest group sizes occurring in October and November (during post-rut aggregations), and in May, when openings green up and attract elk. Smallest group sizes occurred during the June-July period. Bull-only groups remained relatively constant throughout the year (Moran 1973). Moran's (1973) work, however, was based on pooling 700+ group observations over a 5 year period (1963-1968), during which the population size of the Michigan elk herd varied from >2000 to <300 individuals.

This study found seasonal patterns in elk group sizes in Michigan to be similar to those reported for migratory Western elk herds (Knight 1970, Houston 1982). Mixed groups showed the greatest annual variation, and were largest during the winter and smallest during summer (Table 20). Cow-calf groups varied little annually; they tended, however, to be slightly larger in the late spring and early winter and smallest in the summer, when cows went off to calve. No cow-calf only groups were observed during the winter (Table 20). Similar to findings of Moran (1973), bull-only groups tended to vary little in size annually.

Moran (1973) found the largest groups of elk to occur during the immediate post-rut period (October-December). In contrast to this, the largest social groups in this study were observed during winter and early spring (Table 20). These large groupings are likely a response to, initially, seasonal limitations on resource availability (Geist 1982, Clutton-Brock et al. 1982) and, later, a result of elk being attracted to limited openings as these openings greened up in the spring (Moran 1973). Moran (1973) also noted large groupings of elk in openings during the spring green-up period.

The lack of annual variation in the sizes of bull-only groups, and the smaller sizes of bull-only groups, likely represents a behavioral adaptation to the forested nature of the Michigan elk range, in combination with an evolutionary anti-predator strategy (Clutton-Brock et al. 1982, Geist 1982). During the summer, bull elk require greater quantities of food than do cows, both to maximize fat reserves and for antler development. Behaviorally, bulls in primarily forested ranges will therefore search for patches of highly productive food resources (Geist 1982). This results in a secluded, highly mobile lifestyle to minimize both predation and competition, with relatively large home ranges and less fidelity to home ranges than cows (Lowe 1966, Mitchell et al. 1977, Franklin and Lieb 1979, Geist 1982). Bulls thus adopt a "hider" strategy, being less vocal than cows, being alone or in small groups, and utilizing openings less often than cows (Franklin and Lieb 1979, Geist 1982). Thus, bull-only groups are expected to be smaller than cow-calf or mixed groups, and remain relatively small throughout the year, as a consequence of the "hider" strategy. These patterns were seen for elk in Michigan both in this study, and by Moran (1973).

A contributing factor to the small group "hider" strategy of bulls involves potential or evolutionary predation pressure (Geist 1982). As bulls are less abundant than cows, they are very conspicuous in a cow herd, especially if they are large antlered and bodied. Differing significantly in appearance from cows, they are more likely to attract the attention of predators. This could be extremely disadvantageous to bulls, especially following the rut, when their physical condition is poor. Physically spent post-rut bulls could easily fall to predators, with each fallen bull encouraging the development of an exclusively bull search image in predators. Therefore, to minimize predation, bulls must either change their physical appearance, mimicking cows, or segregate from cows (Bromley 1976, Geist and Bromley 1978, Geist 1982). Once separated from cows, large bulls may hide in cover to recuperate from the effects of the rut ("hider" strategy), or they may form large groups in the open. Large bands in the open would be expected where elk depend upon open landscapes and grassy vegetation such as with the Sun River elk in Idaho (Knight 1970), while in areas where fewer elk are present, or in primarily forested habitats, bulls would be expected to develop a hider strategy after the rut (Franklin et al. 1975, Geist 1982). Elk in Michigan, inhabiting a primarily forested range, would be expected to show an evolutionarily derived "hider" response to minimize predation, exploit patchy food resources, and recuperate post-rut. Such a response predicts small group sizes throughout the year; this pattern was observed both in this study (Table 20) and by Moran (1973).

In contrast to the above theory, Clutton-Brock et al. (1982) felt that segregation of the sexes in red deer was most likely due to differing nutritional requirements of stags and hinds. On the Scottish mainland, red deer segregation was associated with the use of different vegetation types by the sexes (Watson and Staines 1978). Similarly, the degree of segregation of hinds and stags on Rhum varied with different plant communities, increasing where food supplies were short (Clutton-Brock et al. 1982). Additionally, segregation became more pronounced when stags reached age 3 and older, at which point their diets begin to diverge from hinds. Such a hypothesis, however, while accounting for the annual separation of bull and cow elk observed, does not specifically account for the smaller sizes of bull-only groups, nor for the more wandering nature of bulls. Moran (1973) felt that movements of single bulls and small bull groups were not as food oriented as were cow movements. Geist's (1982) antipredator strategy of bull independence predicts a greater tendency for bulls to be independent and roam, behaviors commonly seen in elk populations (Altmann 1952, Lowe 1966, Moran 1973, Franklin and Lieb 1979, Houston 1982, Beyer 1987). Thus, it is most likely that the pattern of highly mobile, secretive small groups seen in bulls in Michigan is primarily an evolutionary response to avoid predation and forage effectively on patches in primarily forested range. Such behaviors are very common in red deer, which occupy habitat more similar to the Michigan elk range than do other North American elk populations (Raesfield and Vorreyer 1964 in Geist 1982, Clutton-Brock et al. 1982).

As noted above, bull-only groups in Michigan are significantly smaller than mixed groups. Cow-calf groups, in the seasons in which they occur, tend to be intermediate, though not significantly different in sizes from bull-only groups (Table 20). The same factors described above predicting small bull-only groups annually also account for the smaller overall sizes of bull-only groups relative to mixed groups; bulls tend to employ a "hider" strategy in areas of sufficient cover, while cow-calf and mixed groups use primarily a grouping predator avoidance strategy (Geist 1982), although they also will adopt a "hider" strategy depending upon habitat conditions (Hirth 1977, Geist 1982, Clutton-Brock et al. 1982). Cow-calf only groups were observed only during the summer and fall in this study, and tended to be composed of 1 or 2 cows with their calves, or an adult cow, yearling cow, and calf. These groups did not significantly differ from bull-only groups in mean sizes, perhaps indicating a preference of most individual cows to raise their calf solitarily, adopting a more secretive "hider" strategy, while a smaller proportion of cows raised their calves in larger mixed groups (Table 19). Moran (1973) also found little differences in sizes between bull-only and cow-calf groups in his studies of the Michigan elk.

Social Group Constancy

Franklin and Lieb (1979) found that coastal California Roosevelt elk individuals tended to stay exclusively within the same cow-calf group. They hypothesized that sedentary elk populations with abundant food resources which are free of hunting exploitation, such as their study population, would favor the development of long term associations and bonding between individuals, resulting in stabilized cow-calf groups. Similar trends were also reported for a non-hunted sedentary elk population in Olympic National Park, Washington (Jenkins 1980). Other studies suggest that elk tend to show little cohesion between individuals. Elk in the Sun River, Idaho, herd (Knight 1970), the Yellowstone Mirror Plateau herd (Shoesmith 1979), the Northern Yellowstone herd (Houston 1982), and the Madison River, Montana, herd (Craighead et al. 1973) all showed little cohesion in social group membership. All of these studies, however, dealt with migratory elk populations.

Moran (1973) felt that social group membership in the non-migratory Michigan elk herd was highly dynamic. His conclusions, however, were based on pooled observations over a 5 year period, with methodology not specifically intended to evaluate the constancy of group membership. Franklin and Lieb (1979) felt that the dynamic nature of group membership reported by Moran (1973) for the sedentary Michigan elk was solely a result of methodological bias, although others disagreed (Geist 1982).

This study found group membership to be highly dynamic for the Michigan elk (Table 21). Groups tended to frequently coalesce and split with no apparent pattern; the fragmenting and combining of groups was likely a product of chance encounters, rather than familial or other relationships. Thus, despite the sedentary nature of Michigan elk, and the availability of ample food resources, no stable social group membership pattern was shown by the Michigan elk herd, in contrast to the prediction of Franklin and Lieb (1979).

Geist (1982) and Clutton-Brock et al. (1982) felt that in regions of low food availability, or in areas where food is seasonally limited, food is not a defensible resource. Thus, individuals compete passively by eating preferred foods faster; they also use the behavior of conspecifics as a clue to the location of better foods and quickly move to take advantage of these resources. Geist (1982) speculated that the more intense this passive competition, the more individuals must be independent agents. Thus, individuals may be influenced very little by social bonds even if living in a group; social groups would therefore tend to show little cohesion.

This theory elegantly explains the nature of elk social groups. The migratory Western herds noted above are all subject to severe seasonal food resource limitations; hence, they are migratory, and social groups, due to competition for the seasonally limited resources, tend to be labile. Franklin and Lieb (1979), in contrast, studied a population that was sedentary, with abundant preferred foods available without seasonal limitations. Individuals had little to compete for, allowing the development of close bonds and a static group membership. In Michigan, as speculated by Geist (1982), elk face extensive areas of forested cover, only scattered small openings, and a seasonal restriction on the availability of preferred foods and movements (winter snow cover). Geist (1982) felt that these conditions favored movements by individuals in an opportunistic search for forage. Thus, the Michigan elk herd, although sedentary, would be expected to show little constancy in social group membership. A highly dynamic group membership was exactly the pattern initially observed by Moran (1973) and again documented in this study for the Michigan elk herd.

Group Size and Habitat

Ungulate social group size appears to be inversely related to habitat cover, both within a species occurring in different habitats, and within a population exposed to a variety of vegetation types (Dasmann and Taber 1956, Picton 1960, Knight 1970, Jungius 1971, Walther 1972, Franklin et al. 1975, Mitchell et al. 1977, Hirth 1977, Geist 1982, Clutton-Brock et al. 1982, Takatsuki 1983, Maublanc et al. 1985 in Merkt 1987, Merkt 1987, Leader-Williams 1988). Hirth (1977) found social groups of white-tailed deer to be larger in more open vegetation types in both the Welder Ranch in Texas and, to a lesser extent, the George Reserve in Michigan. Clutton-Brock et al. (1982) similarly noted that red deer groups tended to be larger in open areas versus forested. Although studies directly evaluating social group size as a function of habitat are limited for ungulates (Hirth 1977), complimentary findings have been reported for Grant's gazelle (Gazella granti) in Tanzania (Walther 1972), reedbuck (Redunca arundinum) in South Africa (Jungius 1971), Roosevelt elk (C. e. roosevelti) in North America (Franklin et al. 1975), mule deer (O. hemionus) (Dasmann and Taber 1956), sika deer (C. nippon) (Takatsuki 1983), and roe deer (Capreolus capreolus) (Maublanc et al. 1985 in Merkt 1987). Hirth (1977) felt that the evidence available was sufficient to suggest that a definite pattern relating group size to habitat commonly exists among ungulates, whereby ungulates form larger groups in more open habitats. This pattern is generally attributed to predation avoidance behavior (Hirth 1977, Bertram 1978) or a means of optimizing feeding efficiency (Hirth 1977, Clutton-Brock et al. 1982).

In this study, Michigan elk did not show this inverse relationship between group size and cover density (Tables 22-24). For all bull, cow-calf, and mixed groups in all seasons, only mixed groups differed significantly in group sizes between vegetation types, and then only in 2 of 5 seasons; Post-CALF mixed groups were significantly larger in denser cover than in more open cover, while mixed groups during the RUT season were significantly larger in more open cover types. Thus, elk in Michigan are not following the typical inverse relationship between cover and group size.

In the most comprehensive work relating group size to habitat, Hirth (1977) found that deer social groups on the Welder Refuge, Texas, were significantly smaller in the densest cover types, and largest in open cover. This pattern held for all social groups (buck, doe, yearling, and all groups). This relationship was less developed for deer on the George Reserve in Michigan, however, where only all groups pooled showed a difference in group size based on vegetation type. Hirth (1977) felt that the pattern was less developed on the George Reserve because of the vegetative cover--a largely wooded area broken up only by scattered small ($\leq$25 ha) openings. Hirth (1977) felt that the absence of a group size response to cover density was due to the small size of the open fields and the close proximity of protective cover.

Thus, it appears that the nature of the available habitat may influence the degree of development of a group size-cover relationship. The Michigan elk range is similar to the George Reserve in that it is primarily forested, with only ~15% of the range in openings, most of which are small (Moran 1973, Bender et al. 1991). Similar to the situation at the George Reserve, then, elk in Michigan may not alter group size in response to available cover simply because they are never more than a few hundred meters from protective cover.

The most likely reason for increasing group size as cover declines is as an adaptation to avoid predation (Dasmann and Taber 1956, Eisenberg 1966, McCullough 1969, Hamilton 1971, Jungius 1971, Estes 1974, Hirth 1977, Bertram 1978, Geist 1982). This predation-avoidance hypothesis holds that a large animal, such as an ungulate, is less likely to be detected in heavy cover if it is alone or in a small group; in dense cover, a single animal, or a small group, can be effectively concealed, while a large group cannot. Conversely, in open areas most ungulates are too large to feed and remain concealed while doing so. Thus, large groups are favored as the collective senses of all the individuals can be used to detect approaching predators. Additionally, since the probability of detection is high in the open, the probability of an individual animal being taken by a predator is reduced by being in a group, by a factor roughly equal to the number of individuals in the group (Hamilton 1971, Hirth 1977). The relationship of group size to available cover is therefore most likely an evolutionary response to predation pressure, although others have suggested that feeding relationships might be equally as important (Altmann 1974, Estes 1974, Jarman 1974, Clutton-Brock et al. 1982), especially for female group sizes.

Predation pressure on reintroduced elk in Michigan has largely been insignificant throughout the history of the herd. The only large predators present in the elk range are the black bear (Ursus americanus) and the coyote (Canis latrans), and these are present in either too small a population to affect elk (bear) or are an insignificant predator on an animal as large as an elk (coyote). Additionally, elk in Michigan do not converge onto traditional calving areas, as do some Western USA elk herds (Skovlin 1982). This behavior also contributes to the insignificance of predation by decreasing the vulnerability of newborn calves, a significant portion of which can be taken locally by predators such as black bears in Western herds utilizing traditional calving areas (Taber et al. 1982).

This absence of predation on elk in Michigan also likely contributes to the lack of a group size-cover inverse relationship. Ungulates in general are very behaviorally plastic and adaptable (Geist 1982). It is likely that in a minimum of 10-12 generations in the absence of significant predation pressure, elk in Michigan have adapted to the absence of the threat. The general lack of wariness in Michigan elk (Beyer 1987, Bender et al. 1991, **Chapter 1**) to people, the primary cause of exploitation on the herd, is indicative of this. Thus, in the absence of environmental reinforcement, elk in Michigan may be losing, to some degree, the grouping anti-predator strategy.

