POPULATION GROWTH AND DISPERSAL OF REINTRODUCED CALIFORNIA BIGHORN IN NORTHWESTERN NEVADA

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ABSTRACT.

Population characteristics and dispersal of California bighorn sheep (*Ovis canadensis californiana*) were investigated 12 years after the 1968 release of 8 animals on the Sheldon National Wildlife Refuge in Nevada. Analyses suggested: (1) population growth may have slowed from 1974 to 1980 as a result of intraspecific competition for high quality lambing terrain; (2) female bighorn sheep may experience alternate periods of range expansion and consolidation associated with environmental dispersal; and (3) rams may approximate innate dispersal.

INTRODUCTION

In recent years bighorn sheep (*O. canadensis*) have been the subject of numerous reestablishment efforts in various western states (Delaney 1983, deVos and Remington 1981, Guymon 1980, Johnson 1980, Rowland and Schmidt 1981). Rates of population growth and dispersal are important measures of transplant success. Although population growth rate has been reported (Woodgerd 1964), rates and patterns of dispersal for bighorns are still largely hypothetical (Bailey 1980, Geist 1971, McCutchen 1981), and may be related to a number of environmental conditions. Size of occupied range has been documented for some reintroduced herds of California bighorn sheep (Dave Ganskopp, Oregon State University, Corvallis, Oregon, personal communication; Kornet 1978; Van Dyke 1978), but rates of dispersal have not been calculated for California bighorn.

During the summer of 1968, 8 California bighorn from Hart Mountain in Oregon were released within historic range (Cowan 1940, Hall 1946, McQuivey 1978) in a 700 ha (1,700 ac) enclosure on Sheldon National Wildlife Refuge (SNWR) in northwestern Nevada. This paper presents population growth and dispersal information for this population 12 years after release, and compares rates of spread of this herd and 3 other reintroduced populations of California bighorns.

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STUDY AREA

SNWR contains extensive tables of volcanic origin that have been cut by many water courses. Extensive cliffs border some of the water courses, and most of the tables are edged by low rimrock. The study area lies in Humboldt County in the Hell Creek and Virgin Creek drainages. Elevation varies from 1,500 m to 2,000 m (5,000-6,600 ft.).

The area is arid. Precipitation ranges from 20 cm to 28 cm (8-11 in.) annually. Vegetation consists primarily of sagebrush (*Artemisia spp.*) communities with an understory of bunchgrasses and forbs. Several deciduous plants including quaking aspen (*Populus tremuloides*) and willow (*Salix spp.*) are found near permanent water. Curlleaf mountain mahogany (*Cercocarpus ledifolius*) occurs in small isolated clusters on rocky areas at higher elevations. Additional ungulates inhabiting the area are mule deer (*Odocoileus hemionus*), pronghorn antelope (*Antilocapra americana*), domestic cattle (*Bos taurus*), and feral horses (*Equus caballus*).

METHODS

Field work spanned 16 months between June 1978 and August 1980. Sex and age composition of bighorn sheep groups, and distribution information were collected by direct observation with 8x32 mm binoculars and a 30x spotting scope. An observation point was established on a ridge facing the Hell Creek area inhabited by the ewe/lamb portion of the population. Both the Hell Creek area and the Virgin Canyon area occupied by the ram band were traversed on foot twice monthly to facilitate collection of demographic information. Population counts made during observations were augmented by 3 aerial surveys and 1 drive count. Several animals, individually recognizable by artificial marks and horn and/or pelage characteristics, facilitated population counts and determination of movements.

Sheep were usually observed at more than 0.8 km (0.5 mi.), thus rams were classified by horn size criteria developed by Geist (1971). Age estimates by the horn ring method (Geist 1966) indicated that animals in this population exhibited slower horn growth than was found by Geist (1971). Therefore, Class I rams were considered 2 to 3 years old, Class II rams were 4 to 6 years old, and Class III rams were 7 plus years old. No rams were observed which fit horn size characteristics given for Geist's (1971) Class IV category. Ewes were classified as yearlings, 2 years, and adults.

