ESTIMATES OF INTRINSIC GROWTH RATES IN THREE ELK POPULATIONS IN WASHINGTON

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Abstract: Population growth rates during the initial phase of irruption in three elk (Cervus elaphus) populations in Washington state were compared. Two of the elk populations experienced irruptive growth after introduction into new geographic areas (Rocky Mountain elk), while the other grew exponentially during recolonization of the Mt. St. Helens blast zone (Roosevelt elk). Maximum observed growth rates in the three populations differed, depending on degree of hunting mortality and immigration.

The growth rate of the Mt. St. Helens population exceeded "intrinsic growth rate" (i.e., "r" max.) due to reproduction alone. Immigration was believed to be a significant contribution to growth. The Cedar River Watershed elk population in the western Washington Cascades was below "r max" because elk were lost to illegal hunting mortality, and emigration. The Arid Lands Ecology Reserve elk population, in sagebrush-steppe of central Washington most closely approached maximum "r-max" because emigration, and mortality were minimal. Immigration was not a significant factor.

The comparisons indicate potential affects of the different mortality, reproduction, immigration, and emigration levels. The results also indicate that potential elk population growth rates vary under different environmental conditions.

A population's intrinsic growth rate, "r", is an important population characteristic that is used in a great number of population models (i.e., logistic growth, sustained yield models, etc.). An estimate of "r" can be useful in evaluating the demographic vigor of a given population relative to other populations or under different habitat management systems. Birch (1960) suggested that "r" was a measure of a population's genetic fitness. Unfortunately, the value of "r" is seldom known.

Measures of population growth have been variously defined. The "biotic potential" of a population is defined as the "theoretical, genetically imposed upper limit on a populations rate of growth" (Bailey, 1984:144). The "intrinsic rate of growth" has been defined as the rate at which a population
grows when no resources (e.g. food, shelter, space, and water) is in short supply (Caughley 1977). This growth rate is the genetically imposed upper limit, interacting with the quality of the environment (Andrewartha and Birch 1954). Quality here refers to weather, suitability of food, suitability of nesting sites, and so on (Caughley 1977), and not amount of food, cover, etc. Figure 1 contracts "biotic potential", "intrinsic growth rate", and logistic growth.

![Graphical comparison of growth types](image)

**TIME**

Figure 1. A graphical comparison of the different types of growth.

In the present paper we compare intrinsic growth rates for three elk (*Cervus elaphus*) populations based on annual population estimates spanning time periods of five or more years. The intrinsic growth rate "r" is defined as the growth rate of a population that is not experiencing any density-dependent regulation (i.e., not having passed the inflection point of logistic growth). Mortality factors such as accidents, predation, and old-age may be operative on the population. Reproductive rates are considered to be at maximum levels possible, given conditions in the specific environment (i.e., forage quality, weather, and so on).

The three populations studied are all "irruptive" populations; that is, populations invading new territories (Bailey 1984). Two of the populations represent elk range expansions, while the third represents elk recolonizing an area depopulated by volcanic disturbance.

**STUDY AREAS**

Two of the three populations studied were located in the coastal coniferous forest zone of western Washington, while the third was located in the shrub-steppe of eastern Washington. The habitat conditions in each area were distinctly different.
The Cedar River Watershed (CRW) elk population is located 65 km east of Seattle in the Cascade Mountains. The study area is intensively managed coniferous forest. The CRW covers approximately 365 km², with elevations ranging from 180 to 1520 meters. By 1985, nearly the entire CRW had been converted to second growth Douglas fir forest. Vegetation, climate, and topography are described in Schoen (1977).

Elk first appeared in the CRW in the mid-1960's, probably as a result of introductions of Rocky Mountain elk (C. elaphus nelsoni) from Yellowstone in the early 1900's in Pierce County to the south, and Yakima County to the west (Schoen 1977). Closure of CRW to hunter access has prevented legal harvest of elk in the study area.

