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Progress Report

MODELING ELK & DEER POPULATION DYNAMICS IN IDAHO

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PROGRESS REPORT
STATEWIDE WILDLIFE RESEARCH

STATE: Idaho
PROJECT: W-160-R-32
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Dynamics in Idaho

MODELING ELK AND DEER POPULATION DYNAMICS IN IDAHO

Abstract

Rocky Mountain elk and deer populations continue to exhibit large-scale changes in Idaho and throughout the western states. The preliminary results presented here are part of a larger study initiated to study the effects of competition and other factors on the dynamics of elk, mule deer, and white-tailed deer populations in order to predict population responses to various inter- and intra-specific factors. Here, we present estimates of mule deer and elk equilibrium densities and results from a model that predicts snow depth intended for use to estimate inter-annual changes in winter severity and amounts of winter range for mule deer and elk. We also demonstrate an application of satellite imagery to index forage quality in mule deer and elk summer ranges. Lastly, we show relative effects of competition and habitat condition on mule deer and elk in selected areas of Idaho.

Introduction

Rocky Mountain elk (*Cervus elaphus nelsoni*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*Odocoileus virginianus)* populations extensively overlap throughout western North America. In Idaho and throughout the western states, their populations are experiencing large-scale changes (Unsworth et al. 1995), and numerous intrinsic and extrinsic factors may influence such population fluctuations. Combined, these factors may have confounding effects on the fluctuations of deer and elk populations, which complicate our ability to predict the effects of management decisions. Combining these spatially and temporally variable factors in a predictive model that accounts for relative and interactive effects, including intra- and inter-specific competition, may provide accurate predictions of management decisions like harvest limits or predator control. Such models will assist wildlife managers in maintaining productive deer and elk herds at the regional level.

For analyses of population dynamics that include competition, it is useful to describe the range of population sizes of 2 species that results in one maintaining a zero population growth ($r = 0$) or equilibrium density (K) (Williams et al. 2002). “Ecological” carrying capacity has been defined as the size of a population when it is at equilibrium with its food supply (Caughley 1979), and can be derived from empirical relationships between population growth rate and population size (Houston 1982). Boyce (1990) and Boyce and Merrill (1991) relaxed the equilibrium assumption for elk by effectively making K a function of variable weather. Merrill and Boyce (1991) took this same approach, but also included variation in summer forage quality. We view ecological carrying capacity from a more complex "system-level" approach similar to that described by Coughenour and Singer (1996), considering carrying capacity as the size of the population when it is in equilibrium with many intrinsic and extrinsic factors acting simultaneously on the population, and apply this view throughout our research by considering effects of numerous factors and interactions.

Our overall objective is to estimate competitive effects among these 3 species, examine the influence of intrinsic and extrinsic factors on the dynamics of their populations while accounting for competition, and to use this information to predict population responses to changes in these factors across their ranges in Idaho. This led to the development of 4 specific objectives:

1. Estimate the equilibrium density (carrying capacity) for white-tailed deer, mule deer, and elk separately in selected Idaho Department of Fish and Game (IDFG) delineated Game Management Units (GMU).

2. Estimate annual changes in habitat condition, weather severity, predation pressure, and harvest in each GMU.

3. Develop statistical models to identify and estimate the relative and interactive influences of each factor and on growth rates of elk and deer populations.

4. Develop a predictive multi-cervid model that simultaneously predicts the population size of each species in response to integrated changes in these factors, including management decisions such as harvest limits or predator control.

This report is divided into 3 topics that address recent progress on aspects of Objectives 1, 2, and 3. Further detailed results and those for Objective 4 will be addressed in future reports.

Study Area

These preliminary analyses were performed on data collected in IDFG's GMUs 11, 21, and 36B, located in central Idaho (Figure 1). These were chosen because they contain relatively continuous strings of time series response and predictor datasets required for this study and occur in 2 different ecoregions (Columbia Plateau and Northern Rockies) (Omernik and Gallant 1986) in the larger study area. They support forest, shrub, and grassland vegetation, livestock grazing, timber harvest, agriculture, and recreation.

Methods

Equilibrium Densities

Our response variables were instantaneous rates of annual population growth

$$r_t = \mathrm{Ln}(N_t/N_{t-1}),$$

computed from winter densities, were N_t is the winter density at time t and N_{t-1} is winter density the winter prior to time t. Winter densities were derived from estimates of annual population sizes collected during midwinter (Jan-Feb) aerial sightability surveys between 1992 and 2002 (IDFG 2002, IDFG 2003), which are unbiased estimates of actual population size and composition (Samuel et al. 1987). We used area (ha) of winter range in each GMU to standardize population size as density per ha of winter range. This was intended to avoid biased low estimates that could occur if we used the area of GMUs. This is because GMU boundaries encompass summer, winter, transitional, and unsuitable habitats, and elk and deer are generally restricted to winter ranges during sightability counts. Furthermore, GMU boundaries may not correspond to population demography or spatial patterns exhibited by these large ungulates (Svancara et al. 2002).

Winter range areas for mule deer and elk were digitized static boundaries that represented "part of the overall range where 90 percent of the individuals are located during the average 5 winters out of 10 from the first heavy snowfall to spring green-up, or during a site-specific period of winter" (unpublished data, Dr. Todd Black at Utah State University, Logan; Rocky Mountain Elk Foundation 1999). These winter ranges were digitized from 1:250,000 scale relief maps and are, therefore, appropriate for analyzing population-level responses across large spatial extents, such as those in this study.

Relationships between population growth, competition, and other independent predictors X_is, were evaluated using the Ricker model (Ricker 1954, May 1974) of the general form

$$r_t = r_{\max} + bN_{t-1}$$

Where $r_{\max}$ is the maximum rate of population growth that is possible at time t, b is the intra-specific competition coefficient, N_{t-1} is the population size associated with intra-specific competition at time t. When population growth is zero ($r = 0$), the corresponding density represents the equilibrium density (K) (Williams et al. 2002).

Annual Variability in Snow Depth and Summer Forage

Snow depth is being modeled across Idaho at a 1-km^2 resolution over the past 24 years, starting in 1980. We intend to use this model to estimate the extent and quality of winter ranges for elk and deer each year during this period. The following methods pertain to our initial modeling of relationships between available weather data and snow depth, which is currently being used to build a statewide database of snow depth.