The occupied range for this population was outlined on a 7.5 minute USGS topographic map. This outline included locations of all observed sheep as well as nearby areas where sheep sign had been found or that offered good escape terrain. Land area was then determined with a compensating polar planimeter. Rates of spread were calculated following Caughley (1977:69) as radial equivalents.

RESULTS

POPULATION GROWTH

Population growth of sheep on SNWR has been erratic. After the initial 6 year period, in which the population increased at 27.9% per year ($r = 0.246$), the population stabilized at 29-35 animals during this study (Table 1). There was a preponderance of females after the initial 6 years of growth (67 males:100 females), yet males outnumbered females in 1978 (120:100), and by 1980 the ratio approached equality (108:100).

Most lambs were born in the last week of April during 1980 and 1981, but 1 new lamb was recorded as late as mid-July. Natality and survival of the lambs to 2-3 months of age was high during the initial 6 years ($\bar{x}$ = 94 lambs:100 ewes; Carter 1975, Richardson 1973), as well as for 3 of the 4 years of this study ($\bar{x}$ = 83:100). The low number of lambs in 1979 (25:100) may have resulted from stress during gestation and early lactation caused by a live trapping operation, an unusually cold winter, and/or a dry spring. Survival of lambs

Table 1. Estimated herd composition for California bighorn sheep on Sheldon National Wildlife Refuge (Hansen 1982).[a]

Year	Class of Ram				Class of Ewe			Lamb	Unkn	Total
	III	II	I	Yrlg	Ad	2 Yr	Yrlg			
1968	-	1	1	-	3	-	-	3	-	8
1969	-	2	-	1	3	-	2	3	-	11
1970	1	1	1	1	3	2	2	3	-	14
1971	1	1	2	2	4	2	1	4	-	17
1972	2	1	3	2	6	1	2	5	-	22
1973	2	2	4	2	7	2	3	6	-	28
1974	2	3	3	3	9	3	3	9	-	35
1975-77					NO DATA					
1978	2	3	5	3	8[b]		3	7	1	32
1979	2	6	3	3	8	2	2	2	-	28
1980	3	8	3	1	10	3	-	7	-	35

[a]1968-1974 data from Richardson (1973) and Carter (1975).
[b]Individual ages could not be determined.

through their first winter, from 2-3 months to 14-15 months of age, was high ($\bar{x}$ = 100%) during 1968 to 1974, but lower ($\bar{x}$ = 67%) for 1978 to 1980. Survival was high for adult rams during all years, and high for adult ewes with the possible exception of 1975 to 1977.

Eleven confirmed losses have been documented since 1968, and sheep bones were found in 4 locations other than where documented losses occurred. Nine of these 15 losses were from unknown causes. Of the 6 losses for which causes were determined, 3 resulted from live trapping operations, 2 animals were entangled in the enclosure fence while attempting to cross rock cribs, and one 6-7 month old lamb was killed by a mountain lion (*Felis concolor*) after being chased into a fence. The lion was probably following the fall migration of deer through the area (Hansen 1982). Resident golden eagles (*Aquila chrysaetos*) nesting in the lambing area were observed executing 2 unsuccessful attacks on lambs during the spring of 1980. One animal included in the unknown category was a mature ewe that may have been diseased (Richardson 1973); another was a lamb that disappeared after being observed in 1980 with an injured leg. An adult ewe that died during a live trapping operation in February 1979, had few internal parasites. No evidence of disease or external parasites was noted in the population during this study.