In conclusion, elk in Michigan do not show the general ungulate trend of an inverse relationship between group size and habitat cover. As this relationship is likely an evolutionary response to predation pressure, the close proximity of protective cover in the elk range (a result of the forested nature, with few large openings) and the general absence of a serious predation threat to elk in Michigan are the most probably factors responsible for this lack of response.

Harems

Harem sizes are small in Michigan, with mean sizes of 6.11 (0.75) elk/harem in 1990 and 5.75 (0.66) elk in 1991. These sizes are distinctly smaller than those of elk populations elsewhere, and are more suggestive of breeding group sizes in red deer populations in Europe (Clutton-Brock et al. 1982). Additionally, harems in Michigan are often established in atypical vegetation types such as savannahs or thinned timber, rather than the more typical grassy openings. Grassy openings used also tend to be small, usually less than 2 ha. This use of small openings, savannah, and timber for breeding grounds is again more suggestive of forest dwelling red deer than typical Western elk populations (Geist 1978, 1982; Clutton-Brock et al. 1982); however, this may also simply represent the use of what harem-suitable habitat is available.

Elk harems in Michigan often have more than 1 bull present. The additional bulls present in 19-22% of observed harems were yearlings or other young bulls ($\leq$4X4), suggesting that young bulls are not being actively dispersed by harem masters. Aggressive dispersal of juvenile bulls by harem masters is a behavior typical of elk populations (Geist 1978), but less so of red deer, especially for 1.5-2.5 year-olds (Clutton-Brock et al. 1982).

All harems observed in Michigan were held by a 6X6 or larger bull, with the exception of 4 1990 harems, 3 of which were held by 5X5 bulls, and 1 by a 4X4. However, numerous other prime-aged bulls were observed without harems during this study. The small harem sizes and high percentage of prime but non-breeding bulls, along with the use of atypical rutting areas, all indicate the development of a breeding system of many small, more secretive harems in Michigan, more similar to European red deer than other North American elk populations.

The small harem, more secretive nature of elk rutting in Michigan is likely the result of a combination of high bull:cow ratios with a large percentage of prime-aged bulls ($\geq$40% 5X5 or larger--see **Chapter 5**) and the primarily forested nature of the elk range. Large breeding group sizes tend to be found in species occupying open environments, where males can defend and control harems consisting of 20 females or more (Struhsaker 1967, Horwood and Masters 1970 _in_ Clutton-Brock et al. 1982, Schaller and Hamer 1978, Clutton-Brock et al. 1982). This is the general pattern shown by elk, which are a colonizing ecotonal species adapted for open habitats relative to their ancestral red deer (Geist 1982). However, within a species social group sizes can be influenced by habitat (Hirth 1977, Geist 1982). This also appears true of harem sizes in elk and red deer; in forests or in heavily hunted populations, males of elk or red deer may tend single females rather than defend harems (Altmann 1956, Burckhardt 1958 _in_ Clutton-

Brock et al. 1982). Smaller harem sizes in forested habitats are common in red deer (Clutton-Brock et al. 1982), and it is likely that this behavioral strategy of smaller harem sizes is being expressed in elk in Michigan at least partially in response to the mostly forested nature of their range. The primarily forested nature of the Michigan elk range is much more similar to continental European red deer ranges than to the open ranges used by Western North American elk populations; hence, elk in Michigan may be reverting to a more fundamental behavioral strategy, shown by their ancestral stock, red deer, in response to habitat structure.

The forested nature of the Michigan elk range may also affect harem sizes by limiting the distances over which harem-masters may attract cows. Elk bugling is a high-frequency advertisement adapted to carrying long distances in open cover; in areas characterized by tall vegetation, however, high frequency sounds quickly lose energy and are absorbed by the vegetation, dramatically reducing the distance over which they may be heard (Geist 1982). Low-frequency sounds, in contrast, such as the "roaring" of red deer, carry much farther in forested areas. Thus, elk in Michigan may be limited in the distance in which they can advertise their presence by bugling. Their high-frequency bugling is poorly adapted to the forest vegetation, so bugling elk may be audible only to very close cows, thus restricting harem sizes since only local elk may be aware of the bugler's presence.

The high bull:cow ratios ($\geq$60:100) seen in the Michigan herd also undoubtedly affects the rutting strategy of bulls. In 1990 and 1991, 53% and 46%, respectively, of lone bulls observed during the rut were 5X5 or larger, and thus presumably capable of holding a harem. With so many potential rivals around, harem sizes are likely to be small simply in response to the large numbers of harem-capable bulls present in the herd. Also, since many harem-capable bulls are present without a harem, a harem-master might be benefitted energetically by adopting a more secretive set of rutting behaviors. By adopting behaviors such as tolerance of immature bulls who pose no breeding threat to his harem, less vocalization unless being actively challenged by another prime bull, and herding his harem in atypical cover such as open timber, scrub-shrub, and very small openings (where the harem master can still retain sight of the harem, but where the harem is much more difficult for other bulls to locate than if held in a large opening), a harem bull can decrease the number of times he is challenged by other harem-capable bulls. This would allow harem-masters to increase their probability of keeping their harems and siring offspring, while reducing the energetic demands of constantly confronting other bulls. These behaviors, which would logically favor a rutting system characterized by numerous small secretive harems, are all seen in elk in Michigan. Such a breeding system is very similar to red deer in forested ranges where sex ratios approach 1:1. In these populations, red deer stags typically lose less body weight during the rut than do those in populations characterized by lower sex ratios, suggesting that the energetic demands of holding large harems in areas with a large number of competitor bulls are too great, i.e. the energetic costs of successful reproduction favor the establishment of smaller harems (Raesfield and Vorreyer 1964 in Geist 1982, Geist 1982). Such a breeding strategy would not be seen in Western North American elk populations as the typically low bull:cow ratios of these herds, in combination with the more open ranges occupied, allow a harem-master to gather and control a large harem and still likely not be challenged by more than 1 or 2 other prime bulls. Thus, the presence of large numbers of prime bulls in the Michigan herd likely results in intense competition among these bulls for control of harems, resulting in smaller harem sizes and, in conjunction with the forested nature of their habitat, more secretive breeding behaviors to allow the retention of these small harems by the harem-master.

SUMMARY AND CONCLUSIONS

The social group dynamics of elk in Michigan are unique in many ways relative to other North American elk populations. Although annual patterns in social group sizes, relative sizes of social groups by sex, and the loose nature of social group bonds seen in Michigan are typical of most elk populations, the actual social group sizes and behaviors, especially rutting behavior, are more suggestive of European red deer. Many of the behaviors seen in the Michigan herd likely represent responses to both the high bull:cow ratios seen in the herd, and the forested nature of the Michigan elk range.

The behavioral uniqueness of Michigan's herd is most evident in the lack of social group constancy shown by elk, the lack of a group size-cover relationship, and the rutting system characterized by small, secretive harems. In contrast to expectations involving sedentary elk herds, social groups in Michigan are very dynamic. Although resources are abundant in the Michigan range, winter apparently influences resource availability enough that elk still operate individually in locating and utilizing food resources. This passive competition apparently prevents the development of the high level of social bonding necessary to form static social group memberships, as seen in some coastal elk populations free of any seasonal effects on resource availability.

Elk in Michigan do not demonstrate the typical ungulate pattern of forming larger groups when in more open cover, and smaller groups when in dense cover. The small sizes of openings in the Michigan elk range, and subsequent close proximity of security cover, likely influences the lack of group size response shown by the Michigan herd. Also, this inverse relationship between group size and degree of cover is likely an evolutionary response to predation pressure. The reintroduced Michigan elk herd has been essentially free of predation, and in the ~70 years since reintroduction, elk have likely adapted, behaviorally or otherwise, to the lack of a predation threat.

The densely covered, forested nature of Michigan's elk range, in combination with the historically high bull:cow ratios seen in the herd, have resulted in a unique system of smaller, secretive harems held in atypical areas. This system likely results from adaptations to (1) minimize energy expenditures of harem bulls by not having to constantly defend their harems, (2) maximize use of the limited available habitat suitable for rutting activities, (3) the maximum number of cows a harem bull can control given the dense cover typical of the Michigan elk range in general, (4) the distribution of cows among the large number of harem bulls, and, perhaps, (5) limitations on advertising distances of bulls due, again, to the forested habitat. A consequence (or perhaps causative agent--see **Chapter 4**) of this secretive breeding strategy is that juvenile bulls, who pose little breeding threat to harem bulls, are not being actively dispersed by harem-masters, likely to prevent drawing the unwanted attention of other harem-capable bulls to the harem. This breeding system is remarkably similar to that shown by forest-dwelling red deer populations.

Chapter 4: Movements of Yearling Bulls in Michigan

Movements of yearling elk, particularly dispersal movements of bulls, play a significant role in the dynamics of elk populations. Dispersal movements of young ungulates are thought to result in increased vulnerability and hence greater mortality in the immature age-classes. If such movements are more pronounced in one sex, such as in cervid males, highly skewed sex-ratios can result. Skewed sex-ratios in turn can affect population productivity, potential harvest, and habitat needs and utilization. Thus, the dispersal movements of immature elk can potentially have a significant effect on the population dynamics, structure, and recreational attributes of the Michigan elk herd.

The high bull:cow ratio present in the Michigan elk herd ($\geq$60:100) indicates that bull elk are plentiful in the elk range. The presence of large numbers of older bulls may result in increased dispersal movements among immature bulls. Concern in Michigan exists over agricultural and forestry depredation problems caused by the elk herd. Dispersal movements of young bulls into peripheral areas of the elk range, which are predominately agricultural, may result in increased frequency of such problems. Conversely, real political and sociological barriers exist preventing expansion of the elk herd into areas outside the traditional elk range in Michigan. These barriers, which in effect make the Michigan herd an enclosed population, may act to limit or prevent major dispersive movements by young bulls. The goal of this Chapter is to determine the nature of dispersal movements of yearling bulls in Michigan. Specific objectives include:

(1) Compare seasonal movements of yearling bull and cow elk.

(2) Compare home range sizes of yearling bull and cow elk.

(3) Evaluate differences in distribution patterns of adult and immature bull elk.

(4) Evaluate the tolerance of adult bull elk towards immature bulls during the rut.

METHODS

Bull Distribution

The geographic locations of each bull elk harvested during the 1984-1990 elk seasons were plotted, and X-Y coordinates determined for each harvested bull. A geographic mean of all bull kills was determined, and linear distances from the geographic mean to each individual kill determined. Mean linear distances from the geographic mean were compared by age-class, and by combining age-classes to equilibrate sample size in the following manner: yearlings, 2.5 year-olds, 3.5 year-olds, 4.5 year-olds, 5.5 year-olds, 6.5-7.5 year-olds, and $\geq$8.5 year-olds. A significantly greater mean distance for an age class from the geographic mean would be indicative of dispersal movements, as these animals would have been consistently harvested towards the periphery of the elk range.

Movements and Home Range

Elk calves were immobilized and radio-collared during September-November 1989, 1990, and 1991 (see **Chapter 5** for immobilization details). Radio-collared calves were subsequently located at least weekly throughout the duration of this study. Mean minimum, mean, and maximum seasonal distances moved from point of capture were compared between bulls and cows for the following traditional dispersal seasons: Pre-CALF (March-June), Post-CALF (July-October), and Post-RUT (November-February). Additionally, minimum convex polygon home-ranges were calculated for all elk radio-collared as calves in 1990. The ARC/INFO Geographic Information System (GIS) (ESRI, Inc., Redlands, CA) was used to plot all locations from Fall 1990-May 1992 and calculate home ranges for the radio-collared calves/yearlings.

Harem Bull Dynamics

Elk harems were monitored in 1990 and 1991 for group compositions. All observations were made in the evenings during peak harem activity. The composition of each distinct harem was recorded to determine the presence or absence of yearling and other immature bulls in or adjacent to the harem. The presence of younger age-class bulls within a harem would indicate lack of aggressive dispersal of young bulls by harem-master bulls.

Data Analysis

All comparisons were made using the non-parametric Kruskal-Wallis ANOVA (Siegel 1956). A generalized Scheffe-type test was used for multiple comparisons (Miller 1981). The level of statistical significance was set at $\underline{a}=0.10$.

RESULTS

Bull Distribution

Mean distances from the geographic center of harvested bull elk did not differ among age-classes ($\underline{p}=0.2839$) (Table 25). Similarly, mean distances from the geographic mean did not differ among grouped age-classes ($\underline{p}=0.1416$) (Table 25). Although the differences were not statistically significant, older age-classes and older age-groupings tended to occur further from the geographic center than did yearlings and 2.5 year-olds.

Table 25. Distances (km) of harvested bull elk from the geographic mean by age-class and grouped age-classes, 1984-1990.

	AGE														
	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	11.5	12.5	13.5	6.5-7.5	≥8.5
MEAN	11.15	11.20	12.94	13.68	13.39	12.42	12.23	12.81	10.23	12.71	--	7.67	16.15	12.32	12.28
(SE)	(0.79)	(0.58)	(0.82)	(0.79)	(0.87)	(1.37)	(1.32)	(1.79)	(2.80)	(3.08)	--	(1.27)	(5.33)	(0.93)	(1.16)

Movements and Home Range

Yearling bulls and cows did not differ in minimum, mean, and maximum seasonal movements for any season (Table 26). Movements of cow calves/yearlings tended to be greater than bull movements during the Pre-CALF and Post-CALF periods (Table 26). As yearlings aged, bull movements tended to become larger than cows (Table 26).

Minimum convex polygon home-ranges did not differ between bulls and cows ($\underline{p}$=0.4751). Mean home-range sizes were 26.0(3.3) km^2 for bulls and 29.7(2.4) km^2 for cows.

Harem Bull Dynamics

A total of 27 distinct harems were observed in 1990; 16 distinct harems were observed in 1991. Twenty-two point two percent of the 1990 harems, and 18.8% of the 1991 harems, included >1 bull elk. Mean harem sizes were 6.11 (0.75) and 5.75 (0.66) elk in 1990 and 1991, respectively; these were reduced to 5.48 (0.64) and 5.38 (0.58), respectively, when the additional bulls were excluded from the harem count, indicating that additional males represented 10.3% and 6.4% of total harem membership in 1990 and 1991, respectively. The additional bulls present in these harems were yearlings or other young ($\leq$4X4) bulls, suggesting that young bulls are not being actively dispersed by harem masters in Michigan.

