Correlates to Colonizations of New Patches by Translocated Populations of Bighorn Sheep

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Abstract

By 1950, bighorn sheep were extirpated from large areas of their range. Most extant populations of bighorn sheep (*Ovis canadensis*) in the Intermountain West consist of <100 individuals occurring in a fragmented distribution across the landscape. Dispersal and successful colonizations of unoccupied habitat patches has been rarely reported, and, in particular, translocated populations have been characterized by limited population growth and limited dispersal rates. Restoration of the species is greatly assisted by dispersal and successful colonization of new patches within a metapopulation structure versus the existing scenario of negligible dispersal and fragmented, small populations. We investigated the correlates for the rate of colonizations of 79 suitable, but unoccupied, patches by 31 translocated populations of bighorn sheep released into nearby patches of habitat. Population growth rates of bighorn sheep in the release patches were correlated to N_e of the founder group, and early contact with a second released population in a nearby release patch (logistic regression, p = 0.08). Largest population size of all extant released populations in 1994 was correlated to potential N_e of the founder group, the number of different source populations represented in the founder, and early contact with a second released population (p = 0.016). Dispersal rates were 100% higher in rams than ewes (p = 0.001). Successful colonizations of unoccupied patches (n = 24 of 79 were colonized) were associated with rapid growth rates in the released population, years since release, larger area of suitable habitat in the release patch, larger population sizes, and a seasonal migratory tendency in the released population (p = 0.05). Fewer water barriers, more open vegetation and more rugged, broken terrain in the intervening habitat were also associated with colonizations (p = <0.05). We concluded that high dispersal rates and rapid reoccupation of large areas could occur if bighorn sheep are placed in large patches of habitat with few barriers to movements to other patches and with no domestic sheep present. Many restorations in the past that did not meet these criteria may have contributed to an insular population structure of bighorn sheep with limited observations of dispersal.

Key words: bighorn sheep, colonization, patch size, dispersal, corridor features, *Ovis canadensis canadensis*, *O. c. nelsoni*.

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Introduction

Fragmentation and insularity of populations of wild vertebrates is a pervasive problem in increasingly human-altered landscapes. Small isolated populations of animals may be at higher risk of extirpation than large, contiguous populations (Gilpin & Soulé 1986). Beier and Noss (1998) recently argued that landscape connectivity enhances population viability for many species, and that undisturbed environments were, in general, more continuous than those disturbed by humans. Here we report on a species that currently occurs in small, isolated populations, that formerly occupied a much wider range (Buechner 1960; Wishart 1978), and that has been rarely reported to disperse. The distribution of the species was likely naturally fragmented to some extent (Geist 1971; Schwartz et al. 1986; Bleich et al. 1990). But unregulated hunting, habitat destruction, overgrazing of rangelands, and diseases contracted from domestic livestock contributed to large scale declines and further fragmentation of the species during the 1870–1950 period (Cowan 1940; Buechner 1960; Wishart 1978; Monson 1980; Thorne et al. 1985). Most (64–88%) extant populations of bighorn sheep within the western United States currently consist of less than 100 individuals (McCutcheon 1981; Thorne

et al. 1985; Singer 1994). About 55–58% of present-day populations stem from translocations (Bailey 1990; Singer 1994). Only about 40% of these translocations were judged successful (Leslie 1980; Bailey 1990; Singer et al. 2000*a*), thus slowing the restoration process. Information on factors that contribute to successful dispersal and colonization, in particular, would greatly accelerate the restoration process.

Historically, bighorn sheep likely occurred in a naturally fragmented distribution, because bighorn sheep are habitat specialists that prefer open patches of steep, cliffy habitat, and these patches of habitat tend to occur in islands on mountains separated by flat areas or dense forests (Van Dyke et al. 1983; Risenhoover et al. 1988; Smith et al. 1991). Traditional views held that: (1) suitable habitats are climax vegetation types that change slowly; (2) the species is a classic K-selected species that lives in matrilineal groups; (3) subadults are retained in groups; (4) movements and migrations are learned from older animals (Geist 1971; Festa-Bianchet 1986); and thus, (5) colonizations of new habitat is rare. Present day support for these views include mtDNA differences between nearby mountain ranges inferring restricted movements by ewes (Ramey 1995; Boyce et al. 1999), the present-day evidence of an insular distribution of the species, persistence of many small populations of 50 or less (Krausman & Leopold 1986; Stevens 1994; Wehausen 1999), strong fidelity of ewes to home ranges (Dodd 1983), and the near absence of new colonizations. Bleich et al. (1996) reported only one instance of a ewe emigrating and reproducing in a new mountain range, while McQuivey (1978) reported only four such dispersals by marked ewes.