DISPERSAL

The bighorn sheep on SNWR occupied approximately 38 km^2 (15 mi^2) in 1980; 11 km^2 (4 mi^2) in the Hell Creek area, 17 km^2 (7 mi^2) in the Virgin Canyon area, and 10 km^2 (4 mi^2) in the connecting travel corridor and irregularly used areas. Density over the entire range was 0.9 sheep/km^2 (2.3 sheep/mi^2). Rate of spread calculated from the occupied range size of the ewe/lamb band for 1968 was 0.19 km/yr (0.12 mi/yr) radial equivalent; while for the herd as a whole this rate was 0.29 km/yr (0.18 mi/yr). Rates of spread calculated from entire ranges of 3 other populations of reintroduced California bighorn (Ganskopp, Oregon State University, Corvallis, Oregon, personal communication; Kornet 1978; Van Dyke 1978) varied from 0.25 km/yr (0.16 mi/yr) to 0.45 km/yr (0.28 mi/yr) (Table 2). Some of this variability undoubtedly resulted from differences in technique for calculating occupied range size, yet radial equivalent dispersal values for Hart Mountain and SNWR, where enclosures were used, both were lower than those for Steen's Mountain and Leslie Gulch, where sheep were not enclosed.

On SNWR, the enclosure fence may have been an effective barrier for several years; however, when population densities within the enclosure reached about 5 sheep/km^2 (13 sheep/mi^2) in

Table 2. Radial equivalent rates of spread for California bighorn sheep, Himalayan thar, and Barbary sheep (Hansen 1982).

Species	Location	Years Since Release	Rate of Spread (km/yr)	Source
California bighorn	Sheldon NWR, NV	12	0.29	Hansen 1982
	Hart Mt. NWR, OR	24	0.25	Kornet 1978
	Steen's Mtn., OR	17	0.33	Van Dyke 1978
	Leslie Gulch, OR	14	0.45	Ganskopp, pers. comm.
Himalayan thar	New Zealand		0.67	Caughley 1970
Barbary sheep	New Mexico	36	1.3	Dickinson and Simpson 1979

1974, nearly twice the highest recorded natural densities (Wilson and Douglas 1982), the animals found a way out of the enclosure. Then ewes began exploring the surrounding area, and by 1980 regularly used an area almost twice the size of the enclosure. Whereas much of the surrounding area was fair to good sheep habitat, there was little or no good lambing terrain within 5 kilometers (3 miles) of the enclosure, and in 1979 and 1980 all known lambs were born in the enclosure. Not until 1981 was a female bighorn observed 8 kilometers (5 miles) from the enclosure near an area of good lambing terrain in the Virgin Canyon.

A similar pattern may be found on nearby Hart Mountain where, about 15-20 years after reintroduction, a new subgroup of breeding females was established 12 km (8 miles) north of the original lambing area. A second subgroup was established 12 km (eight miles) to the south approximately 25 years after initial release. Dispersal to the north required crossing of a gravel road, while to the south, the release enclosure bisected the escarpment face. Although rams regularly traveled around the enclosure for many years, ewes with young lambs were first observed to the south in 1981, 5 years after removal of the enclosure fence.

DISCUSSION

GROWTH

The population growth curve of SNWR suggests that some factor or factors began to have a limiting influence on the population between 1975 and 1978 (Table 1). No unusual human disturbance was known to have occurred at that time, and I found no evidence of significant loss to disease. Several predators were present in the area, and are known to have killed 1 sheep and attacked others. Also, 2 animals are known to have died of accidents involving the enclosure fence. Furthermore, high rates of lamb production and survival were evident before and, in most years, after 1975 to 1978. Hence, the apparent factors limiting this population were predation and accidents.

The defense of bighorn sheep against predation is the use of adequate escape terrain. Holl (1982) found that in the San Gabriel Mountains of southern California a minimum of 150 ac (60 ha) of escape terrain was necessary to support 10 ewes on winter ranges. On SNWR, 10% of the area used by ewes, or about 330 ac (135 ha), was escape terrain. From this, an escape terrain carrying capacity for Hell Creek might be calculated at 22 ewes. But, the population counts indicate no more than 10 to 15 ewes were able to consistently recruit lambs in the Hell Creek area.