Table 26. Mean (SE) minimum, maximum, and mean distances (in kilometers) moved from point of capture of bull and cow elk radio-collared during Fall, 1990.

	MOVEMENT PERIOD					
	Pre-CALF		Post-CALF		Post-RUT	
Movement	Bull	Cow	Bull	Cow	Bull	Cow
MEAN	2.30(0.26)	2.65(0.26)	2.94(0.64)	2.96(0.43)	3.77(0.82)	2.83(0.37)
MINIMUM	0.87(0.18)	0.97(0.21)	1.63(0.60)	1.51(0.35)	1.82(0.58)	1.01(0.19)
MAXIMUM	3.80(0.53)	4.54(0.40)	4.34(0.76)	4.49(0.63)	6.19(1.30)	4.59(0.40)

DISCUSSION

Elk dispersal patterns have not been well documented in the literature. In general, however, female calves tend to establish themselves in or adjacent to their mother's territory, becoming part of a cow matrilineal band (Franklin and Lieb 1979, Clutton-Brock et al. 1982, Geist 1982). Male calves, in contrast, are usually driven out by their mothers once they become yearlings; mothers usually will react aggressively to the approach of 1-2 year-old male offspring (Franklin and Lieb 1979).

Yearling bulls are usually dispersed twice. The first dispersal occurs prior to its mother giving birth to another calf. The second occurs during the fall, when younger bulls are driven off by harem bulls (Altmann 1963, Franklin and Lieb 1979, Clutton-Brock et al. 1982, Houston 1982). Once dispersed, yearling bulls typically join other young bulls in bull-only groups (Franklin and Lieb 1979, Clutton-Brock et al. 1982). In some populations, however, juvenile bulls do not disperse until age 2.5 or later (Clutton-Brock et al. 1982, Hurley and Sargeant 1991).

In this study, yearling bulls showed no dispersive movements relative to yearling cows (Table 26), nor did they exhibit larger home ranges. Additionally, the location of yearling bulls killed during the 1984-1991 hunting seasons plotted inside the locations of other age-classes, suggesting that yearling bulls are not being forced to peripheral areas of the Michigan elk range by other dominant bulls (Table 25). Harem bulls in Michigan also tolerate the presence of yearling and other young bulls in or adjacent to their harems, again indicating that yearling bulls are not being subject to the second classic dispersal period (the rut) in Michigan. These results suggest that yearling bulls in Michigan are not being actively displaced by dominant bulls, and thus are able to stay in close proximity to their mother's range if they choose to do so. These results are contrary to what has been traditionally believed about yearling elk movements.

The absence of dispersal movements shown by yearling bulls in this study is not necessarily unexpected, however. By definition, dispersal movements require that additional available range be present for elk to move into. The elk range in Michigan, however, is restricted to the areas currently occupied by elk due to political and sociological barriers. Areas peripheral to the existing range represent a classical "mortality vacuum" (Owen-Smith 1981) where animals are unable to establish, due to special hunts designed specifically to target peripheral animals (the October elk hunts), and by regulations encouraging exploitation of elk in these peripheral areas (all Michigan elk hunters may hunt these peripheral areas regardless of which Elk Management Unit they have a permit for; switching to other EMU's is much more restricted). Additionally, poaching losses are higher in these peripheral areas (T. Carlson, MDNR, pers. commun., Beyer 1987). Since heritabilities of high survival-value fitness traits are high (H. Prince, MSU, pers. commun.), selection may have acted to eliminate long-range dispersal traits in elk in Michigan. Thus, yearling bull elk in Michigan may not show dispersal movements simply because there are no readily available areas to disperse to.

Dispersal movements of young elk can also be confused with the greater movements shown by bull elk in general. During spring and summer, bulls must gain weight more rapidly than cows, both to support their larger body sizes and subsidize rutting activities, as well as for antler development. Typically occupying poorer ranges than cows, bulls therefore tend to move greater distances than do cows, searching for patches of abundant high-quality forage (Clutton-Brock et al. 1982, Geist 1982). During the fall and winter, following the rut, bulls also show greater movements than cows, partly as an evolutionary response for predator avoidance (a "hider" strategy) and, secondarily, to again find patches of abundant nutritionally superior forage needed to recover from the rut. Thus, seasonal home ranges and movements of bulls tend to be larger than for cows (Franklin and Lieb 1979, Clutton-Brock et al. 1982, Geist 1982, Beyer 1987, Hurley and Sargeant 1991). This pattern has been demonstrated for adult elk in Michigan by Beyer (1987). This study, however, found no differences in movements and home ranges of yearling bulls or cows (Table 26). This suggests that the increased movements seen in bull elk may not occur until age 2.5 or later in Michigan. Such increased relative movements, however, are not necessarily dispersal movements; they may instead simply be the natural tendency of bulls to wander more than cows (Clutton-Brock et al. 1982, Geist 1982). True dispersal movements involve the complete abandonment of a home range and the establishment of a new disjunct home range.

Movements of bulls relative to cows may become greater in elk in Michigan at age 2.5 or older. Clutton-Brock et al. (1982) found peak dispersal for red deer to occur between the ages of 2 and 3, when immature stags left their mother's home ranges and joined stag only groups. Movements of dispersing red deer tended to be long; 70% of stags in England established new ranges >2 km from their birth places (RDCR 1978 in Clutton-Brock et al. 1982). Hurley and Sargeant (1991) also reported that bull elk dispersed from ranges occupied as yearlings at age 2.5 in the Bob Marshall Wilderness, western Montana. The mean distance between pre- and post-dispersal activity centers was 24.6 km, compared to mean distances of 3.6 km for cow elk. Additionally, home range sizes of 2.5 year-old bulls were significantly larger than all other sex- and age-classes, again attributed to exploratory movements by the dispersing 2.5 year old bulls (Hurley and Sargeant 1991). Thus, increased movements of bulls relative to cows, or even dispersal movements, may not be seen in elk in Michigan until age 2.5 or older. However, no calves radio-collared during Fall 1990 have yet shown dispersal movements as of September 1992.

Indirect evidence suggesting that young bull dispersal may be uncommon in Michigan involves the traditionally high bull:cow ratio seen in the herd (>60:100). Although bull elk in general show greater age-specific mortality than cows (causing bull:cow ratios to drop significantly from ~1:1), dispersal carries an additional significant risk of mortality for young bulls (Flook 1970, Clutton-Brock et al. 1982, Geist 1982, Hurley and Sargeant 1991), which leads to even lower bull:cow ratios in elk herds. Flook (1970) found bull:cow ratios of 85:100 in fenced areas of Elk Island National Park, Alberta, where dispersal was prevented by the enclosing of the herd. Comparable ratios in nearby Banff or Jasper National Parks, Alberta, where elk herds are not enclosed, were 37:100. The impedance of yearling dispersal and elimination of the associated mortality was felt to be responsible for these highly different ratios (Flook 1970, Geist 1982). Similarly, Murphy (1963) documented a high 55:100 bull:cow ratio in an enclosed population of elk in

Missouri. Hurley and Sargeant (1991) also noted that mortality rates were higher for dispersing 2.5 year-old bull elk than any other sex- or age-class in Montana. The authors felt that this additional mortality was significant enough that a yearling-only harvest scheme may not be effective in increasing the number of mature bulls. The potential magnitude of the increased mortality associated with dispersing immature bulls was also demonstrated by Heptner et al. (1961) (in Geist 1982) in the USSR with comparisons between elk and red deer populations. Red deer bull:cow ratios in 4 reserves ranged from 63-83:100, while elk bull:cow ratios on 2 reserves were 27-33:100. Since elk are a colonizing or dispersing form relative to red deer, dispersal theory predicts that red deer should have higher bull:cow ratios than elk due to lower bull mortality rates (Geist 1982). Thus, the significantly lower bull:cow ratios seen in elk relative to red deer in the USSR reserves again shows that dispersing immature elk are highly vulnerable and subsequently suffer increased mortality relative to established bulls, resulting in naturally low bull:cow ratios in elk populations where animals are free to disperse.

Bull:cow ratios have traditionally been high in the Michigan herd, usually greater than 50-60:100 (Moran 1973, Beyer 1987, **Chapter 5**). Moran (1973) attributed this high ratio to "the classic structure of an unexploited elk herd under average range conditions", due to the similarity with the 55:100 bull:cow ratio observed by Murphy (1963) for an unexploited captive elk herd in Missouri. However, the much lower bull:cow ratios documented for unexploited elk populations by Flook (1970) in Canada and Heptner et al. 1961) in the USSR indicate that lack of hunting exploitation alone may not result in high bull:cow ratios. Additionally, and perhaps most importantly, the Michigan herd is an enclosed population, although the boundaries are political and sociological rather than physical. The low probability of successfully abandoning the traditional elk range in Michigan may drive the lack of dispersal-type movements shown by yearlings in this study, resulting in decreased early bull mortality and subsequent high bull:cow ratios, which typify confined elk populations (Murphy 1963, Flook 1970, Geist 1982). The absence of harvest likely also contributes to high bull:cow ratios, but Flook's (1970) ratios on elk populations in Banff and Jasper National Parks suggest that the absence of harvest is insufficient alone to create the high bull:cow ratios seen in largely unexploited confined elk populations in Missouri (Murphy 1963), on Elk Island (Flook 1970), and in the pre-1984 Michigan herd (Moran 1973). The historic high bull:cow ratios of the Michigan elk herd thus provide other indirect evidence that dispersal movements of yearling or other young bulls may be uncommon in this population.

SUMMARY AND CONCLUSIONS

Although yearling bull dispersal was not observed in Michigan, the lack of juvenile dispersal is still very important to the dynamics of Michigan's elk herd. Yearling bulls are not being actively dispersed by dominant bulls, and thus are likely much less vulnerable than juvenile bulls in typical Western USA elk populations. The absence of yearling bull dispersal, and subsequent low juvenile bull mortality rates relative to Western elk populations, contributes significantly to many of the unique attributes of the Michigan herd.

The historically high bull:cow ratios seen in the Michigan herd are at least partially attributable to the lack of juvenile bull dispersal. By minimizing mortality in this segment of the bull population, more bulls survive into older age-classes, resulting in the high bull:cow ratios historically seen in the Michigan herd. These high bull:cow ratios may in turn provide positive feedback to further minimize dispersal. With so many bulls around, elk in Michigan have apparently adopted a breeding system based on numerous small, secretive harems to avoid constant harem possession conflicts (**Chapter 3**). In this "secretive" rutting system, juvenile bulls, who pose little breeding threat to harem-masters, are tolerated, as the act of driving them away would likely bring unwanted attention to the harem from other harem-capable bulls. Thus, a positive feedback mechanism may be present in Michigan, whereby high bull:cow ratios ====> tolerance of juvenile bulls in or adjacent to harems ====> lack of dispersal by juvenile bulls ====> lower juvenile bull mortality ====> high bull:cow ratios. Which variable, the absence of juvenile dispersal or a high bull:cow ratio, drives this hypothetical relationship is unclear.

The lack of juvenile dispersal may be the result of several factors. As outlined above, high bull:cow ratios may result in the abandonment of aggressive juvenile dispersal by dominant breeding bulls. Also, dispersal, by definition, requires that range be available to move into. The enclosed nature of the Michigan elk range may have resulted in the elimination, by selection, of juvenile dispersal traits, as the survival of elk leaving the current range is nil, and traits highly correlated with survival show the highest heritabilities. Thus, dispersal may be limited simply because there is no place to disperse to. Similarly, the impetus for juvenile dispersal may be lacking in Michigan. Total elk density is low, per capita resource availability is high, and juvenile bulls are not being actively dispersed by dominant bulls. Dispersal may therefore not be seen simply because juvenile bulls have no reason to disperse. Finally, it is possible that greater dispersal movements may not be seen until bulls reach age 2.5, as is common in red deer and some Western elk populations (although no dispersal movements have yet been observed for 2.5 year-old elk radio-collared as calves during Fall, 1990). However, bulls in general exhibit greater movements than do cows, partly as a consequence of food acquisition behaviors and partly as a predator-avoidance behavior. The greater movements of bulls in general should not be confused with true dispersal movements, which involve the complete, or at least seasonal, abandonment of a previous home range.

Chapter 5. Population Demographics and Modelling of Elk in Michigan

Elk population management in Michigan is accomplished through annual controlled hunting seasons held since 1984. Aimed at regulating total elk numbers while maintaining a desired herd structure, the MDNR, in effect, employs a trophy management harvesting strategy centered on a heavy cow harvest in conjunction with a more limited any-bull harvest. The overall goal of MDNR population management is to maintain "a viable elk population, in harmony with the environment, affording optimal recreational opportunities" (MDNR 1984).

The population dynamics of the Michigan elk herd were modeled by Beyer (1987) using the computer simulation model POP-II (Fossil Creek Software, Ft. Collins, CO). The MDNR has used this model (1987 model) to determine harvest quotas and as the population management tool for the elk herd since its development. Although concern existed over the lack of data used in model development, parameters of the model have not been modified nor predictions tested since model development. From 1987-1990, the model appeared to provide an accurate estimate of elk numbers relative to the MDNR annual censuses. The January, 1992, census, however, produced a count of 1121 elk for an estimated population size of 1200. This count indicated that previous MDNR censuses were negatively biased, and that the population projections of the elk model were also low.

The goal of this Chapter is to modify the 1987 elk management model to more accurately reflect population levels and characteristics of the Michigan elk herd, thereby providing a more effective population management tool. Specific objectives include:

(1) Determine mortality and reproductive rates for the Michigan elk herd.

(2) Determine current sex- and age-composition of the Michigan elk herd.

(3) Modify the 1987 MDNR elk population model to more accurately reflect the true population parameters of the Michigan elk herd.

(4) Develop distinct elk population models for the 4 MDNR Elk Management Units (EMUs).

(5) Project alternative population management strategies for the Michigan elk herd.

GENERAL METHODS

Population Modelling

The dynamics of Michigan's elk herd were modelled by Beyer (1987) using the computer population model POP-II, Version 6.03 (Fossil Creek Software, Ft. Collins, CO) (Bartholow 1986). This existing computer simulation model was evaluated and modified in this study.