We used daily measures of precipitation (cm), maximum temperature (°C), and minimum temperature (°C) from the DAYMET U.S. Data Center (http://www.daymet.org/) (Thornton et al. 1997) and monthly summaries of snowfall and snow depth from the Western U.S. Climate Historical Summaries (http://www.wrcc.dri.edu/summary/climsmid.html), recorded at 16 randomly selected Snotel sites across Idaho. We computed 5 measures of monthly accumulations of daily precipitation, based on different temperatures that were anticipated to coincide with snowfall (Table 1). Two measures of snowfall were used to predict snow depth (Table 2).

We divided Idaho into 2 regions along the major separation line between the Northern Rockies and Snake River Plateau ecological regions (Figure 1) because preliminary analyses suggested spatial autocorrelation along a north-south gradient. Estimation of snow depth followed a 3-step process and was performed separately for each region. First, we used simple linear regression models to identify the predictor(s) that best explained variation in snowfall and used Akaike's Information Criterion (AIC) (Akaike 1973) to compare models and selecting the 'best' model for predicting snowfall. Second, we used simple linear regression models to compare use of average versus accumulated average snowfall to predict snow depth and used AIC to compare models. Lastly, we used the best model in step 2 to predict snow depth from snowfall predicted in step 1 by applying the model coefficients to the predicted snowfall.

We heuristically evaluated the suitability of our best snow depth model in region 1 with DAYMET and Western U.S. Climate Historical Summaries data from a Snotel site (Elk River Ranger Station) not used in model development.

Summer forage was evaluated using the normalized difference vegetation index (NDVI) (Lillesand and Kiefer 2000), a satellite-derived vegetation index at a 30x30 m resolution. The data we used were annual NDVI values that were from Landsat 4 satellite imagery flown in July each year, developed and corrected for spatial error and clouds by Beck and Gessler (2004), and spanned 15 years, beginning in 1989. The NDVI is one of the most popular and simplistic spectral vegetation indices used for detecting change (Wilson and Sader 2002, Sader et al. 2003). It is a ratio of near-infrared and infrared wavelengths and is preferred for large-scale vegetation monitoring because it helps compensate for changing illumination conditions, surface slope, and aspect (Lillesand and Kiefer 2000). It may, therefore, be suitable for assessing the quality of rapidly photosynthesizing grasses and broadleaf shrubs in mule deer and elk summer ranges.

We measured and graphed the mean and standard deviation of the NDVI in each summer range for mule deer (unpublished data, Dr. Todd Black at Utah State University, Logan) and elk (Rocky Mountain Elk Foundation 1999) to heuristically assess the efficacy of using NDVI to estimate change in summer forage.

Effects of Density Dependence, Inter-specific Competition, Winter Snow, Summer Forage, and Harvest on Population Growth

We used winter densities, winter snow accumulation, and summer forage (NDVI indices) described in previous sections of this report and harvest metrics and snow accumulation from IDFG (2004) as predictors of r (Table 3). We also used harvest per day for mule deer and harvested males per hunter for elk (IDFG 2004). Winter densities were used as measures of intra- and inter-specific competition. We predicted r_t from winter densities at t-1, winter snow accumulation at t-1, summer forage during summer in the middle of population growth periods, and harvest during fall and early winter of the growth period.

Relationships between population growth, competition, and other independent predictors X_is, were evaluated using a modified version of the Ricker model (Ricker 1954, May 1974) that Garton et al. (2001) used of the general form

$$r_{(1t)} = r_{\max} + b_1 N_{(1t)} + b_i X_i$$

where $r_{\max}$ is the maximum rate of population growth that is possible for species one at time t, b_1 is the intra-specific competition coefficient, b_2 is the inter-specific competition coefficient, b_i is the regression coefficient for each additional predictor variable (e.g., inter-specific competition or extrinsic variable), $N_{(1t)}$ is the population size associated with intra-specific competition at time t, and X_i is the variable corresponding to b_i (e.g., population size of the inter-specific competitor at time t).

Our baseline model contained density of the species corresponding to the population growth rate because density dependence was assumed to be present. We added the other predictors to this base model one at a time and compared these additive models with AIC (Akaike 1973).

Analyses and models for each GMU were currently based on the availability of data because we are still in the process of gathering and computing predictors in GMUs. Thus, preliminary analyses for each GMU in this report do not contain a complete set of predictors.

Results and Discussion

Equilibrium Densities

The equilibrium density of mule deer in GMU 11 from 1992-2002 was 1.25 deer/km^2 of winter range (Figure 2 [A]). During that period, the population maintained growth rates between ¯0.42 and 0.42 and densities from 0.68 to 1.62 deer/km^2 of winter range from 1992 to 2002.

The equilibrium density of mule deer in GMU 21 from 1993-2003 was 6.4 deer/km^2 of winter range (Figure 2 [B]). Growth rates ranged from ¯0.85-0.84, and densities from 2.66-10.01 deer/km^2 of winter range between 1993 and 2002.

The equilibrium density of mule deer in GMU 36B from 1994-2002 was 3.64 deer/km^2 of winter range (Figure 2 [C]). Growth rates ranged from 0.47-0.46, and densities from 2.61-5.47 deer/km^2 of winter range between 1993 and 2002.

Elk had a lower equilibrium density in GMU 36B (0.59 elk/km^2 of winter range between 1989-2000 [Figure 3]) than mule deer. Their growth rates ranged from ¯0.073-0.31, and their densities from 0.13-0.62 elk/km^2 of winter range during that period.

The dynamics of mule deer populations in GMUs 21 and 36B appear to have been similar compared to GMU 11. One reason for this may be due to differing environments (GMU 11 is located in the Columbia Plateau ecoregion, whereas 21 and 36B are in the Northern Rockies [Figure 1]). While numerous factors need to be examined to better understand the differences reported here, we also recognize that our sample size for GMU 11 was small compared to GMUs 21 and 36B. We intend on improving sample sizes by lengthening data strings (see IDFG 2004), and employing these analyses in many more GMUs.