The Mt. St. Helens (MSH) elk population included in the present study is found in northwest section of the volcanic blast zone. The study area includes 225 km² within portions of the Green and North Fork Toutle River drainages, and ranges in elevation from 240 to 1200 meters. This area was similar to the CRW before the 1980 volcanic eruption, which eliminated most of the existing coniferous forests in the study area. Current vegetation communities in the study area generally resemble recent clear-cuts that have been burned. Recovery of the vegetation in the blast zone has been described by Means et al. (1982), Adams and Adams (1982), and Stevens et al. (in press).

The majority of the elk in the MSH study area were killed in the May, 1980 eruption. The elk herd in the area before the eruption was thought to have resulted from remnant herds of Roosevelt elk (C. elaphus roosevelti), with possible mixing of Rocky Mountain elk introduced into the Yakima area west of the Cascade Crest (Merrill et al. in press). Since 1982, elk have been harvested in controlled permit hunts.

The Arid Lands Ecological Reserve (ALE) is a 330 km² portion of the U.S. Dept. of Energy's Hanford Site, located in south-central Washington, 16 km northwest of Richland. Elevations vary from 150 to 1090 meters. The ALE site lies in the rain shadow of the Cascade Mountains on the west, resulting in an arid climate, with hot summers and cool winters. The ALE site is located in the Artemesia tridentata/Agropyron spicatum, shrub-steppe zone (Daubenmire 1970). The study site is described in detail by McCorquodale (1985) and Vaughn and Rickard (1977).

Elk were first noted on the ALE Reserve in 1972 (Rickard et al. 1977). They are thought to have come to the site from elk introduced in the Yakima area. The elk are not hunted as long as they remain in the ALE Reserve, which is closed to hunter access.

METHODS

Population Estimates

Elk population estimates for the three areas were obtained using several different methods. Population estimates of the CRW elk were obtained for the period from 1970 to 1982. Elk numbers were estimated from helicopter counts, road transects censuses (Schoen 1977), and mark-recapture censuses (Paige, in prep.).
The MSH elk population estimates for the period 1982-1985 were derived from helicopter counts of elk in quadrats chosen randomly without replacement (Merrill et al. in press). The 1981 estimate was provided by the Washington Department of Game.

The ALE elk population size was determined from direct aerial counts of the entire population (McCorquodale 1985).

Calculation of Growth Rates

The growth rates of the three elk populations were calculated from population estimates made in the same time period each year, over a number of years. The population growth rate, "r", was calculated by least squares linear regression of the natural log of elk population numbers over time. The slope of the line is the estimate of "r".

RESULTS

The factors known to be affecting elk population growth in the three study areas are summarized in Table 1. The estimations of intrinsic growth rates in the three populations range from 0.21 to 0.32 (Table 2). The CRW population had the lowest r value, and the greatest amount of variation (Figure 2). This variation may be due to the use of different techniques used to estimate population size. However, since 1977 the estimates were all calculated by mark-recapture methods.

The observed growth rate in the MSH elk population of 0.29 is greater than can be accounted for by reproduction alone (Figure 3). When the population estimates are adjusted to reflect the population growth without the removal of elk through controlled permit hunting, the growth rate would be 0.35 (Figure 4, curve A).

The expected MSH elk population growth, based on reproductive potential and available age structure data, assuming the only mortality was legal hunting, results in a growth rate of 0.24 (Figure 4, curve C). This comparison indicates that between 34 percent (1982) and 68 percent (1984) of the observed population growth may be attributed to immigration. These percentages would be even greater if natural mortality was a factor in these years (Merrill et al. in press). If the MSH elk population estimates were adjusted to eliminate hunting mortality and immigration, the growth rate would be approximately 0.30.