Initial inputs of POP-II include an initial population age-structure, age-, sex-, and season-specific mortality rates, and age-specific natality rates (Bartholow 1986). Additional information which can be added to the model include annual sex- and age-specific harvests, sex- and age-specific harvest efforts, and a weather severity index. POP-II then models population dynamics based on a biological year, beginning just after calf drop, in the following bookkeeping fashion:

$P_{N+1} = (((P_N - M_S) - M_H) - M_W) + R$, where

P_{N+1} = Population the following June

P_N = Population this June

M_S = Summer mortality

M_H = Harvest mortality

M_W = Winter mortality

R = Recruitment

The model thus begins with the population at the start of the biological year (approximately mid-June for the Michigan elk) and proceeds with the following steps (from Bartholow 1986):

(1) Subtraction of age- and sex-specific preseason natural mortality (poaching, predation, accidents, disease, etc.). This period follows from just after calf drop until the hunting season (early December).

(2) Subtraction of harvest mortality (including a pre-selected wounding loss). Harvests simulated in POP-II can mimic the age structure of the actual harvest by use of the relative effort value option. These effort values allow the partitioning of the harvest among different age-classes.

(3) Subtraction of age- and sex-specific postseason

natural mortality (starvation, accidents, predation, poaching, disease, etc). The postseason period covers the time from the end of the hunting season to immediately prior to calf drop (late May through early June).

(4) Addition of recruitment based on age-specific natality rates. The final model step is to advance all surviving individuals 1 age-class and place the recruitment into the initial age-class.

Population Parameters

Mortality Rates

Calf Mortality. Winter calf mortality was assessed by radio-collaring 2, 14, and 12 elk calves during October-November, 1989-1991, respectively. Calves were immobilized by darting individuals with a powder-charged Cap Chur gun (NASCO, Ft. Atkinson, WI) propelling a dart containing the muscle paralytic agent succinylcholine chloride (Succrostrin; E.R. Squibb and Sons Inc., Princeton, NJ). Once immobilized, calves were fitted with collars equipped with motion sensitive (mortality mode) radio transmitters (Telonics, Mesa AZ). Care for immobilized animals was described by Beyer (1987).

Newly collared calves were monitored at least once per week to assess mortality throughout the winter period of mid-December through May (based on POP-II's biological year). As more than 1 young is extremely rare in elk (Taber et al. 1982), mortality analysis simply involved calculating the percentage of collared calves that die during the winter period.

An additional index of winter calf mortality was determined by comparing cow:calf ratios from fall sex- and age-counts to spring cow:calf ratios. Cow:calf ratios were determined from helicopter and/or ground counts of elk. To maintain statistical independence, individual elk were not counted more than once during these periods.

Summer calf mortality was estimated by monitoring the survival of calves of previously radio-collared cow elk. Summer calf mortality covered the period from birth (~June 1) through the beginning of the MDNR annual elk hunt (early December), again based on POP-II's biological year. Radio-collared cows were repeatedly observed to assess (1) whether they calved and (2) summer survival of the calf. Summer calf mortality was calculated as the percent of calves from radio-collared cows that did not survive to December.

Summer calf mortality was also estimated by use of MDNR's elk hunt biological data, specifically the monitoring of lactation rates of harvested cows (Moran et al. 1987, Moran and Schmitt 1988, 1989; Carlson et al. 1990, S. Schmitt, MDNR, pers. commun.). Lactation rates provided information on whether a calf was still suckling at time of harvest; hence, an estimate of summer calf survival when compared with pregnancy data from the previous year (S. Schmitt, MDNR, pers. commun.).

Adult Mortality. Adult mortality analysis was attempted using 2 methodologies. Survival analyses on 72 elk radio-collared at various times from 1981-present was attempted utilizing a staggered-entry Kaplan-Meier estimator (Pollock et al. 1989). Additionally, annual and pooled data from the 764 harvested elk to date were analyzed by time-specific life-table analysis (Conley 1978). Life-table analysis was attempted on cow elk only due to known bias in bull elk harvesting among age-classes (Beyer 1987).

Natality Rates

Natality was estimated by monitoring the reproductive success of 13 previously radio-collared cows in 1990, and of 10 radio-collared cows in 1991, as described under **Calf Mortality**. Additionally, adult cow pregnancy rates from 1984-1991 were obtained from the MDNR elk hunt biological data summaries of harvested animals (Schmitt et al. 1985, 1986; Moran et al. 1987, Moran and Schmitt 1988, 1989; Carlson et al. 1990, S. Schmitt, MDNR, pers. commun.).

Sex- and Age-Ratios

Sex- and age-counts of the elk herd were done in late Fall, 1990 and 1991. Counts were made from a helicopter and by trained ground crews. All counted elk were classified into the following sex- and age-categories: (1) calf, (2) adult cow, (3) spike (yearling) bull, (4) immature bull, and (5) prime-aged/trophy bull (5X5 or better rack).

Spring cow:calf ratios were determined in April 1990 and 1991 using a ground count only. For Spring cow:calf counts, only numbers of cow and calf elk were recorded.

MDNR elk censuses in December, 1991, and January, 1992, provided additional information on bull:cow ratios. Elk counted in the December helicopter census were classified by sex- and age-category. All elk counted in the January ground and air census that were classified as either (1) bulls or (2) cows and calves were used to estimate bull:cow ratios (elk classified as unknown were not used). To determine a bull:cow ratio from the January data, it was assumed that the herd exhibited a calf:cow ratio of 50:100. This allowed determination of the approximate number of cows counted, and thus an estimate of bull:cow ratios.

For all herd ratios estimated, 90% confidence intervals were calculated using the methodology of Wyoming Game and Fish (1982).

Bull harvest antler data from 1984-1990 were analyzed to determine which age-classes of elk could produce prime bulls for viewing purposes (≥5X5).

RESULTS

Sex- and Age-composition

Fall 1990 and 1991 sex- and age-composition counts resulted in the recording of 499 and 467 elk, respectively (Table 27). Thirty-eight percent of bulls counted in Fall

Table 27. Fall and Spring sex- and age-composition counts of the Michigan elk herd, 1990-1992.

	Number				Ratios[1]		
Count	Bulls	Cows	Calves	Total	Bull	Cow	Calf
Fall 1990	131	236	132	499	55.5±7.9 :	100 :	55.9±7.9
Fall 1991	135	220	112	467	61.4±8.2 :	100 :	50.9±8.0
Spring 1991	---	162	79	241		100 :	48.8±9.2
Spring 1992	---	161	78	239		100 :	48.4±9.2
Dec 1991[2]	66	109	58	233	60.6±14.2:	100 :	53.2±13.6
Jan 1992[3]	255	420	---	675	60.7±4.6 :	100	

---

[1] Ratios ±90% confidence interval.

[2] Data from MDNR-MSU December 1991 helicopter census of elk population.

[3] Data from MDNR January 1992 combined ground and air elk census.

1990 were 5X5 or larger. In 1991, 43% of bulls counted were 5X5 or larger.

Spring 1990 calf counts produced a calf:cow ratio of 48.8±9.2:100 from 241 cows and calves tallied (Table 27). Spring 1991 calf counts resulted in the tallying of 239 cows and calves for a calf:cow ratio of 48.4±9.2:100 (Table 27).

An additional assessment of bull:cow ratios was provided by classifying elk counted during the MDNR's December and January censuses. The December aerial census resulted in 233 elk being classified for a bull:cow ratio of 60.6±14.2:100. The January census resulted in 675 elk being classified for a bull:cow ratio of 60.7±4.6:100.

Analysis of the age-distribution and antler development of bulls harvested from 1984-1990 indicated that 31% of 2.5 year-olds and 62% of 3.5 year-olds achieved antler development of ≥5X5. Minimum antler development for all age-classes ≥4.5 years-old was 5X5.

Natality

Long-term pregnancy data from MDNR elk check stations averaged 28.6% (SE=2.2) for yearling cows and 86.8% (SE=1.7) for adult cows. Pooled data from all hunts produced natality estimates of 27.8 calves/100 yearlings and 86.6 calves/100 adult cows.

Observations of calving rates of radio-collared cows produced natality estimates of 85% (11 of 13 radio-collared cows calving) in 1990 and 80% (8 of 10) in 1991. These rates are minimum estimates, however, as any calves lost at, or shortly after, birth were unlikely to have ever been observed with the cow.

Mortality

Calf Mortality. All radio-collared calves in 1989 lost their collars due to a mechanical defect. None of 14 radio-collared calves in 1990, and again 0 of 12 radio-collared calves in 1991, died from natural causes during the 1990 and 1991 Winter periods, respectively.

The overall seasonal mortality rates of adult elk in Michigan are unknown. Assuming winter overall mortality rates for cows of 0-5% in 1% increments, however, comparisons of mean Fall and Spring cow:calf ratios produce mean overwinter calf mortality estimates of 7.1, 6.6, 6.1, 5.6, 5.1, and 4.5% for 1990. Comparable estimates for 1991 were 2.5, 2.0, 1.5, 1.0, 0.5, and 0.0%, respectively. Extreme ninety-percent confidence intervals for these mean ranges are 0.0-24.2% for 1990, and 0.0-19.7% for 1991.

Minimum Summer calf mortality rates observed for radio-collared cows were 7.7% in 1990 (1 of 11 calves of radio-collared cows lost) and 12.5% in 1991 (1 of 8 calves of radio-collared cows lost). These rates are minimum estimates for Summer mortality, however, as they cover only the period from which the calf is first observed with the cow.

Summer calf mortality rates determined from comparisons of pregnancy and lactation rates from harvested elk averaged 10.2% (SE=1.57) from 1986-1990. These estimates were only for adult (2.5 year-olds or older) cows; as yearlings were not included, these estimates likely represent minimum estimates.

Adult Mortality. Data were inadequate to estimate adult elk natural mortality rates. Of 58 cow elk radio-collared throughout the course of elk research in Michigan, only 7 succumbed to natural mortality factors. Conversely, 37 were either legally or illegally killed. Similarly, no radio-collared bull has ever succumbed to anything other than human-induced mortality. Time-specific life-table analysis of cow elk harvested from 1984-1990 likewise was unable to provide useful mortality information. Calculated mortality rates varied greatly in the analysis, with older age-classes frequently having greater numbers of harvested elk than younger age-classes (Table 28).

Table 28. Time-specific life table mortality analysis of cow elk harvested in Michigan, 1984-1991.

AGE	n	l_x	d_x	mortality rate
1.5	95	1.000	0.084	8.4
2.5	87	0.916	0.053	5.3
3.5	82	0.863	0.189	18.9
4.5	64	0.674	0.264	26.4
5.5	39	0.410	0.000	0.0
6.5	39	0.410	-0.053	+5.3
7.5	44	0.463	0.242	24.2
8.5	21	0.221	0.053	5.3
9.5	16	0.168	0.031	3.1
10.5	13	0.137	0.032	3.2
11.5	10	0.105	-0.011	+1.1
12.5	11	0.116	0.074	7.4
13.5	4	0.042	-0.053	+5.3
14.5	9	0.095	0.063	6.3
15.5	3	0.032	-0.010	+1.0
16.5	4	0.042	0.010	1.0
17.5	3	0.032	0.011	1.1
18.5	2	0.021	0.010	1.0
19.5	1	0.011	0.011	1.1
20.5	0	0.000	-0.011	+1.1
21.5	1	0.011	-0.010	+1.0
22.5	2	0.021	0.021	2.1
23.5	0	0.000	0.000	0.0

Section 1: Model Development and Justification

Evaluation of Current (1987) MDNR Elk Population Model

The 1987 MDNR elk model (Beyer 1987) apparently provided accurate population size projections relative to MDNR census estimates (Table 29). The 1992 MDNR population estimate of 1200 elk, however, indicated that previous censuses were negatively biased, and hence 1987 model projections actually underestimated population size. Additionally, predicted bull:cow ratios of the 1987 MDNR elk model are 10-20% higher than ratios observed during 1990 and 1991 sex- and age-composition counts. Other parameters of the current elk model fall within 1990 and 1991 population estimates (i.e. cow:calf ratios and bull age-structure).

Thus, the 1987 MDNR elk model underestimates population size, and fails to accurately (within 90% confidence intervals) predict population sex-ratios (Table 29). These are perhaps the 2 most vital projections of the model; herd size, to allocate harvest to achieve MDNR population management goals, and bull:cow ratios, to evaluate the impact of the annual hunts on the bull segment of the herd, the most desirable segment for viewing purposes. For optimal management of the Michigan elk herd, it was thus necessary to modify the 1987 MDNR elk model to enhance the

Table 29. Current (1987) MDNR elk population model predictions and observed elk herd population parameters.

	Population Size[1]		Mean Bull:Cow:Calf Ratio[2]		Percent Bulls $\geq$5X5[2]	
YEAR	MODEL	ESTIMATE	MODEL	ESTIMATE	MODEL	ESTIMATE
1975	---	200	---	---	---	---
1976	234	---	---	---	---	---
1977	276	300	---	---	---	---
1978	326	---	---	---	---	---
1979	386	---	---	---	---	---
1980	452	500	---	---	---	---
1981	531	---	---	---	---	---
1982	623	---	---	---	---	---
1983	729	750	---	---	---	---
1984	853	850	---	---	---	---
1985	944	940	---	---	---	---
1986	961	950	---	---	---	---
1987	994	1000	---	---	---	---
1988	1024-1132[3]	1020	---	---	---	---
1989	985-1069	----	---	---	---	---
1990	961-1042	980	70.4:100:52.0	55.5:100:55.9	40-45	38
1991	902-977	---	70.4:100:52.2	61.4:100:50.9	40-45	43
1992	891-964	1200				

[1] Estimated population size (January for MDNR estimates).
[2] Population ratios November-December.
[3] Values are post-hunt (December) and final (May) population sizes, respectively.

predictive ability of the model for population management purposes.

Development of New Model

Four population parameters must be estimated to run POP-II simulations for a population. These 4 parameters are:

(1) Sex- and age-specific mortality rates.

(2) Harvest levels and allocation.

(3) Reproductive rates.

(4) Initial population size and structure.

Modification of the 1987 MDNR elk model consisted of manipulating mortality and reproductive parameters, and altering bull harvest allocation by changing age-specific hunter effort values.

Reproductive Rates. Recruitment of new individuals into the population depends upon 2 factors in POP-II: (1) age-specific fecundity and (2) sex-ratio at birth.