Annual Variability in Snow Depth and Summer Forage

Monthly snowfall in region 1 was predicted best by accumulation of precipitation from days when the daily average temperature was <0°C (F = 247.5, d.f. = 559, adj R^2 = 0.31 [Table 4]),

Snowfall = 13.37 + 5.50 * daily precipitation when daily average temperature is <0°C.

This model appeared to adequately predict observed snowfall in several Snotel sites intended for validation (Figure 4). It predicted slightly lower peak levels of snowfall, but it did predict the variability in amount of snowfall through time, and peaks were typically greater than the maximum cutoff depth that is suitable for movement by elk and mule deer.

Snowfall in region 2 was predicted equally well from precipitation accumulated from days when the maximum temperature was <4°C and when daily average temperature was <0°C (Table 4). We chose the latter model to maintain consistency with the predictor that was best for region 1, but used the new model coefficients to predict snowfall (F = 55.01, d.f. = 574, adj R^2 = 0.09 [Table 4]),

Snowfall = 6.64 + 2.64 * daily precipitation when daily average temperature is <0°C).

Snow depth was predicted best from the accumulated average snowfall (F = 217.3, d.f. = 46, adj R^2 = 0.82 [Table 5]),

Snow depth = $^{-}5.12$ + 0.35 * accumulated average snowfall.

This model implies that snow depth is negligible until average snowfall accumulates to >14.63 cm, and that on average, snow depth increases by 3.5 cm for every 10 cm of snowfall (Figure 5).

The mean NDVI in the summer range of GMU 36B was consistently lower than that of GMU 21, suggesting that GMU 21 supported higher quality summer forage in July for mule deer and elk, but annual variation tracked closely between the 2 GMUs (Figure 6). This same pattern was present in the standard deviation of NDVI (Figure 7).

The lower mean NDVI in GMU 36B may be due to different elevations in the 2 summer ranges, which can influence development and photosynthesis of plants, and thus, NDVI in July when the satellite imagery were obtained. The matching dynamics in annual variation may be due to their both being in Northern Rockies ecoregion (Figure 1), and also suggest that summer forage in both GMUs experience similar environmental conditions, such as precipitation.

The mean NDVI in the summer range of GMU 11 generally fell within the range between GMUs 21 and 36B but widely varied (Figure 6), indicating relatively high variability in the quality of summer forage from one year to the next in GMU 11. This coincided with greater variability in NDVI in the summer range of GMU 11 compared that of GMUs 21 and 36B during the same year. The greater variability of summer forage among years, as well as within summer range in

GMU 11 is likely due to more severe summer temperatures and environmental conditions in the Columbia Plateau ecoregion compared to the Northern Rockies. It may also be attributed to the high amount of human development (e.g., agriculture) in GMU 11 (Figure 8 [A]) compared to GMUs 21 and 36B (Figure 8 [B and C]), and annual variability in NDVI in these areas may be more severe than in natural vegetation.

Effects of Density Dependence, Inter-specific Competition, Winter Snow, Summer Forage, and Harvest on Population Growth

The population of mule deer that winter in GMU 11 is effected by several intrinsic and extrinsic factors (Table 6). The models we constructed that hypothesized intra-specific competition, and 3 extrinsic factors effecting population growth, were all competing (ΔAIC<2.0 [Burnham and Anderson 1998]). Therefore, it is plausible that intra-specific competition, summer forage quality, harvest per day, and inter-specific competition by elk have singular and additive effects on mule deer populations in GMU 11 (Table 6). However, degrees of freedom were low, preventing us from constructing models with increasing complexity to evaluate relative effects of each of these factors. Nonetheless, the complexity of factors affecting this population coincides with the highly variable environments in the Columbia Plateau ecoregion.

Mule deer in GMU 21 are affected by intra-specific competition and winter snow accumulation (Table 6), with no evidence that harvest per day or summer forage quality affected them (ΔAIC > 12.6). In GMU 36B, the mule deer population was affected by intra-specific competition and summer forage quality (Table 6), with a lack of evidence for snow accumulation, harvest per day, or inter-specific competition by elk (ΔAIC > 3.9). Although the model hypothesizing intra-specific competition and snow accumulation had a ΔAIC = 3.9, it is plausible that snow accumulation may be determined to also be important to this population with further analyses that involve more complex models and larger datasets.

Elk in GMU 36B were affected by intra-specific competition and summer forage quality (Table 6) with no evidence that intra-specific competition alone was important (ΔAIC > 6.9). Data were lacking for this analysis, resulting in the construction of only these 2 models. We hypothesize that additional factors may affect elk in this GMU, and in others, and are currently collecting additional predictor datasets and increasing sample sizes.

Management Implications

A statistical model that predicts the effects of intrinsic and extrinsic factors on population growth rates of elk and deer will give wildlife managers the ability to predict the consequences of management decisions such as habitat alterations, harvest seasons, and predator control, while considering the effects of competition. Using this model, managers will have the capability of predicting the outcome of various management scenarios within a given GMU prior to implementing a management activity. Such scientific information will foster a better understanding of game management and aid in the effective management and conservation of elk, deer, and wolves.