Only the most inaccessible portions of escape terrain are used by ewes for lambing (Hansen 1982:58, Van Dyke et al. 1983:6). In Hell Creek only about 1 percent of available escape terrain was used for lambing. Consequently, intraspecific competition for lambing terrain may have forced ewes with young lambs into less secure areas, potentially increasing their susceptibility to predation. The apparent loss of adult ewes and the recorded incident of lion predation in the late fall suggest general escape terrain may also have been a factor. Additionally, dispersal from the enclosure that was induced by high sheep densities increased exposure of sheep to the hazard of fence crossing, thus increasing accidents. Therefore, rather than predation, the actual factor limiting this population was probably the availability of high quality escape and lambing terrain.

DISPERSAL

Howard (1960), and later Caughley (1977), defined dispersal of individuals as, "movement an animal makes from its point of origin to the place where it reproduces or would have reproduced if it had survived and found a mate." In discussing bighorn dispersal, it is important to distinguish between rams and ewes. Bighorn sheep are traditional in their range use (Geist 1971:79), and ewes normally drop their lambs in the lambing area where they themselves were born. However, occasionally ewes wander considerably as 2 year olds (Kopec 1982:104). If an area favorable to lambing is found, a ewe may return there to drop her lambs, and in so doing, establish a new lambing area (Geist 1971:128). From this new lambing area future generations of ewes may disperse to yet other areas, thus expanding the population's range size. Rams frequently move large distances during the rut (Geist 1971:89, Witham and Smith 1979); however, rams of an isolated population will find no ewes in their travels, and will leave no offspring except in the original lambing range. Hence, individual dispersal of rams does not in itself produce population range expansion.

Rate of spread, a measure of population range expansion, is strongly dependent on environmental conditions (Caughley 1977). Discontinuity of preferred habitats, either natural (Geist 1971:127) or artificial, may inhibit dispersal, and thereby range expansion of bighorn sheep. Evidence from SNWR and Hart Mountain suggests that: (1) discontinuous areas of lambing habitat separated by as little as 5 kilometers (3 miles) may form limited barriers to female bighorn dispersal even when the intervening land may be considered fair to good sheep habitat; and (2) whereas ewes may explore considerable distances under favorable conditions, they do not do so as readily as rams, and consequently artificial obstructions that rams readily cross may significantly slow female dispersal.

Male bighorn sheep (Geist 1971:90) and Barbary sheep (*Ammotragus lervia*) (Dickinson and Simpson 1979:42) both move long distances in an apparently "irrational" manner. From this Dickinson and Simpson (1979:42) suggested that dispersal in Barbary sheep was analagous to innate dispersal (Caughley 1977, Howard 1960). Bighorn rams may also approximate innate dispersal during establishment of individual rutting ranges. But, Dickinson and Simpson (1979:36) calculated rates of spread of "breeding groups", and excluded outlying male sightings. They found breeding group rates of spread fluctuated at approximately 5 year intervals, and suggested that alternate periods of dispersal and range consolidation were responsible. Thus, the fluctuating rates of spread may have been a density dependent process, and may therefore be indicative of environmental dispersal (Caughley 1977, Howard 1960) rather than innate dispersal as suggested for rams. Dispersal of bighorn ewes on SNWR is evidently following a similar pattern; a pattern that can be likened to colonization in oceanic island chains (Brown and Gibson 1983:218, Williamson 1981:40), in that land areas providing adequate habitats, especially lambing terrain, are often isolated from each other, as are islands, producing partial barriers to dispersal, or "filters" (Brown and Gibson 1983:218).

Further studies of range expansion of reintroduced bighorn sheep populations are needed: (1) to establish the effectiveness of environmental conditions that inhibit dispersal of female bighorns and so inhibit population range expansion; and (2) to determine the differences in patterns and rates of male and female bighorn sheep dispersal. To document potential rate fluctuations, occupied range size should be collected by wildlife managers at about 5 year intervals.

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