Estimates of pregnancy rates from 7 years of harvest data averaged 27.8-28.6% for yearling cows and 86.6-86.8% for adult cows. Minimum calving rates of radio-collared adult cows averaged 80-85% for 1990-1991. Natality estimates from the harvest data are likely much closer to actual values than the observations of radio-collared cows, as the sample sizes are an order of magnitude larger, and observations of radio-collared cows underestimate calving rates due to missing calves that die at or shortly after birth. Thus, reproductive values of 27 calves/100 yearling cows and 86 calves/100 adult cows were used in model development. These rates are close to the long term pregnancy rates, but still allow for a small percentage of pregnancies that may not be carried to term. These reproductive rates are considerably greater than those used by Beyer (1987) (20 calves/100 yearlings, 85/100 adult cows), which is consistent with the underestimation of population size shown by the 1987 MDNR elk model.

Sex-ratio at birth is the second variable affecting the number of cows and bulls born into the population. Numerous studies on a variety of ungulates have shown sex-ratios at birth to be skewed towards females when populations are considerably under carrying capacity, i.e. when nutritional levels of reproductive females are high (Taber et al. 1982, Verme 1983, Verme and Ullrey 1984, DeGayner and Jordan 1987). Skewed sex-ratios favoring females at birth have been demonstrated in, for example, white-tailed deer (Verme 1969, McCullough 1979, Verme and Ozoga 1981, Verme 1983, DeGayner and Jordan 1987), mule deer (Robinette et al. 1957), and goats (Sachdeva et al. 1973).

The Michigan elk herd is managed under a population management strategy designed to limit population density, and thus provide high per capita resource availability. The low densities of the herd, high nutritional quality of the range, and subsequent high nutritional status of individual elk is shown by the extremely high reproductive rates and large body-sizes seen in the Michigan elk herd relative to other elk populations. Such reproductive and nutritional conditions strongly suggest that sex-ratios at birth are likely skewed towards females in the Michigan herd. The 1987 MDNR elk model establishes a sex-ratio at birth of 50:50 (Beyer 1987); this results in bull:cow ratios that are greater than those observed in this study. One effect of skewing sex-ratios at birth towards females is to decrease the predicted bull:cow ratios in the model, without having to severely alter bull mortality rates.

Thus, based on the strength of empirical and theoretical evidence, and observed sex-ratios in the Michigan herd relative to the 1987 MDNR elk model predictions, sex-ratios at birth were skewed towards females in this model. Iteration was used to determine the sex-ratio providing the best fit to observed population parameters. This ratio was 48:52 bulls:cows at birth.

Mortality Rates. Survival data from radio-collared elk and age-structure data from harvested elk were inadequate to estimate biologically-based adult mortality rates in this study. Adult mortality rates in the 1987 MDNR elk model were iteratively derived to balance model population projections against MDNR population estimates (Beyer 1987). These mortality rates, along with reproductive rates now known to be too low, resulted in population projections shown by the 1992 census to be much too low. The age-structure produced by these rates, however, fit the age-structure observed in the bull segment adequately (40-43% 5X5 bulls, as compared with observed values of 38-43%). Thus, the adult mortality rates of the existing model were left unaltered, as they provided an adequate fit to observed herd age-structure. Balancing model projections with MDNR population estimates was therefore accomplished by altering calf and yearling mortality rates.

Balancing model projections to the 1992 MDNR population estimate (as well as to previous population estimates, although these are likely negatively biased, at least at higher elk numbers) was achieved primarily by altering summer calf mortality. The 1987 MDNR elk model has summer calf mortality rates which are considerably (2-4%) lower than the winter calf mortality rates (Beyer 1987). However, most of the literature available on elk and red deer suggests that summer calf mortality rates are near equal to, or even greater than, winter calf mortality rates, due primarily to the density-independent nature of summer calf mortality, and the great vulnerability of new-borns to disease, parasitism, and accidents. This has been shown for red deer (Wegge 1975, Arman et al. 1978, Guinness et al.

1978, Clutton-Brock et al. 1982), Tule elk (C. e. nannodes) (McCullough 1969, Gogan and Barrett 1987), Roosevelt elk (Harn 1960, Harper et al. 1967), Rocky Mountain elk (Green 1950, Taber 1976, Houston 1982), and Rocky Mountain elk in Michigan (Moran 1973). Additionally, minimum estimates of summer calf mortality produced by this study ranged from 7.7% in 1990 to 12.5% in 1991; estimates from comparisons of pregnancy and lactation rates of harvested adult cow elk averaged 10.2% from 1984-1990. All 3 of these estimates are minimum estimates due to their methodology, yet all are 2-4% greater than the summer calf mortality rates used in the 1987 MDNR elk model. Therefore, since the new recruitment values used in this model resulted initially in population projections greater than 1992 MDNR census estimates, increases in summer calf mortality rates (to 8.5% for both cows and bulls) was the principal mechanism used to balance model projections to MDNR census estimates (Table 30).

Data were inadequate to accurately estimate winter calf mortality rates. Since the winter calf mortality rates in the 1987 MDNR elk model fall within the wide range of estimates produced by this study, winter calf mortality rates were not altered, and only summer calf mortality rates were modified to balance population projections (Table 30).

Table 30. Initial population proportions, size, and mortality rates for the new general elk population model.

AGE CLASS	Initial Population Proportion		Pre-Season Mortality		Post-Season Mortality	
	BULL	COW	BULL	COW	BULL	COW
0.5	31	31	8.5	8.5	10.0	10.0
1.5	24	24	7.5	3.0	8.0	5.0
2.5	16	20	7.0	2.0	8.0	2.0
3.5	10	18	7.0	2.0	10.0	2.0
4.5	8	15	7.0	2.0	12.0	3.0
5.5	6	11	7.0	2.0	15.0	3.0
6.5	4	7	8.0	2.0	20.0	4.0
7.5	3	5	8.0	3.0	25.0	4.0
8.5	2	4	8.0	3.0	30.0	4.0
9.5	1	3	8.0	3.0	35.0	5.0
10.5	0	2	12.0	3.0	40.0	6.0
11.5	0	1	15.0	5.0	45.0	10.0
12.5	0	0	20.0	8.0	50.0	15.0
13.5	0	0	25.0	8.0	60.0	25.0
14.5	0	0	25.0	10.0	100.0	100.0

INITIAL POPULATION SIZE = 225

Relative Hunter Effort Values

POP-II uses relative hunter effort values to allocate harvest by age-class. Beyer (1987) developed relative effort values to proportion the projected harvests in the 1987 MDNR elk model to mimic the age-structure of the actual 1984-1986 harvests. Chi-square (Siegel 1956) analysis indicated that predicted bull harvest age-structures from the 1987 model differed significantly ($\underline{a}$=0.10) from the age-structure of the actual 1984-1991 Michigan bull elk harvests, however (Table 31). New bull relative effort values were thus derived by iteration that allowed projected bull harvests to mimic actual harvest age-structure (Table 31).

Evaluation of New General Elk Population Model

Three population parameter estimates are available to assess the predictive ability of the new model:

(1) MDNR population estimates, especially the 1992 census.

(2) Herd sex- and age-composition estimates.

(3) The age-composition of the bull segment, specifically the percentage of 5X5 or larger bulls.

Comparisons of model projections to parameter estimates (Table 32) indicate that the new model provides a close fit to the estimated herd parameters. MDNR population estimates tend to be lower than model predictions; these estimates,

Table 31. Actual and simulated bull harvests by age-class from the 1987 MDNR elk model and the new general model.

AGE CLASS	Actual Harvest[1]	Projected 1987 Model[2]	Projected New Model[3]
1.5	47	42 (1)	47 (1)
2.5	89	97 (3)	95 (2.5)
3.5	65	91 (4)	65 (2.5)
4.5	68	74 (5)	74 (4)
5.5+	134	101 (5)	121 (5)

[1] Actual numbers of bull elk harvested 1984-1991.

[2] Projected bull harvests of 1987 MDNR elk model 1984-1991 (age-specific relative effort values in parentheses).

[3] Projected bull harvests of new general elk model 1984-1991 (age-specific relative effort values in parentheses).

Table 32. Predictions of new elk population model and observed elk herd population parameters.

	Population Size		Mean Bull:Cow:Calf Ratio[1]		Percent Bulls $\geq$5X5[1]	
YEAR	MODEL[2]	ESTIMATE[3]	MODEL	ESTIMATE	MODEL	ESTIMATE
1975	197-213	200	---	---	---	---
1976	233-252	---	---	---	---	---
1977	276-299	300	---	---	---	---
1978	326-353	---	---	---	---	---
1979	385-418	---	---	---	---	---
1980	455-493	500	---	---	---	---
1981	536-582	---	---	---	---	---
1982	633-687	---	---	---	---	---
1983	746-810	750	---	---	---	---
1984	878-954	850	---	---	---	---
1985	984-1069	940	---	---	---	---
1986	1028-1118	950	---	---	---	---
1987	1096-1190	1000	---	---	---	---
1988	1146-1243	1020	---	---	---	---
1989	1121-1213	----	---	---	---	---
1990	1134-1226	980	62.9:100:52.7	55.5:100:55.9	39-44	38
1991	1119-1209	---	62.4:100:52.9	61.4:100:50.9	40-43	43
1992	1160-1253	1200				

---

[1] Population ratios November-December.
[2] Projected post-hunt (December) and final (May) population sizes, respectively.
[3] Estimated January population size.

however, are likely negatively biased as indicated by the 1992 census of 1200 elk. Additionally, an independent aerial census estimate of 1279±301 elk (Otten et al. 1992) also corroborated the new model's 1992 population estimate. Thus, the new model appears to be a good predictor of elk population size and herd structure. Adoption of the new model should provide the MDNR with a more precise means of evaluating population management strategies for the Michigan elk herd.

Section 2. Elk Management Unit (EMU) Modelling

The MDNR divides the overall Michigan elk range into 5 Elk Management Units (EMUs), each of which has individual harvest and population level goals (Fig. 2). Very little information is available on elk numbers, population parameters, or dynamics on an EMU level for management purposes. The objective of this Section is to apply the overall elk population model developed in the previous section to the individual EMUs, utilizing the limited amount of data on elk distribution and population structure available for mean projections of EMU dynamics.

METHODS

Population distribution of elk within the EMUs was estimated from the November-December 1991 and January 1992 elk censuses. EMU bull:cow:calf ratios were estimated from the same data, with cow:calf ratios for the January census assumed to be ~100:50. This allowed the derivation of bull:cow:calf ratios from the 2 categories of known elk in the January data: (1) bulls and (2) cows and calves (not differentiated).

Modelling was accomplished by modifying the general elk population model developed in the previous section. Two

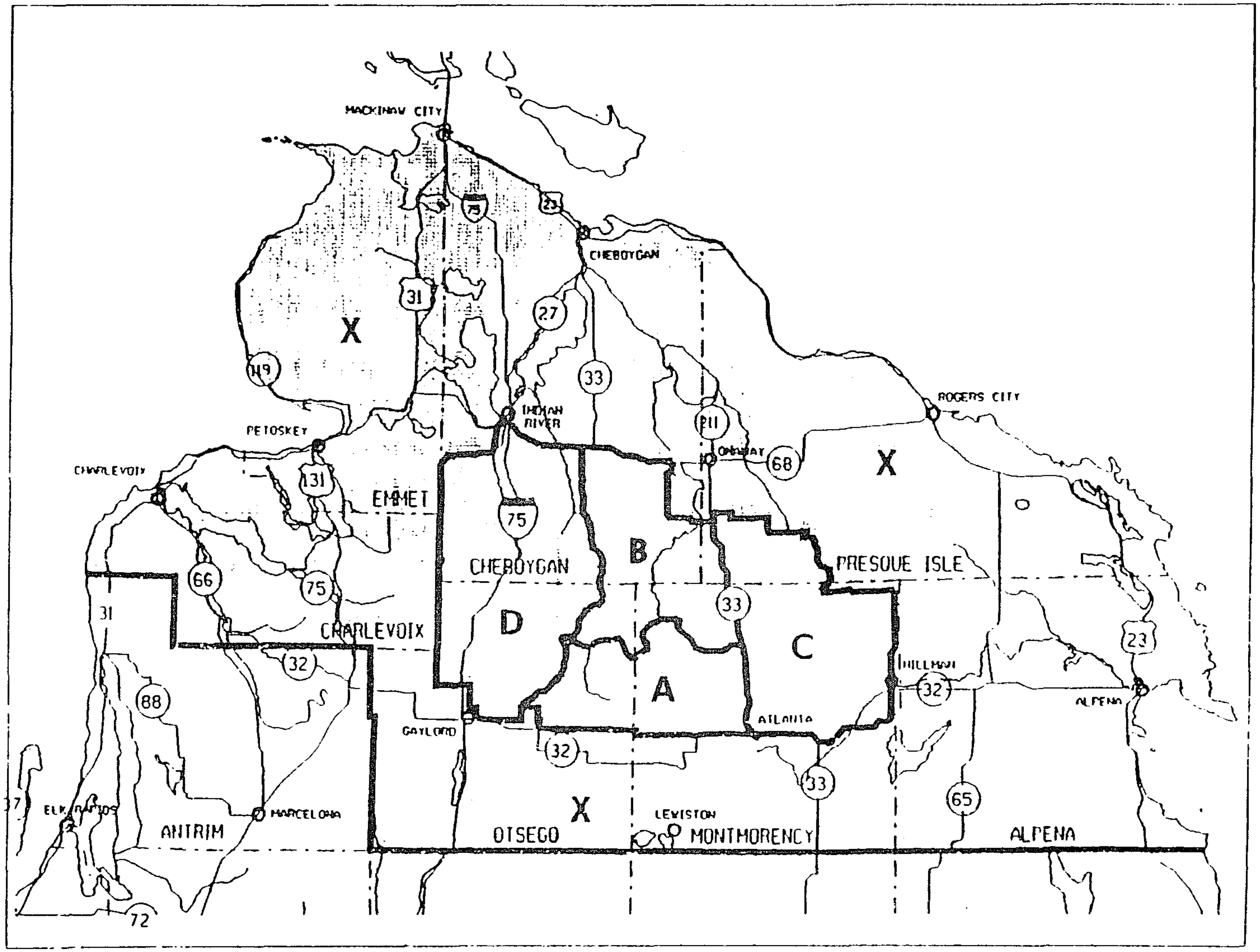

Figure 2. Elk Management Units within the Michigan elk range.

variables in the model were modified: (1) initial age-structure, modified to reflect EMU bull:cow:calf proportions, and (2) initial population size, modified to reflect the percentage of the total herd size determined to be in the EMU immediately prior to calving in 1992.