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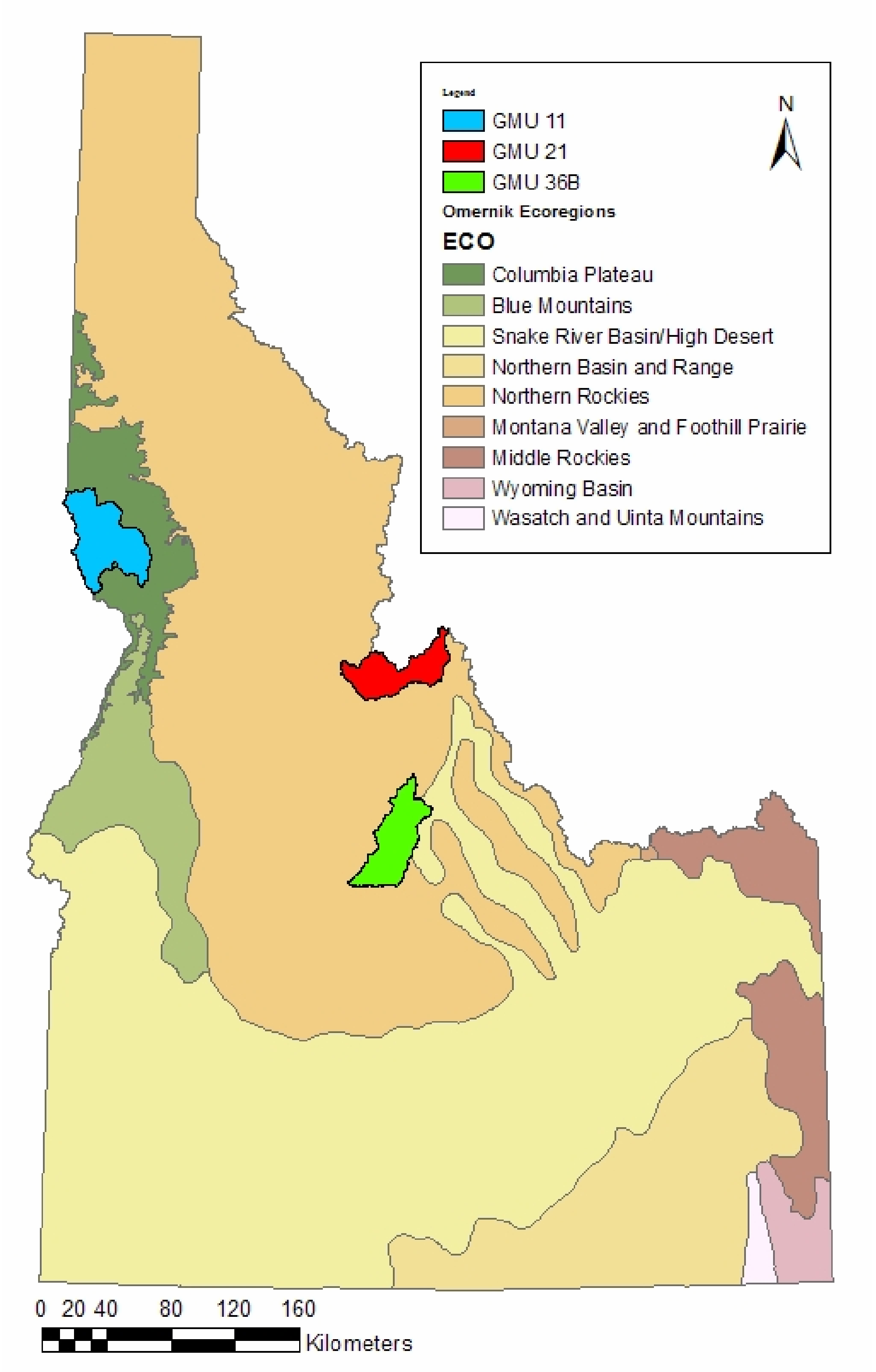

Figure 1. Study areas and ecoregions.

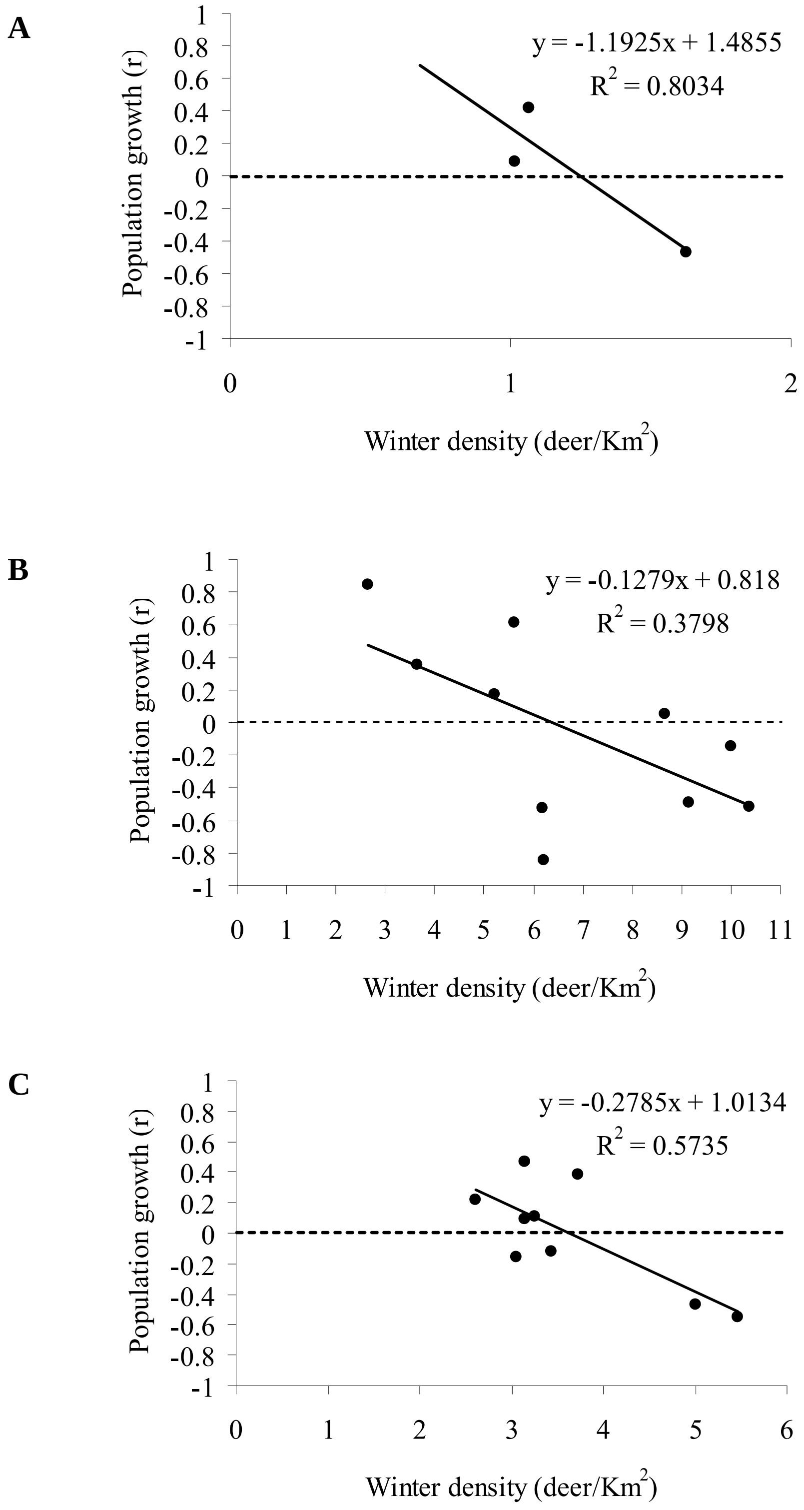

Figure 2. Equilibrium densities of mule deer in GMUs (A) 11, (B) 21, and (C) 36B.