The ALE elk population growth rate was calculated to be 0.22 over the period 1975-1985 (Figure 5). However, in the period from 1982-1985, when the most intensive elk studies were in progress, the growth rate was 0.32. No hunting mortality or immigration were recorded during this latter time period (McCorquodale 1985).
Table 1. Characteristics of the elk populations understudy.

<table>
<thead>
<tr>
<th>Population</th>
<th>Population Regulation Features</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cedar River</td>
<td>Moderate emigration and immigration</td>
</tr>
<tr>
<td>ALE Reserve</td>
<td>Some &quot;illegal&quot; hunting mortality</td>
</tr>
<tr>
<td>ALE Reserve</td>
<td>No known emigration or immigration</td>
</tr>
<tr>
<td>Mt. St. Helens</td>
<td>High immigration</td>
</tr>
<tr>
<td>Mt. St. Helens</td>
<td>Moderate, regulated hunting mortality</td>
</tr>
<tr>
<td>Missouri</td>
<td>No immigration or emigration</td>
</tr>
</tbody>
</table>

Table 2. Estimated "intrinsic growth rate" (r-max) of three elk populations in Washington state, and a captive herd in Missouri.

<table>
<thead>
<tr>
<th>Population</th>
<th>Period</th>
<th>Sample</th>
<th>&quot;r-max&quot;</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cedar River</td>
<td>1970-82</td>
<td>22</td>
<td>0.21*</td>
<td>0.75*</td>
</tr>
<tr>
<td>ALE Reserve</td>
<td>1975-85</td>
<td>9</td>
<td>0.22*</td>
<td>0.98*</td>
</tr>
<tr>
<td>ALE Reserve</td>
<td>1982-85</td>
<td>4</td>
<td>0.32*</td>
<td>0.99*</td>
</tr>
<tr>
<td>Mt. St. Helens</td>
<td>1981-85</td>
<td>5</td>
<td>0.29*</td>
<td>0.99*</td>
</tr>
<tr>
<td>Mt. St. Helens¹</td>
<td>1981-85</td>
<td>5</td>
<td>0.35*</td>
<td>0.99*</td>
</tr>
<tr>
<td>Mt. St. Helens²</td>
<td>1981-85</td>
<td>5</td>
<td>0.24*</td>
<td>0.99*</td>
</tr>
<tr>
<td>Mt. St. Helens³</td>
<td>1981-85</td>
<td>5</td>
<td>0.30*</td>
<td>0.99*</td>
</tr>
<tr>
<td>Missouri</td>
<td>1951-59</td>
<td>2</td>
<td>0.27</td>
<td>-</td>
</tr>
<tr>
<td>Missouri¹</td>
<td>1951-59</td>
<td>2</td>
<td>0.30</td>
<td>-</td>
</tr>
</tbody>
</table>

Mt. St. Helens¹ - Corrected for elk harvests
Mt. St. Helens² - Corrected for elk immigration
Mt. St. Helens³ - Corrected for harvests and immigration
Missouri¹ - Corrected for elk harvests

* Significant at \( P < 0.01 \)
Figure 2. Estimates of elk population size, regressed over time for the Cedar River Watershed.

\[ N_t = 90 \ e^{0.21t} \]
\[ r^2 = 0.75 \]

Figure 3. Estimates of the observed Mt. St. Helens elk population regressed over time.

\[ N_t = 145 \ e^{0.29t} \]
\[ r^2 = 0.99 \]
ELK POPULATION GROWTH - MT. ST. HELENS

A - Corrected for harvests (.35)
B - Observed numbers (.29)
C - No immigration (.24)

Figure 4. A comparison of the observed growth curve, and curves adjusted for immigration (C) and harvest mortality (A).

ELK POPULATION GROWTH - ALE RESERVE

\[ N_t = 7.1 e^{0.22t} \]
\[ r^2 = 0.98 \]

Figure 5. Estimates of elk population size, regressed over time for the ALE Reserve study site.
DISCUSSION

Estimates of intrinsic growth rates are important for determining the speed at which a population can grow and respond to different levels of hunting harvests. Intrinsic growth rates for elk are not readily available. Murphy (1963) reported a growth rate of 0.27 for a lightly harvested, captive elk population, which was corrected to 0.30 when known harvest mortalities were included in the population numbers.