Models were developed only for EMUs A, B, C, and D, as area X has a population goal of 0 elk, and hence acts as a mortality vacuum. Due to the limited amount of data available to construct the EMU models, only population means were estimated. Inferentially determining confidence intervals on the parameter estimates would have produced C.I.s so large as to make EMU modelling useless due to small sample sizes. Instead, as the population parameters were independently estimated from 2 distinct and independent sources of data, Popperian or Lakatosian corroboration was used to assess the viability of the EMU models, an application of an alternative method of scientific inference, falsificationism (Salmon 1967).

RESULTS and DISCUSSION

Counts from both the November-December 1991 and January 1992 censuses produced similar estimates of the proportion of the elk herd in each EMU (Table 33), as well as the bull:cow:calf ratios in each EMU (Table 34). The mean values used to construct the individual EMU models thus can be considered corroborated to the highest degree possible.

Table 33. Proportions of elk herd in each Elk Management Unit (EMU) during November-December 1991 and January 1992 elk censuses.

	Percent of Counted Elk		
EMU	Nov-Dec 1991	Jan 1992	MEAN
A	26	26	26.0
B	28	23	25.5
C	8	8	8.0
D	38	43	40.5

Table 34. Estimated herd sex- and age-structure in each Elk Management Unit (EMU).

	Number per 100 COWS					
	Nov-Dec 1991		Jan 1992		MEAN	
EMU	BULL	CALF	BULL	CALF	BULL	CALF
A	71	46	73	50	72.0	48.0
B	81	43	93	50	87.0	46.5
C	45	42	48	50	47.0	46.0
D	43	51	43	50	43.0	50.5

These means were used to allocate the January 1992 population and the estimated Spring 1992 population into EMUs, reflecting both the proportion of the herd present in each EMU and the sex- and age-structure estimated for each EMU (Table 35). All other parameters from the general elk population model were maintained in the individual EMU models.

Since the population histories of the EMUs are unknown, EMU models cannot be used to reconstruct the dynamics of the elk in each EMU as the general model was for the entire elk population. EMU models therefore serve solely as population management projection tools. Using the recommended MDNR harvests for the upcoming 1992 elk seasons (T. Carlson, MDNR, pers. commun.), EMU models were used to project the impact of these harvests on elk numbers in each EMU (Table 36). From these projections, it can be seen that the effect of the recommended MDNR harvest is to decrease elk numbers in each EMU, especially in EMU D. This result is consistent with past MDNR management goals of decreasing the elk population to a level of ~900-1000, with the additional goal of having most of the herd reduction occur in EMU D, which is characterized by largely privately-owned lands, high levels of elk-agriculture conflicts, and a generally intolerant landowner attitude towards elk. Thus, by modelling harvests on an EMU basis, the MDNR can more effectively target local problem areas such as EMU D, and

Table 35. Initial population structure and sizes for the individual Elk Management Unit (EMU) models.

	EMU A				EMU B				EMU C				EMU D			
	Fall 91[1]		Summ 92[2]		Fall 91		Summ 92		Fall 91		Summ 92		Fall 91		Summ 92	
AGE	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
0.5	32	35	44	47	29	32	39	42	11	12	14	16	57	62	77	84
1.5	28	30	29	32	31	28	26	29	7	10	10	11	33	53	51	56
2.5	24	22	26	29	28	21	28	27	5	8	6	9	25	40	30	50
3.5	17	19	22	22	20	17	26	20	3	7	5	8	18	34	23	39
4.5	11	14	15	19	12	13	18	17	2	5	3	6	11	26	16	33
5.5	6	11	10	14	6	10	11	12	1	4	2	5	6	20	10	25
6.5	3	9	5	11	4	8	5	10	1	3	1	4	4	17	5	19
7.5	2	7	2	9	2	6	3	7	1	2	1	2	2	12	3	16
8.5	1	5	2	7	1	5	2	6	1	1	1	2	1	9	2	11
9.5	1	4	1	4	1	3	1	5	0	1	1	1	1	7	1	9
10.5	0	2	1	4	0	3	1	2	0	1	0	1	0	6	1	7
11.5	0	2	0	3	0	2	0	2	0	1	0	1	0	4	0	5
12.5	0	2	0	2	0	2	0	2	0	1	0	1	0	3	0	3
13.5	0	2	0	1	0	1	0	1	0	1	0	1	0	2	0	2
14.5	0	1	0	1	0	1	0	1	0	0	0	0	0	2	0	2

[1] Structure obtained from November-December 1991 aerial census.

[2] Estimated structure at beginning of 1992 bio-year (after calving).

Table 36. Projection of recommended 1992 elk harvest by Elk Management Unit (EMU).

	Harvest				
EMU	BULLS	C & C[1]	TOTAL	% HARVEST	% GROWTH
A	20	30	50	14.6	-2.6
B	25	35	60	18.5	-9.6
C	8	12	20	18.9	-6.4
D	40	90	130	23.7	-13.2

[1] Cows and calves (antlerless-only permits).

more efficiently allocate harvest to deal with these areas of locally abundant elk. Simultaneously, the general elk population model, with its more generalized but likely much more accurate population parameters, can be used to assess harvest impacts on the overall population and plan long-range population management strategies for the overall elk population.

As just noted, the general elk population model must be used to assess long-term impacts on elk population numbers and parameters. Individual EMU models were constructed based on population proportions and herd structure estimates for each EMU. The productivity and mortality parameters used in the EMU models are identical to the general model. As these rates are constants, attempted long-term projections of the EMU models would result in forcing the sex- and age-structure of each EMU into that projected by the general model, i.e. ~60 bulls:100 cows:50 calves. This overall population mean structure differs from that shown by each individual EMU (Table 34).

Productivity and mortality rates which maintain sex- and age-structures estimated for each EMU for 1991 could have been iteratively developed to allow long-term projections of the EMU models. This, however, was inappropriate for several reasons:

(1) Although differences in productivity and mortality

parameters likely exist among EMUs (for example, EMU D, with plentiful agricultural lands and a high level of winter feeding of elk and deer, would likely show lower mortality and higher productivity rates than EMUs on poorer soils and with less artificial feeding, such as EMU C), no biological basis exists for estimating any EMU-specific productivity or mortality rates, unlike that for the overall population.

(2) Movements between EMUs is common; thus, population proportions and herd structure within an EMU is likely to change annually, sometimes seasonally, perhaps significantly.

(3) Similarly, the observed EMU sex- and age-structures in 1991 may be a result of either (1) EMU-specific productivity and mortality rates driving the EMU population into such a structure or (2) simply an artifact of elk movements that by chance, or design, resulted in the particular population level and structure which was observed during Fall and Winter of 1991-1992.

(4) Finally, the purpose of the EMU models is to determine how best to allocate a harvest once the desired harvest level has been determined. Selection of the desired harvest level is accomplished with the general elk population model which, for reasons noted above, is likely much more accurate than the individual EMU models. Allocation of an annual harvest to EMUs requires projections of only 1 year. Hence, use of the generalized productivity

and mortality rates is likely to result in minimal bias during this short an interval. Additionally, EMU models can thus be re-calibrated annually with new population levels and structures suggested by future MDNR censuses. This allows individual EMU models to most accurately follow changing herd distribution trends and/or shifting sex- and age-structures in each EMU.

Thus, the individual EMU models described in this section should not be viewed as dynamic long-term projection tools. They are likely much more inaccurate than the general elk population model on which they were based, due principally to the limited amount of EMU-specific demographic data available. However, the available data used to develop the EMU models was corroborated to the highest degree possible. The EMU models presented should thus adequately fulfill their purpose of providing a means to allocate the 1992 harvest by EMU. They should not be used for long-term population projections, and initial population structure and levels should be reviewed and reallocated annually to prevent the generalized productivity and mortality rates used in each model from forcing the EMU populations into sex- and age-structures identical to the general elk population model.

Section 3. Alternative Management Strategies for Elk in Michigan

Current MDNR population management of the Michigan elk herd consists of limiting population size and distribution by controlled hunting. This is accomplished through placing the emphasis of the harvest on cows, with a more limited number of bull (hunter's choice) permits. The purpose of this strategy is to maintain populations at a desired level without altering current herd composition, particularly the number of adult bulls, thus not negatively impacting herd viewing opportunities.

Beyer (1987) found elk hunters in Michigan to be aselective in harvesting cow elk. However, hunters harvested older, larger bulls to a greater degree than their presence in the population. From this, Beyer (1987) developed age-specific relative hunter effort values for use in the 1987 MDNR elk population model to mimic the actual age-structure of the bull harvest. Selectivity in bull harvest was also noted in this study (Table 31), and new age-specific relative effort values were derived to mimic actual hunter selection from 1984-1991.

Other population management strategies can also be evaluated for the Michigan elk herd by use of the age-specific relative effort value feature of POP-II. The most common harvesting strategies currently used to maintain or increase the numbers of older age-class bulls include: (1) Strategies which simply limit overall bull harvest (such as that currently employed by the MDNR), (2) strategies which limit overall bull harvest while simultaneously protecting younger bulls (i.e. 4-point or better type systems), and (3) strategies which limit overall bull harvest while simultaneously protecting older age-classes (i.e. spike-only type systems). The objective of this Section is to project and evaluate these alternative population management strategies for the Michigan elk herd using the general elk population model developed in this Chapter.

METHODS

The general elk population model previously developed in this Chapter was used to project the population dynamics of the Michigan elk from 1992-1997. Two differing population goals were used in these projections: stabilized populations of 1000 and 1100 elk, respectively. The current MDNR harvesting strategy (Beyer 1987, as modified by Table 31) was used to iteratively determine annual harvests necessary to achieve these population goals, with the exception of the 1992 harvest, where recommended MDNR harvest levels were used (T. Carlson, MDNR, pers. commun.). Harvests were chosen to not significantly alter current herd sex- and age-composition.

Once harvest levels were derived which accomplished the population level goals, 5 alternative bull harvesting strategies were modeled to evaluate their impacts on herd sex- and age-composition. These alternative harvesting strategies were:

(1) The current MDNR harvesting strategy, allowing a limited any-bull harvest with no restrictions on age-class of harvested bulls.

(2) A strategy where 25% of the limited bull harvest is allocated solely for bulls with 3 antler-points or less.

(3) A strategy identical to (2), but where 50% of the bull harvest is limited to $\leq$3-point elk.

(4) A 4X4 or better strategy, designed to allow the maximum number of yearling elk to enter the older age-classes.

(5) A 5X5 or better strategy, again designed to maximize the number of young elk entering the adult age-classes.

All 5 of these strategies were projected using the harvest levels developed to balance herd population levels at 1000 or 1100, respectively.

RESULTS and DISCUSSION

Among the goals of the MDNR elk management plan is to maintain a herd with a large number of prime-aged bulls for optimal viewing opportunities. Selective harvesting of bulls is a common practice used to produce a herd with a large number of high viewing quality, large-antlered individuals, either by increasing the total number of bulls or the number of trophy animals (Weigand and Mackie 1987). Most schemes limit either the number of yearlings or the number of adult animals taken, while simultaneously placing heavy harvest pressure on the cow segment of the population to limit overall population size and density. Such a population management scheme has been used in Michigan since the re-initiation of elk hunting in 1984. Michigan's harvesting strategy places the emphasis of the harvest on cows to limit the total herd size to ˜1000 and maintain high bull:cow ratios for viewing purposes, while allowing a much more limited any-bull harvest to satisfy hunter demand for bull elk hunting. This system has been effective in maintaining the historically high bull:cow ratios (˜60:100) and large numbers of prime-aged (˜40%) bulls in the herd (Table 32). However, other harvest management strategies do exist which could potentially satisfy MDNR elk management goals to an even greater degree, as well as further enhance the trophy status of the Michigan herd.

Current MDNR permit allocation philosophy and trophy management theory was used to devise harvests that balanced the simulated Michigan herd at either 1000 or 1100 elk from 1992-1997 (Table 37). These harvests are heavily slanted towards cows (to control population growth) yet allow a moderate bull harvest as well. When used in conjunction

Table 37. Simulated harvest levels to achieve elk population goals of 1000 and 1100 animals, respectively.

Population Goal: 1100	HARVEST			
Year	CALF	BULL	COW	TOTAL
1992[1]	14	93	153	260
1993	15	85	120	220
1994	15	65	95	175
1995	15	65	95	175
1996	15	65	95	175
1997	15	65	95	175
Population Goal: 1000				
1992[1]	14	93	153	260
1993	15	90	130	235
1994	15	90	130	235
1995	10	60	90	160
1996	10	60	90	160
1997	10	60	90	160

[1] MDNR recommended 1992 harvest (T. Carlson, MDNR, pers. commun.).

with the age-specific hunter effort values characteristic of Michigan bull and cow elk harvests (Table 38, Beyer 1987), the resulting projections maintain current herd sex- and age-composition (Tables 39 and 40).

Age-specific bull relative effort values were also developed that mimic the other trophy management harvesting strategies (Table 38). These alternative effort values allowed the projection of the Michigan elk population from 1992-1997 under these different management philosophies, utilizing the same overall harvests developed for the current MDNR population management strategy, but allocating bull harvest differently. Each of these alternative harvest strategies apparently achieved MDNR elk management goals, i.e. maintaining current (~60:100) bull:cow ratios along with a large number (~40%) of prime-aged bulls (≥5X5) for viewing purposes (Tables 39 and 40). The alternative strategies differed in how they achieved these outcomes, however. Strategies involving placing heavy harvest on young bulls (≤3 points) resulted in the highest numbers of prime-aged bulls and greatest percentages of older age-class bulls (≥4.5 years-old) while also allowing bulls to reach older age-classes than in any other simulated harvesting strategy (Tables 39 and 40). These strategies accomplished this by allowing fewer bulls to actually reach the prime age-classes, but then having a much lower probability of being harvested once these age-classes were reached. These

Table 38. Relative effort values used in simulating various alternative bull elk harvest strategies in Michigan.

		$\leq$3 Points			
AGE	MDNR[1]	25%[2]	50%[3]	$\geq$4X4[4]	$\geq$5X5[5]
1.5	1	10	20	0	0
2.5	2.5	2	2	3.5	3
3.5	2.5	1	1	4.5	6
4.5	4	2	2	5	10
5.5	5	2	2	5	10
6.5	5	2	2	5	10
7.5	5	2	2	5	10
8.5	5	2	2	5	10
9.5	5	2	2	5	10
10.5	5	2	2	5	10
11.5	5	2	2	5	10
12.5	5	2	2	5	10
13.5	5	2	2	5	10
14.5	5	2	2	5	10

[1] Current limited any-bull harvesting strategy.
[2] 25% of bull permits for only 3 point bulls or less.
[3] 50% of bull permits for only 3 point bulls or less.
[4] All bull permits solely for 4X4 or larger bulls.
[5] All bull permits solely for 5X5 or larger bulls.