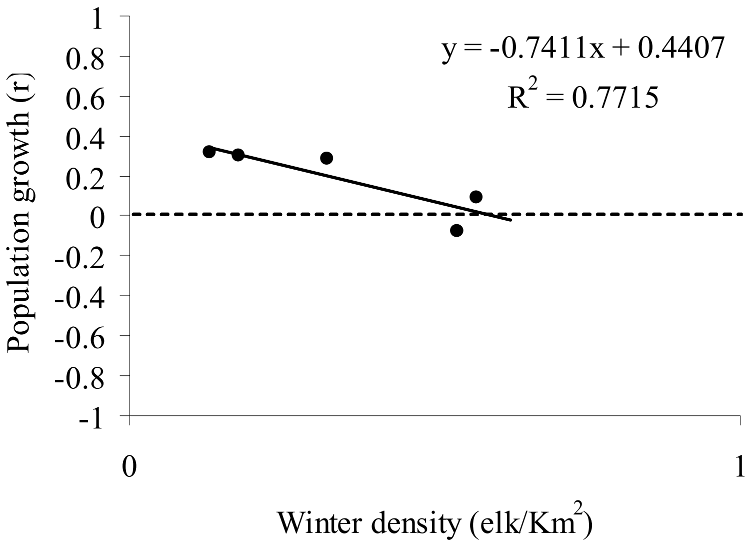

Figure 3. Equilibrium density of elk GMU 36B.

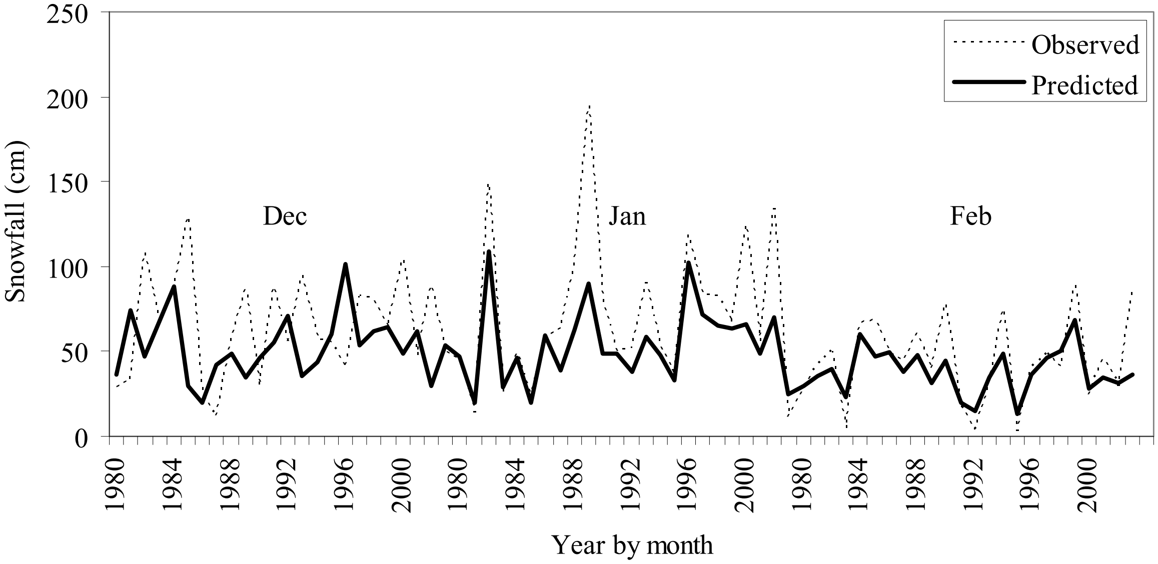

Figure 4. Predicted and observed snowfall in the Region 1, Elk River Ranger Station Snotel site, 1980-2003.

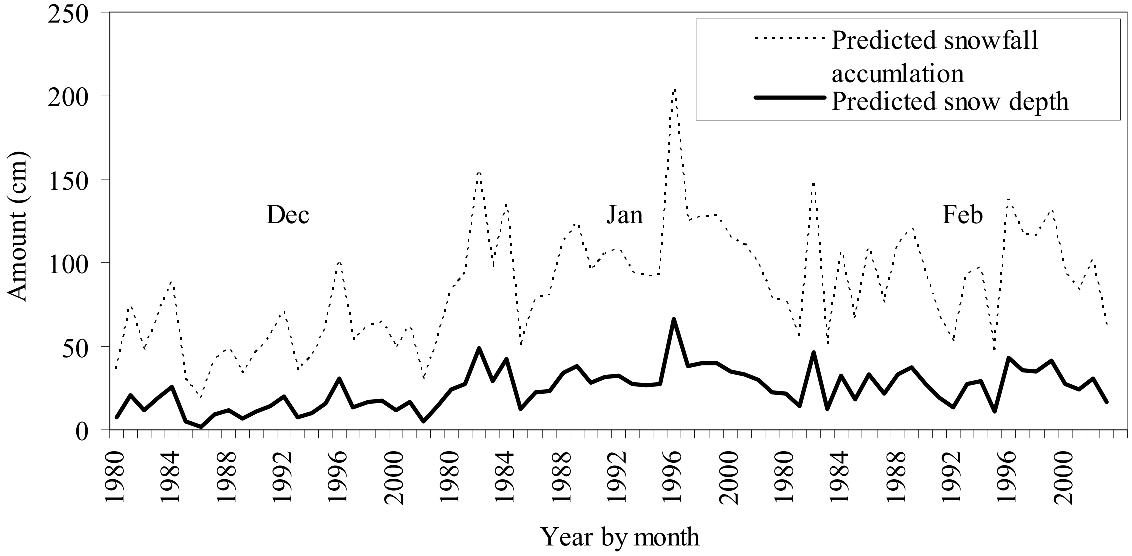

Figure 5. Predicted snowfall and snow depth in the Region 1, Elk River Ranger Station Snotel site, 1980-2003.