Intrinsic growth rates calculated for two Washington elk populations are comparable to that reported by Murphy. Where growth rates do not reflect hunting mortality or substantial immigration, the values ranged from 0.30 to 0.32. The exception is the CRW population.

Demographically, the CRW elk population apparently differs from the other two elk herds in two respects. First, data from herd composition counts and reproductive tract collections suggest that the elk from CRW have lower yearling fecundity; 31 calves per 100 yearlings from MSH (Merrill et al. 1984), and 11 calves for 100 yearlings for CRW (Schoen 1977). Yearling fecundity rates are not available from the ALE study area.

Second, survival rates of elk in the CRW study area are lower than in the other two areas. Elk mortalities, both adult and calf, are commonly noted in CRW (Paige, in prep), while in the ALE area no natural mortalities have been noted, and few natural mortalities have been noted in the MSH area. Nelson and Peek (1982) indirectly assess the affect in changes in calf, yearling, and adult mortality on intrinsic growth rates. Their results indicated that survival rates have a greater impact on the r value than does fecundity, especially the fecundity of yearlings.

The relatively low growth rate observed in the CRW area may reflect less productive elk habitat resulting in lower reproductive and survival rates. The lower survival rates may be due to relatively high poaching rates, and/or lower habitat quality due to the rapid conversion of the majority of the CRW to second growth forest stands. This second hypothesis is supported by lower blood parameter values in CRW, suggesting reduced physical condition in comparison to MSH elk (Merrill et al. 1984, Paige in prep.).

The use of a single statistic, such as r as an index of demographic vigor to predict future population trends has been criticized by Hanks (1981). The high r value of the reindeer population on St. Matthews Island indicated that the population was in "good condition", yet the population experience a spectacular crash. An index of physiological condition, used in conjunction with the growth rates could have resulted in different conclusions regarding demographic vigor.

The understanding of intrinsic growth rates may be most useful in the comparison of conditions between areas. This has been noted in the discussion of the r values for CRW and the other two areas.
While enumeration of population numbers is subject to many types of bias (Caughley 1977), estimates of population numbers in the MSH and ALE study sites are greatly facilitated by the very open terrain. The ALE reserve population estimates are thought to be total population counts. Also, the controlled nature of the ALE site has resulted in a greater precision in the understanding of factors that could affect population growth. Hence, the estimate of $r$ for this population likely represents a realistic estimate of the maximum $r$ for elk.

LITERATURE CITED


DISCUSSION

Question: Can we assume that all these populations are in about the same place in the logistic curve and are comparable. Or, are some of them threatening to run into a density-dependent factor?

Answer: The high, the .99 R-square value would indicate that that model is as good a fit as you could possibly get. So there is no indication of nonlogistic growth. The Cedar River population is a little bit more problematic. There was that little blip you saw in there. We're not sure if that last data point is a real good one. I think the Cedar River one is the only one that might be sort of tapering off but if you take out that one blip and you take out those two points we leveled off and assume that was the case, actually the R-value up to that point would even be higher. So, I think we try to control for that as much as possible.

Question: Did you say that on the Reserve you don't have immigration?

Answer: We don't think there is very much right now. It looks like there was a sort of a single burst of animals that colonized the area, and they may have been augmented. Scott's here and maybe he would like to comment on that so I don't pontificate too much.

Question: That's a good choice of words. I was thinking if you don't have emigration and you know that they're there now, and they weren't before, maybe we ought to build a shrine. Sounds like divine intervention to me.

Answer: Well there was colonization but there is no immigration continuing since, obviously.

Answer: Basically, we had a small group that came in originally and those seem to be the ones that have resulted in the population that is there now.