Table 39. Comparisons of simulated alternative harvest strategies to achieve a population goal of 1000 elk for the Michigan herd, 1992-1997.

Strategy	Year	Pop Size[1]	No. Bulls[2]	B:C:C[3]	%≥5X5[4]	%≥4.5[5]	Max. Age[6]
MDNR	92	1098-1186	422	61.8:100:53.1	44.0	25.8	11
	93	1038-1120	408	63.8:100:51.6	42.1	23.8	11
	94	968-1044	385	63.5:100:51.3	41.7	22.3	10
	95	966-1042	360	63.3:100:51.8	41.6	21.7	10
	96	966-1042	359	63.5:100:52.3	43.6	24.0	10
	97	966-1044	361	63.7:100:52.6	44.6	25.8	10
≤3 Pt 25%	92	1098-1186	422	61.8:100:53.1	44.0	25.8	11
	93	1035-1120	408	63.8:100:51.6	42.1	23.8	11
	94	959-1041	382	63.1:100:51.3	49.3	31.9	11
	95	951-1034	350	61.9:100:51.8	53.1	41.7	11
	96	944-1028	344	61.0:100:52.3	51.5	39.8	11
	97	939-1023	338	60.0:100:52.6	49.7	36.1	11
≤3 Pt 50%	92	1098-1186	422	61.8:100:53.1	44.0	25.8	11
	93	1034-1120	408	63.8:100:51.6	42.1	23.8	11
	94	958-1041	383	63.0:100:51.3	50.5	33.4	11
	95	948-1032	350	61.6:100:51.8	55.1	45.1	11
	96	940-1025	342	60.5:100:52.3	52.8	42.7	11
	97	933-1019	334	59.3:100:52.6	50.8	38.3	12

Table 39. Cont'd.

Strategy	Year	Pop Size[1]	No. Bulls[2]	B:C:C[3]	%≥5X5[4]	%≥4.5[5]	Max. Age[6]
≥4X4	92	1098-1186	422	61.8:100:53.1	44.0	22.8	11
	93	1038-1120	408	63.8:100:51.6	42.1	23.8	11
	94	968-1044	384	63.5:100:51.3	39.9	20.3	10
	95	966-1042	358	63.3:100:51.8	39.1	17.9	10
	96	966-1043	359	63.6:100:52.3	41.6	20.6	10
	97	967-1044	358	63.7:100:52.6	42.5	22.6	10
≥5X5	92	1098-1186	422	61.8:100:53.1	44.0	22.8	11
	93	1039-1120	408	63.8:100:51.6	42.1	23.8	11
	94	970-1045	387	63.7:100:51.3	39.3	18.1	10
	95	970-1044	360	63.8:100:51.8	38.2	15.0	9
	96	971-1046	362	64.2:100:52.3	41.3	19.3	9
	97	972-1048	365	64.6:100:52.6	42.8	21.9	9

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[1] Final (May of following year) and post-hunt (December) populations, respectively.
[2] Total number of bulls in population in November.
[3] November bull:cow:calf ratio.
[4] Percent of November bulls ≥5X5.
[5] Percent of November bulls age 4.5 or older.
[6] Maximum age of bulls in November population.

Table 40. Comparisons of simulated alternative harvest strategies to achieve a population goal of 1100 elk for the Michigan herd 1992-1997.

Strategy	Year	Pop Size[1]	No. Bulls[2]	B:C:C[3]	%≥5X5[4]	%≥4.5[5]	Max. Age[6]
MDNR	92	1098-1186	422	61.8:100:53.1	44.0	25.8	11
	93	1053-1137	408	63.8:100:51.6	42.1	23.8	11
	94	1049-1132	389	63.2:100:51.6	42.1	22.6	11
	95	1051-1135	387	63.0:100:52.8	43.7	23.8	10
	96	1054-1139	388	62.9:100:52.9	44.5	25.8	10
	97	1057-1141	389	62.9:100:52.7	44.1	25.7	10
≤3 Pt 25%	92	1098-1186	422	61.8:100:53.1	44.0	25.8	11
	93	1050-1137	408	63.8:100:51.6	42.1	23.8	11
	94	1041-1129	386	62.8:100:51.6	49.2	31.6	11
	95	1038-1128	380	61.8:100:52.8	52.3	39.7	11
	96	1034-1125	375	60.8:100:52.9	51.4	38.4	11
	97	1030-1122	370	59.7:100:52.7	50.4	37.6	11
≤3 Pt 50%	92	1098-1186	422	61.8:100:53.1	44.0	25.8	11
	93	1050-1137	408	63.8:100:51.6	42.1	23.8	11
	94	1040-1129	388	62.7:100:51.6	50.4	33.2	11
	95	1035-1126	379	61.6:100:52.8	53.7	42.2	11
	96	1030-1123	373	60.4:100:52.9	52.6	40.8	11
	97	1025-1118	367	59.1:100:52.7	51.5	39.8	12

Table 40. Cont'd.

Strategy	Year	Pop Size[1]	No. Bulls[2]	B:C:C[3]	%≥5X5[4]	%≥4.5[5]	Max. Age[6]
≥4X4	92	1098-1186	422	61.8:100:53.1	44.0	25.8	11
	93	1053-1137	408	63.8:100:51.6	42.1	23.8	11
	94	1049-1132	388	63.2:100:51.6	40.5	20.9	10
	95	1051-1135	387	63.0:100:52.8	41.9	20.7	10
	96	1055-1139	387	62.9:100:52.9	42.8	23.0	10
	97	1057-1142	389	62.9:100:52.7	42.8	23.4	10
≥5X5	92	1098-1186	422	61.8:100:53.1	44.0	25.8	11
	93	1054-1137	408	63.8:100:51.6	42.1	23.8	11
	94	1051-1133	390	63.4:100:51.6	39.7	18.5	10
	95	1055-1137	391	63.4:100:52.8	41.6	19.2	10
	96	1059-1142	391	63.5:100:52.9	42.7	22.0	10
	97	1063-1146	394	63.6:100:52.7	42.7	22.0	10

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[1] Final (May of following year) and post-hunt (December) populations, respectively.
[2] Number of bulls in the November population.
[3] November bull:cow:calf ratio.
[4] Percent of November bulls ≥5X5.
[5] Percent of November bull population age 4.5 or older.
[6] Maximum age of bulls in population.

same strategies also resulted in the lowest total number of bulls present in the simulated population relative to the other strategies (Tables 39 and 40). However, some of this difference is likely attributable to the constant non-compensatory natural mortality rates utilized in the model. Rates of natural mortality would likely decrease to lower levels in the heavily exploited younger age-classes in actual, rather than simulated, populations, thereby allowing a greater number of bulls to actually enter the older age-classes.

Harvesting strategies aimed at older bull age-classes (≥4X4 and ≥5X5) in theory allow the maximum number of bulls possible to enter prime age-classes, where they are then heavily exploited. Simulations of these strategies also maintained desired sex- and age-ratios in the Michigan herd (Tables 39 and 40). Although the percent of prime-aged (≥5X5) bulls produced by these strategies was comparable to that produced by the current MDNR harvesting strategy, the numbers of age 4.5 and older bulls were less, and the maximum age achieved by bull elk tended to decline under these harvesting strategies (Tables 39 and 40). This suggests that while an adequate number of bulls ≥5X5 are maintained by these strategies, a significant proportion of these are the 31% of 2.5 year-olds and 62% of 3.5 year-olds that achieve ≥5X5 status in Michigan. Thus, while ≥4X4 and ≥5X5 strategies achieve MDNR bull elk management goals adequately, the actual biological impacts on the herd of shifting bull age-structure downward are not predictable from simulation modelling at this level.

The current MDNR harvesting strategy involves limiting the total bull harvest without placing restrictions on age-classes available to harvest. This strategy produced results intermediate to the strategies limiting either younger or older age-class harvest, and altered the current herd sex- and age-composition the least (Tables 39 and 40). These results were expected, as the current "natural" sex- and age-structure present in the Michigan elk herd was produced by this harvesting strategy.

The results of these harvest simulations are not unexpected. Antler regulations designed to save young bulls (such as the ≥4X4 or ≥5X5 modeled) have shown mixed results in actual practice, although the tendency is for such regulations to not result in greater numbers of prime-aged or trophy bulls in elk populations (Weigand and Mackie 1987). Most of the Western elk-harvesting states surveyed by Weigand and Mackie (1987) instead felt that the only way to maintain trophy class bulls was "not to kill them". Colorado, for example, found that protecting spikes did not increase the number of older bulls; their "quality hunting" (i.e. trophy) areas thus do not have point restrictions, rather they simply limit the total number of bull permits, allowing hunters the opportunity to harvest a spike bull if they choose, thus allowing more bulls to actually reach and survive in the older age-classes (Hernbrode 1987). This strategy is identical to that currently employed by the MDNR for bull elk hunting in Michigan.

In contrast, antler regulations that place the bulk of the harvest pressure on the younger age-classes have more consistently shown themselves to be effective in increasing the numbers of animals in older age-classes. Selective harvesting of does and spikes, along with a more limited adult buck harvest, resulted in greater numbers of older age-class bucks along with increased antler quality on a South Carolina plantation (Franklin et al. 1985). Similarly, Fleming (1983) found that the proportion of older bucks in the herd increased in response to a spike and 3-point only harvesting program, in conjunction with heavy doe harvesting, on an East Texas hunting club. Red deer managers in Germany maintain as many stags as possible in the ages of best trophy production (8-14) via a culling plan that places the emphasis of the harvesting pressure on younger age-classes (typically 20% of fawns, 45% of 1-3 year-olds, 20% of 4-9 year-olds, and 15% of 10+ year-olds are culled) (Ueckermann 1987). The result of this strategy is a population dominated by large trophy animals with a nearly 1:1 sex ratio. Similar results to these were demonstrated by the simulations of ≤3-point strategies on the Michigan elk (Tables 39 and 40). Both produced a bull population dominated by older, presumably more impressively antlered, bulls. However, overall bull populations and bull:cow ratios in the ≤3-point simulations were lower than those in the other bull harvesting strategies, suggesting that harvesting strategies of this type may require a lower total bull harvest to maintain desired bull numbers and/or bull:cow ratios.

The results of simulated harvesting of the Michigan elk population with various alternative bull strategies thus tend to complement the empirical information available in the literature. Limited bull and/or antler regulations designed to maximize the numbers of prime-aged bulls tend to be inconsistent in their results, especially those aimed at protecting younger age-classes. For such strategies to work, the overall population must be kept well below carrying capacity and competition between the sexes must be minimal (Clutton-Brock et al. 1979, Gore et al. 1985, Carpenter and Gill 1987, Ueckermann 1987). Total numbers of bulls must be kept low to prevent compensatory increases in other mortality factors from removing the desired gain in older age-class bulls. Controlling the cow segment of the population is particularly important in management for large numbers of prime-aged bulls, and is effectively accomplished through antlerless hunting permits (Raedeke and Taber 1985).

This is especially true if males and females tend to use different habitats, as with elk and red deer (Clutton-Brock et al. 1985, 1987; Carpenter and Gill 1987). Clutton-Brock et al. (1987) and Carpenter and Gill (1987) both noted that increasing numbers of hinds or cows resulted in poorer stag or bull survivorship, due principally to reduced plant biomass of favored forage species, as stags or bulls could no longer economically feed, and were forced into less favorable areas where survival was lower. One of the failures of regulations aimed at protecting yearling bulls, for example, is that increased survival of yearling bulls due to antler restrictions results in an effective increase in the number of cows (as yearling bulls are more closely associated with cows and calves than with adult bulls), thereby increasing adult mortality (Carpenter and Gill 1987). Other assumptions implicit in the success of limited bull and/or antler regulations include that the population is not limited by food and that no intra-specific competition exists for essential requirements between age-classes (Carpenter and Gill 1987).

The current MDNR harvesting strategy appears to be superior to the alternative bull harvesting strategies modeled for elk in Michigan for achieving MDNR bull elk management goals. By not restricting the age-classes of vulnerable bulls, it avoids many of the assumption pitfalls inherent in antler regulation strategies outlined above, as well as being simpler to implement and enforce. Additionally, it does not significantly alter the present herd bull age-distribution based on model projections (an unsurprising result, as the present age-distribution of bulls was formed by this harvesting strategy), as do the ≤3-point strategies (shift bull age-structure upward) and the older-bull only harvesting strategies (shift bull age-structure downward), thereby avoiding any potential ecological problems such as rutting season and behavior dysfunctions associated elsewhere with altered bull age-structures (Geist 1982, DeMarchi et al. 1987). Also, it is the harvesting system currently in place, and no justification would have to be developed to try and alter the present, apparently effective, system. Finally, according to model projections, it is the only strategy which accomplished the MDNR elk management goals verbatim, i.e. current elk herd sex- and age-structure is maintained.

The results of these harvest simulations suggest that the current harvesting strategy employed by the MDNR is superior to the commonly utilized alternatives for accomplishing MDNR elk population management goals. The quality of these results, however, is only as good as the population simulation model on which they were developed. If parameters used in modelling (censuses, recruitment rates, mortality rates, etc.) are severely under- or overestimated, model projections can be seriously biased (as detailed by Beyer 1987). Additionally, all model parameters are constants; thus, they do not change annually, with changing elk density, with varying winter severity, etc. This constancy of population parameters is biologically ugly, and undoubtedly biases model performance and projections, although to what extent is unknown. Insufficient information currently exists to account for ecological variation in the elk population model; such data typically requires a substantial period of time to collect and evaluate, while elk research in Michigan is limited to 2 or 3 year MS or PhD programs, periods of time insufficient to adequately address questions of ecological variation. Additionally, although very useful in reconstructing the past history of the elk population, knowledge of how ecological variation has affected elk population parameters in the past would likely be of limited utility in population projections such as attempted in this section. This is due, of course, to the inability to predict environmental and other changes in the future accurately. To accommodate this variation in population projections would require information not only on the effect of such variation on population parameters in the past, but on exactly how, when, and where this variation will be expressed in the future as well. Thus, although modelling with means and constant parameters is simplistic, the alternative is often a plethora of widely varying potential outcomes with no objective basis for supporting any particular one. Therefore, while the results of this modelling Chapter, and the performance of the general and EMU-specific elk population models, should be viewed with caution and skepticism, they none-the-less represent the best application of the current level of understanding of elk dynamics in Michigan. It must be emphasized that their proper role should be as one tool to help assess potential outcomes of population management practices; their results should **NEVER** be considered the paradigm that the real world of elk dynamics in Michigan is forced, kicking and screaming, onto.