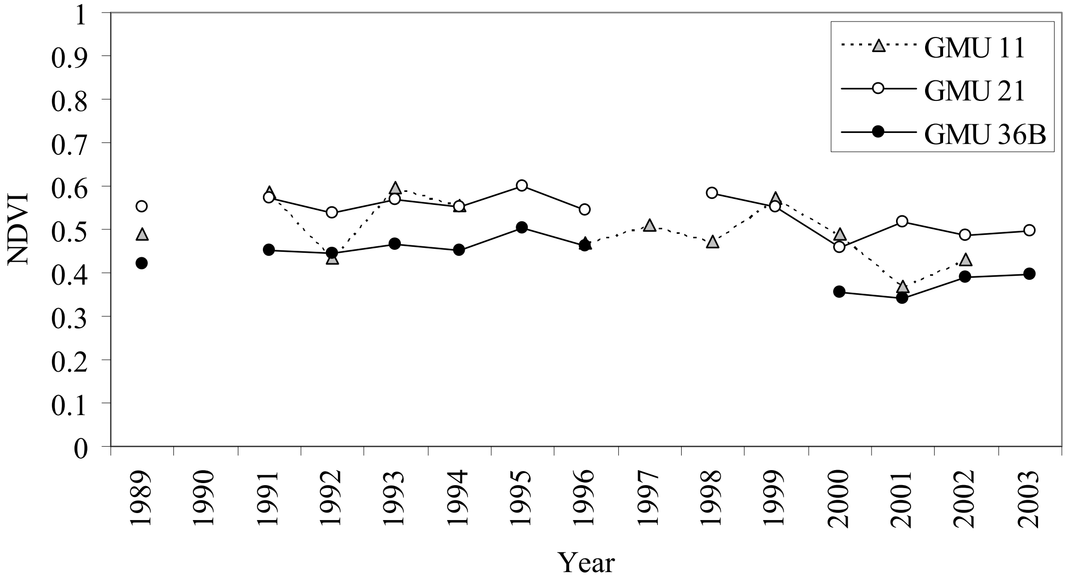

Figure 6. Mean NDVI in mule deer summer ranges in GMUs 11, 21, and 36B.

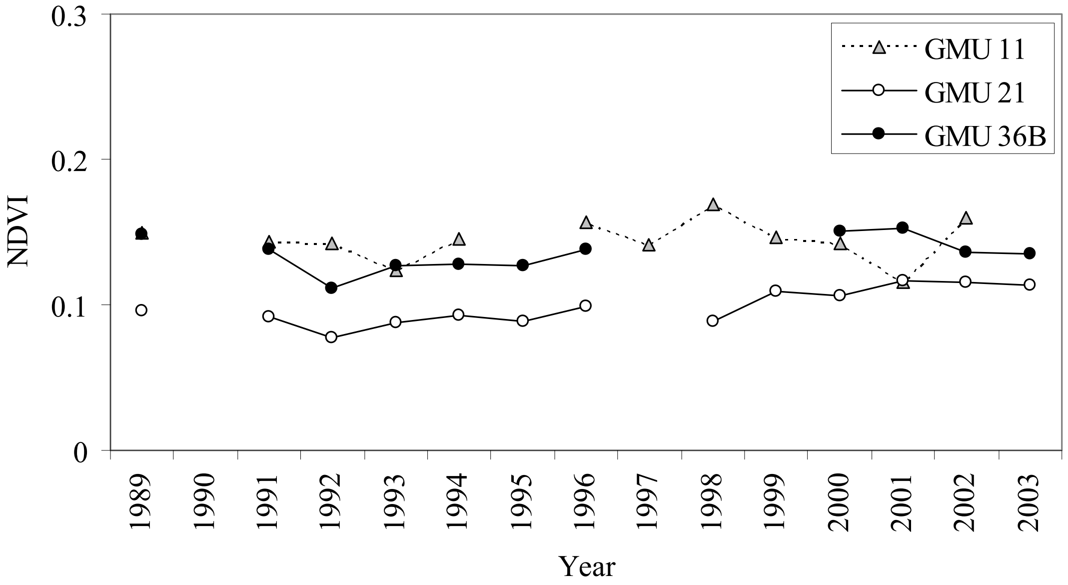

Figure 7. Standard deviation of NDVI in mule deer summer ranges in GMUs 11, 21, and 36B.

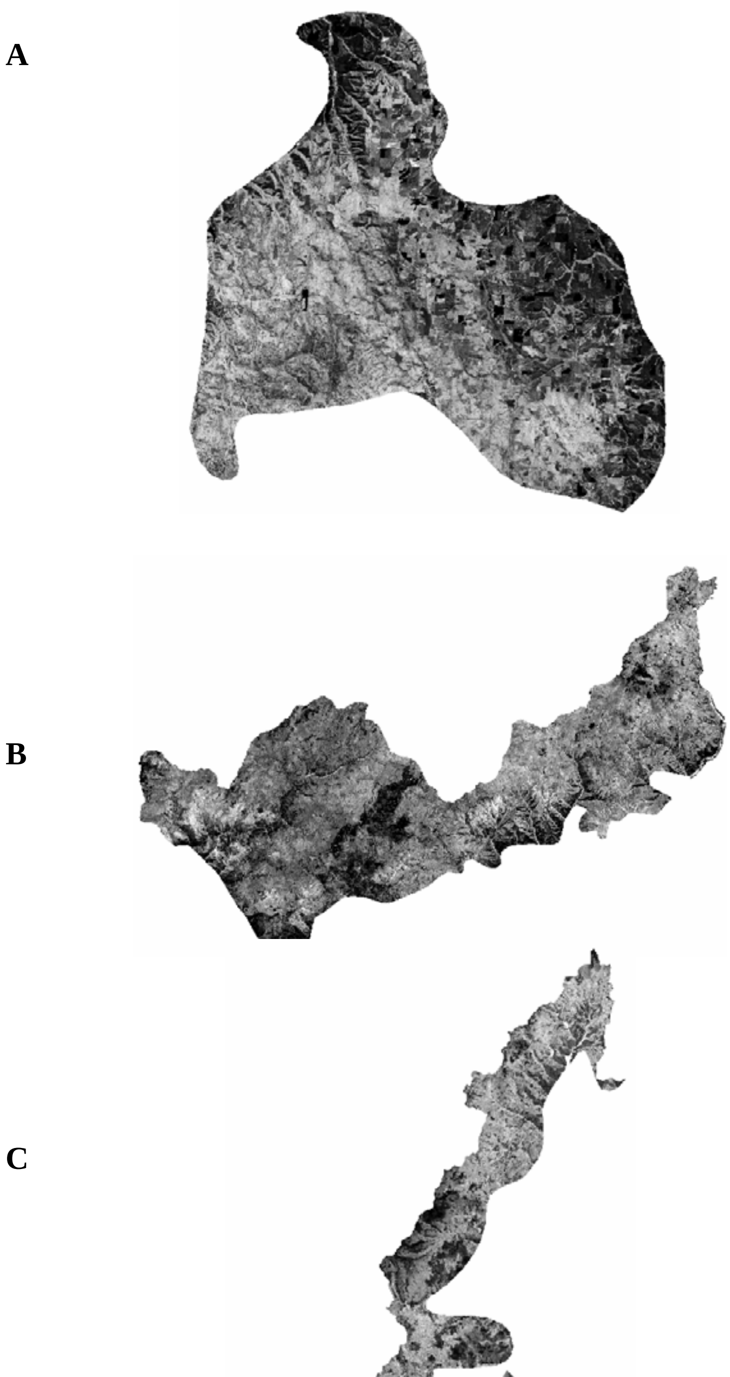

Figure 8. NDVI-values in mule deer summer ranges in GMUs (A) 11, (B) 21, (C) 36B, 1989.

Table 1. Variables used to construct linear regression models for predicting snowfall from daily DAYMET precipitation and temperature data.

Variable	Type	Description[a]
Snowfall	Continuous (response)	Monthly total snowfall (cm)[a]
Precipitation	Continuous (predictor)	Monthly estimate from accumulated daily precipitation[b]
Precipitation when maximum temperature <4°C	Continuous (predictor)	Monthly estimate from accumulated daily precipitation when maximum temperature is <4°C[b]
Precipitation when minimum temperature <0°C	Continuous (predictor)	Monthly estimate from accumulated daily precipitation when minimum temperature is <0°C[b]
Precipitation when average temperature <0°C	Continuous (predictor)	Monthly estimate from accumulated daily precipitation when average temperature [(maximum temp/minimum temp)/2] is <0°C[b]
Precipitation when average temperature <4°C	Continuous (predictor)	Monthly estimate from accumulated daily precipitation when average temperature [(maximum temp/minimum temp)/2] is <4°C[b]

[a] From Western U.S. Climate Historical Summaries (http://www.wrcc.dri.edu/summary/climsmid.html).

[b] From DAYMET U.S. Data Center (http://www.daymet.org/).

Table 2. Variables used to construct linear regression models for predicting snow depth from daily DAYMET precipitation and temperature data.

Variable	Type	Description[a]
Snow depth	Continuous (response)	Average monthly snow depth (cm)[b].
Average snowfall	Continuous (predictor)	Average monthly total snowfall (cm)[b]. Assumes complete melt at end of each month.
Accumulated average snowfall	Continuous (predictor)	Accumulated (December snowfall is added to January, and January's to February) average monthly snowfall (cm)[b].

[a] From Western U.S. Climate Historical Summaries (http://www.wrcc.dri.edu/summary/climsmid.html).

[b] Averaged across years (1980-2003).

Table 3. Variables used to construct linear regression models for predicting their singular and additive effects on population growth rates (*r*).

Variable	Type	Description[a]
Instantaneous population growth rate (*r*)	Continuous (response)	$r_t = \mathrm{Ln}(N_t/N_{t-1})$; computed from winter densities.
Winter density	Continuous (predictor)	Estimated annual population size computed from midwinter aerial surveys divided by the area (ha) of winter range[b].
Harvest per hunter	Continuous (predictor)	Total male and female harvest during general harvest season divided by number of hunting licenses (IDFG 2004).
Harvested males per hunter	Continuous (predictor)	Total male harvest during general harvest season divided by number of hunting licenses (IDFG 2004).
Summer forage quality	Continuous (predictor)	Mean NDVI computed in summer ranges; positive relationship between NDVI and forage quality.
Snow accumulation	Continuous (predictor)	Average annual accumulation of daily snowfall (cm) across 30 random points.

[a] All variables were measured for each GMU.

[b] Mule deer (unpublished data, Dr. Todd Black at Utah State University, Logan); elk (Rocky Mountain Elk Foundation 1999).

Table 4. Linear regression models developed to predict monthly snowfall from daily DAYMET precipitation and temperature data in Idaho.

Model	d.f.	ΔAIC
North and Central Idaho (Region 1)		
Snowfall = Precipitation when average temperature <0°C	559	0.00
Snowfall = Precipitation when maximum temperature <4°C	559	41.19
Snowfall = Precipitation when minimum temperature <0°C	559	75.13
Snowfall = Precipitation when average temperature <4°C	559	108.20
Snowfall = Precipitation	559	131.21
South Idaho (Region 2)		
Snowfall = Precipitation when maximum temperature <4°C	574	0.00
Snowfall = Precipitation when average temperature <0°C	574	1.22
Snowfall = Precipitation when minimum temperature <0°C	574	31.94
Snowfall = Precipitation when average temperature <4°C	574	33.76
Snowfall = Precipitation	574	51.28

Table 5. Linear regression models developed to predict monthly snow depth from snowfall in Idaho.