SUMMARY AND CONCLUSIONS

The general elk population model developed in this Chapter appears to be superior to the 1987 elk population model in predicting elk dynamics in Michigan. It must be emphasized, however, that a model is a representation of reality, and not reality itself. Although potentially useful in predicting population responses in the Michigan herd, the new model, as well as the individual EMU-specific models, should be only 1 method of evaluating responses to population management strategies utilized. Model predictions should never be accepted unquestioningly.

Of the various alternative bull-harvesting strategies evaluated, the current MDNR strategy appears to be the best satisfier of MDNR elk management goals, i.e. maintaining current sex- and age-composition while limiting overall population size. Strategies aimed at harvesting older bulls exclusively result in the gradual decline of this segment; hence, viewer satisfaction would likely be negatively effected. In contrast, strategies placing heavy harvest pressure on young bulls result in a bull population dominated by older age-classes. These strategies would likely result in increased viewer satisfaction with the Michigan elk herd. However, hunter satisfaction would likely be decreased, as a sizeable proportion of bull hunters would be restricted to harvesting only spikes or 3-points, and not prime bulls. The current MDNR harvesting strategy has avoided the problems associated with these alternatives to date. However, by placing no restrictions on the age-classes of harvested bulls, the MDNR strategy runs the risk of developing the problems associated with the trophy-bull only strategies if Michigan hunters should become more selective in bulls taken, i.e. become more selective for larger racks. This change in hunter behavior would effectively change the current MDNR harvesting strategy into a prime-bull only strategy, complete with its associated problems. Since the potential negative impacts associated with the trophy-only strategies--including loss of the older bull segment, behavioral and reproductive dysfunctions such as reduced herd productivity due to dependence on younger bulls for breeding, and viewer dissatisfaction with viewing opportunities--appear to be more serious than those associated with spike or other younger bull strategies, care must be taken to insure that the current MDNR strategy does not evolve into a trophy-only strategy due solely to changes in hunter behavior. Thus, if the MDNR continues to utilize the present bull harvesting strategy, hunter selectivity must be carefully monitored annually to insure that MDNR population management goals are being accomplished, i.e. the prime-aged bull segment of the elk herd is being maintained.

Ecology and Management of Elk in Michigan

Elk ecology in Michigan appears to be driven by 3 overriding factors: (1) the very high bull:cow ratios seen in the elk herd, (2) the forested nature of the elk range, and (3) the current high level of exploitation. These 3 factors have combined to dictate the accommodations elk have made to their habitat in Michigan. The high bull:cow ratios currently, and historically, seen in the herd have resulted in high visibility of prime-aged bulls, and apparent high levels of competition among prime bulls. This, in turn, has dictated the nature of elk population management in Michigan. The primarily forested nature of the elk range apparently has resulted in the expression of behavioral traits more suggestive of red deer than other North American elk populations. Finally, the very high levels of exploitation, both hunting and viewing, are resulting in further adaptations in the elk, the most important of which are increased wariness and decreased visibility. Other factors have also undoubtedly contributed significantly to the ecology of elk in Michigan as well, and deserve further investigation. Two of the most important of these are the genetic history of the herd, and the disease relationships of the herd, particularly with the meningeal worm (_Parelaphostrongylus tenuis_) parasite.

Despite inadequacies in the predictive ability of the 1987 elk population model, the current MDNR harvesting strategy has proven very effective in accomplishing MDNR population management goals. The only principal weakness inherent in the current harvesting strategy lies in its sensitivity to hunter behavior. Should bull elk hunters become more selective for large-racked older bulls, the current harvesting strategy, if unaltered, would result in the gradual decline of older age-class bulls. Since these age-classes are the most favored for viewing, any significant decline would result in a decrease in the total recreational attributes of Michigan's elk herd. If analyses of future harvests indicate a trend of greater selectivity for older age-class bulls, the MDNR should consider allocating a percentage of the bull harvest for ≤3-point bulls only. This would place a higher proportion of the younger age-classes in the harvest, thereby effectively decreasing older bull vulnerability.

Morphologically and behaviorally, elk in Michigan exhibit numerous unique traits, many of which likely represent adaptations to the atypical nature of the Michigan elk range and the unusual elk population structure. Characteristics such as heavy body weights, labile social groups, and lack of yearling dispersal can all be related back to attributes of the Michigan elk range and/or population structure. The trophy antler potential of Michigan bull elk appears to be poor, especially in light of the body weights of Michigan bulls and range conditions which appear optimal for trophy production. However, very few bulls in the peak antler age-categories (age 9.5 and older) have been harvested in Michigan, suggesting poor bull survivorship into trophy age-classes. A thorough genetic investigation of Michigan's elk is needed to clarify the significance of the current morphological (and perhaps behavioral) features shown, especially in light of possible early hybridization with other *Cervus elaphus* subspecies. The unique morphological and behavioral characteristics of Michigan's elk may warrant designation, at least in terms of sportsperson-related issues such as Boone and Crockett or Pope and Young record categories, as a distinct population.

APPENDIX

Appendix: Modelling for Increased Herd Productivity

The effects of increasing herd productivity at a given population size by reducing the proportion of bulls were modeled to evaluate the overall impacts on bull age-structure and potential overall herd harvest. Herd population goals were maintained at 1000 or 1100 elk, respectively, but bull:cow ratios were reduced by harvest to ˜40-50:100. The impacts of the current MDNR harvesting strategy were evaluated and compared with two ≤3-point only harvesting strategies to determine which strategies better met the MDNR goal of maintaining large numbers of prime-aged bulls, under the altered herd structure.

METHODS

The new general elk population model (**Chapter 5**) was used for all projections. Projections were made from 1992-2010 using elk harvests (Table A-1) which (1) decreased bull:cow ratios gradually to the 40-50:100 range, then maintained them at this level, and (2) produced relatively stable populations of 1000 and 1100 elk, respectively. Three different bull harvesting strategies were evaluated:

Table A-1. Harvests utilized in long-term projections of Michigan elk herd with reduced bull:cow ratios.

	Population:1000				Population:1100			
YEAR	Calf	Bull	Cow	Total	Calf	Bull	Cow	Total
1992	14	93	153	260	14	93	153	260
1993	15	90	135	240	15	90	100	205
1994	15	90	120	225	15	90	90	195
1995	15	80	85	180	15	90	90	195
1996	15	80	85	180	15	95	95	205
1997	15	80	85	180	15	95	100	210
1998	15	80	85	180	15	95	100	210
1999	15	80	85	180	15	95	100	210
2000	15	85	90	190	15	100	105	220
2001	15	85	90	190	15	100	105	220
2002	15	85	90	190	15	100	105	220
2003	15	85	95	195	15	100	110	225
2004	15	85	95	195	15	100	110	225
2005	15	85	95	195	15	100	110	225
2006	15	85	95	195	15	100	110	225
2007	15	85	95	195	15	100	110	225
2008	15	85	95	195	15	100	110	225
2009	15	85	95	195	15	100	110	225
2010	15	85	95	195	15	100	110	225

(1) The current MDNR harvesting strategy, allowing a limited any-bull harvest (partitioned as described in **Chapter 5**).

(2) A 3-point or less strategy, in which 25% of the limited bull harvest is allocated to bull elk with 3 or fewer total antler points.

(3) A strategy identical to (2), except that 50% of the bull harvest is restricted to bull elk with 3 or fewer total antler points.

RESULTS AND DISCUSSION

For either population goal, the current MDNR bull harvesting strategy resulted in a significant decline in the prime bull age-classes (≥5X5, and ≥4.5 year-olds) (Tables A-2 and A-3). The MDNR strategy also drove down the maximum age of bulls in the simulated population from 11 to 7.

Either ≤3-point strategy drove both overall population size and bull:cow ratios down lower than the MDNR strategy (Tables A-2 and A-3). However, greater proportions of prime bulls were maintained with the ≤3-point strategies, especially in the older age-classes (4.5 years-old and older). The ≤3-point strategies also allowed bull survivorship into much older age-classes (11-13 year-olds) in the simulated populations than did the MDNR strategy.

Short term total harvests (1992-1997) were increased only 4% (1210 to 1265) and 7% (1180 to 1270) relative to models maintaining bull:cow ratios at ~60:100 for population goals of 1000 and 1100, respectively (**Chapter 5**). However, modelling indicated that the elk herd did not respond to the increased productivity potential provided by the greater

Table A-2. Comparisons of simulated alternative harvest strategies to achieve a population goal of ~1000 elk for the Michigan herd while decreasing bull:cow ratios to 40-50:100, 1992-2010.

Strategy	Year	Pop Size[1]	No. Bulls[2]	B:C:C[3]	%≥5X5[4]	%≥4.5[5]	Max. Age[6]
MDNR	1992	1098-1186	422	61.8:100:53.1	44.0	25.8	11
	1995	953-1027	358	62.7:100:52.0	41.9	21.8	10
	2000	941-1011	305	51.1:100:53.0	35.3	16.1	9
	2005	943-1013	291	47.6:100:52.7	30.6	11.3	7
	2010	949-1019	290	47.1:100:52.8	30.4	11.0	7
≤3 Pt 25%	1992	1098-1186	422	61.8:100:53.1	44.0	25.8	11
	1995	937-1018	348	61.2:100:52.0	53.4	42.0	12
	2000	899-974	269	44.9:100:53.0	41.6	30.1	12
	2005	900-972	248	40.9:100:52.7	36.0	24.6	11
	2010	909-981	252	40.9:100:52.8	36.6	25.0	11
≤3 Pt 50%	1992	1098-1186	422	61.8:100:53.1	44.0	25.8	11
	1995	935-1017	348	61.0:100:52.0	55.7	46.0	11
	2000	889-965	260	43.4:100:53.0	42.1	31.9	13
	2005	891-963	241	39.4:100:52.7	36.3	26.1	12
	2010	901-973	244	39.6:100:52.8	36.6	26.2	12

[1] Final (May of following year) and post-hunt (December) populations, respectively.
[2] Total number of bulls in population in November.
[3] November bull:cow:calf ratio.
[4] Percent of November bulls ≥5X5.
[5] Percent of November bulls age 4.5 or older.
[6] Maximum age of bulls in November population.

Table A-3. Comparisons of simulated alternative harvest strategies to achieve a population goal of ~1100 elk for the Michigan herd while decreasing bull:cow ratio to 40-50:100, 1992-2010.

Strategy	Year	Pop Size[1]	No. Bulls[2]	B:C:C[3]	%≥5X5[4]	%≥4.5[5]	Max. Age[6]
MDNR	1992	1098-1186	422	61.8:100:53.1	44.0	25.8	11
	1995	1061-1142	368	56.8:100:53.2	40.7	21.2	10
	2000	1065-1143	332	48.3:100:52.8	32.0	12.7	8
	2005	1068-1146	321	45.8:100:52.6	27.8	9.7	7
	2010	1071-1150	321	45.5:100:52.6	28.5	9.3	7
≤3 Pt 25%	1992	1098-1186	422	61.8:100:53.1	44.0	25.8	11
	1995	1045-1134	358	55.6:100:53.2	51.9	40.8	11
	2000	1021-1104	293	42.7:100:52.8	39.0	27.6	12
	2005	1022-1103	280	39.7:100:52.6	35.5	24.3	12
	2010	1028-1108	280	39.7:100:52.6	35.1	24.0	12
≤3 Pt 50%	1992	1098-1186	422	61.8:100:53.1	44.0	25.8	11
	1995	1043-1133	358	55.4:100:53.2	54.1	44.7	11
	2000	1010-1095	285	41.3:100:52.8	39.7	29.8	13
	2005	1012-1093	268	38.3:100:52.6	34.9	25.0	12
	2010	1019-1100	272	38.5:100:52.6	35.4	25.4	12

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[1] Final (May of following year) and post-hunt (December) populations, respectively.
[2] Total number of bulls in population in November.
[3] November bull:cow:calf ratio.
[4] Percent of November bulls ≥5X5.
[5] Percent of November bulls age 4.5 or older.
[6] Maximum age of bulls in November population.

numbers of cow elk until ~10 years after the 1992 season. At this point, bull:cow ratios reached the desired ~40-50:100 level and stabilized. Sustainable harvests from this point on were then approximately 18% (195 vs. 160) and 23% (225 vs. 175) greater than sustainable harvests from the higher bull:cow ratio populations.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Modelling projections suggest that the current MDNR harvesting strategy is prone to over-exploitation of the older bull age-classes as bull:cow ratios drop below the current ~60:100 level. The loss of bulls ≥8.5 years-old, and the low proportion of prime bulls (≥5X5) maintained in the simulated populations, would likely result in unsatisfactory viewing opportunities, as well as hunter dissatisfaction at the low numbers of branch-antlered bulls present in the population. Increased hunting opportunities, however, could potentially result in higher overall satisfaction with the consumptive exploitation uses of the herd.

The ≤3-point bull harvesting strategies modelled work on the theory that greatly reduced hunting vulnerability once bulls live past age 1.5 will result in increased survivorship into older age-classes. Simulated populations under either ≤3-point strategy modelled showed just these results; the proportion of 5X5 or larger bulls declined only slightly relative to current herd levels, while the proportion of bulls 4.5 years-old and older remained stable or increased. Thus, although fewer bulls overall would be present in the Michigan elk population (~40 per 100 cows), a similar percentage of these would be in the older, prime-viewing classes as with the current herd. This would likely result in less viewer and/or trophy hunter dissatisfaction.

Potential sustainable yields from the Michigan elk herd can be increased ~20% without altering overall herd population size by decreasing the proportion of bulls present in the herd. Under this management option, however, the current MDNR harvesting strategy would fail to meet all management goals, i.e. maintenance of a large number of older age-class bulls. Harvesting strategies restricting a percentage of bull permits to ≤3-point bulls only, however, would allow the MDNR to maintain the older bull age-classes under this management option, thereby minimally impacting the viewing opportunities available with the altered herd sex-structure. The impacts of increased harvesting on elk wariness, however, would likely result in decreased bull visibility above and beyond that produced by simply decreasing overall bull numbers. Potential management problems associated with increased elk wariness and decreased visibility are detailed in **Chapter 1.**

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