Model	d.f.	ΔAIC
Snow depth = Accumulated average snowfall	46	0.00
Snow depth = Average snowfall	46	35.19

Table 6. Linear regression models developed to predict singular and additive effects of density dependence, inter-specific competition, winter snow, summer forage, and harvest on population growth on population growth rates (*r*).

Model	d.f.	ΔAIC
Mule deer in GMU 11		
r = Intra-specific competition	2	0.00
r = Intra-specific competition + summer forage quality	1	1.17
r = Intra-specific competition + harvest per day	1	1.23
r = Intra-specific competition + inter-specific competition by elk	1	1.52
Mule deer in GMU 21		
r = Intra-specific competition + snow accumulation	1	0
r = Intra-specific competition + harvest per day	3	12.63
r = Intra-specific competition	8	19.30
r = Intra-specific competition + summer forage quality	6	20.99
Mule deer in GMU 36B		
r = Intra-specific competition + summer forage quality	3	0
r = Intra-specific competition + snow accumulation	2	3.90
r = Intra-specific competition + harvest per day	3	5.06
r = Intra-specific competition	7	8.17
r = Intra-specific competition + inter-specific competition by elk	4	8.81
Elk in GMU 36B		
r = Intra-specific competition + summer forage quality	3	0
r = Intra-specific competition	2	6.97

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IDAHO DEPARTMENT OF FISH AND GAME

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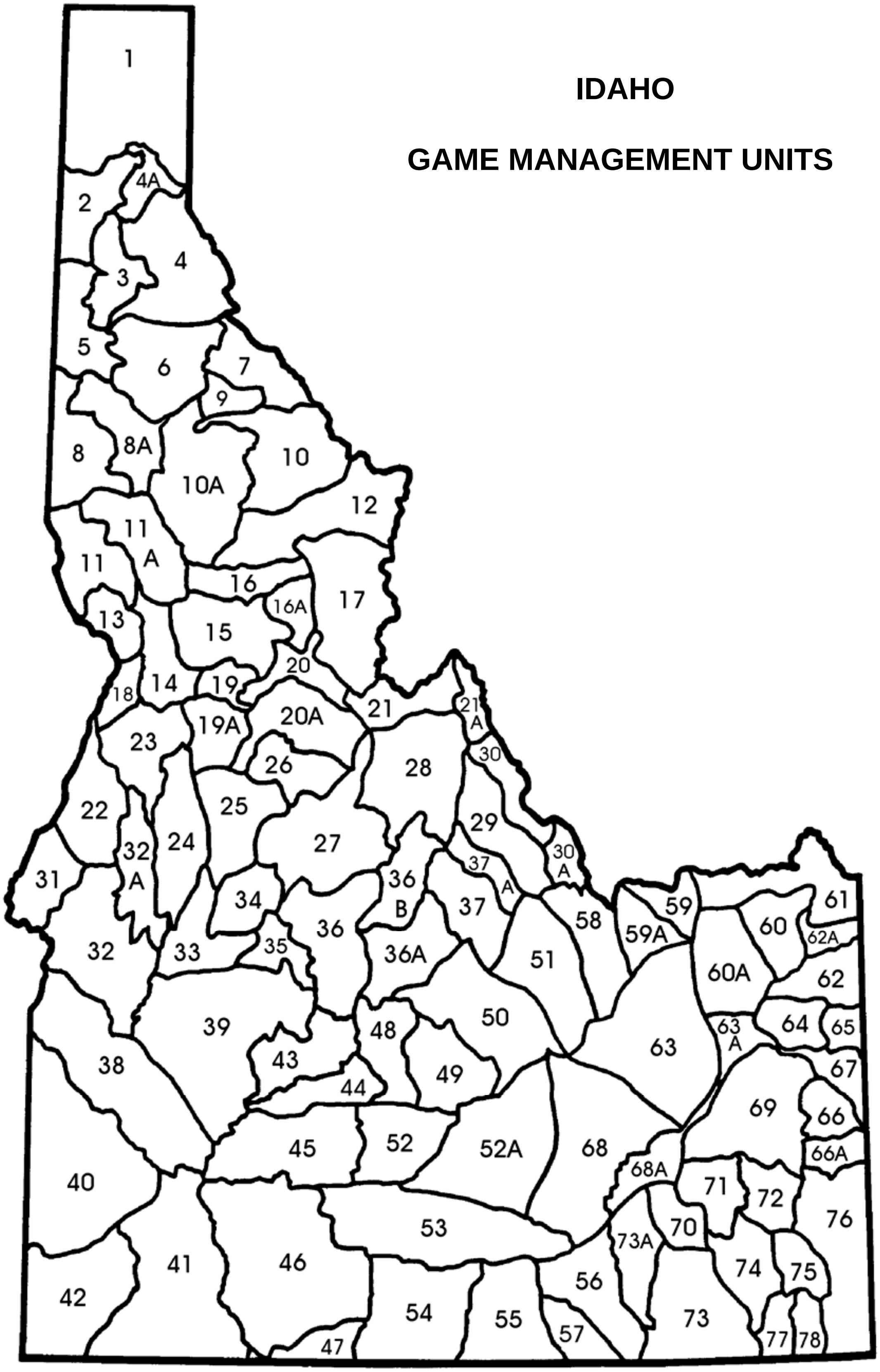
IDAHO

GAME MANAGEMENT UNITS



FEDERAL AID IN WILDLIFE RESTORATION

The Federal Aid in Wildlife Restoration Program consists of funds from a 10% to 11% manufacturer’s excise tax collected from the sale of handguns, sporting rifles, shotguns, ammunition, and archery equipment. The Federal Aid program then allots the funds back to states through a formula based on each state’s geographic area and the number of paid hunting license holders in the state. The Idaho Department of Fish and Game uses the funds to help restore, conserve, manage, and enhance wild birds and mammals for the public benefit. These funds are also used to educate hunters to develop the skills, knowledge, and attitudes necessary to be responsible, ethical hunters. Seventy-five percent of the funds for this project are from Federal Aid. The other 25% comes from license-generated funds.