Several authors have proposed that bighorn sheep may naturally occur in large metapopulations consisting of populations on isolated mountains that are connected by intermountain travel of 10–20 km by ewes and rams (Cochran & Smith 1983; Schwartz et al. 1986; Bleich et al. 1990, 1996). The highly connected populations of about 73,000 Dall sheep (*Ovis dalli*) that occur on every mountain and steep hill in Alaska also imply high dispersal, successful colonizations, and a metapopulation structure (Singer 1982; Heimer 1985). Dispersing Dall sheep were frequently observed during a period of population increase in the early 1980s (F. Singer & E. C. Murphy, personal observation). A past metapopulation structure also for bighorn sheep was suggested by similarities in microsatellite DNA, inferring extensive movements by rams across geographic distances (Luikart & Allendorf 1996; Boyce et al. 1997; Gutiérrez-Espeleta et al. 1998) although mtDNA suggest past low levels of movements by ewes (Boyce et al. 1999). Also, the spread of pasteurellosis across 170 km during two breeding seasons was attributed to extensive movements of breeding rams (Onderka & Wishart 1984). A metapopulation structure requires dispersal rates adequate to recolonize vacated or newly occupiable patches of habitat (Hanski 1989; McCullough 1996). Extinctions of local populations of bighorn sheep by a variety of causes (including disease that killed entire populations, periodic drought, post-fire succession, possibly predation, and periodic severe winter weather in northern climates) have been reported (Buechner 1960; Weaver & Mensch 1971; Wishart 1978; Wehausen et al. 1987; Torres et al. 1994; Bleich et al. 1996; see Fig. 1). Subsequently, newly suitable patches would have been created periodically by large fires, relief from drought, milder winters, recovery by nondiseased groups, and post-glacial succession (Geist 1971, 1975; Fig. 1). It is possible that bighorn sheep existed mostly in metapopulations but human disturbance has accelerated extinction rates in these metapopulations, and bighorn sheep populations now occur in a nonequilibrial state (Harrison 1994).

Increaser dispersal is defined as dispersal during periods of the most rapid population increases prior to habitat saturation. Increaser dispersal is most typical of small mammals (Lidicker 1976; Krebs 1978; Beacham 1979; Stenseth 1983). Sinclair (1992) felt that saturation dispersal (i.e., dispersal from saturated habitats) was typical of most ungulates (McCullough 1985; LaBonte et al. 1998). Increaser versus saturation dispersal can alter the rate of restoration. Presaturation or increaser dispersal will result in a faster recovery, since dispersal is most likely at highest rates of increase (highest lambda's, λ) and when the habitat is not yet fully occupied (highest λ's typically occur at about 50–70% occupation of the habitat in ungulates). A saturation dispersal model for

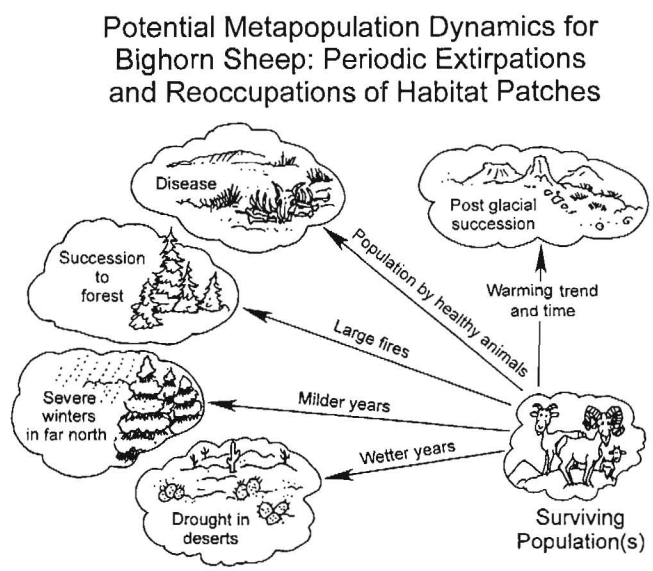

Figure 1. Factors that create new habitat patches for bighorn sheep and that encourage a metapopulation structure consisting of periodic extirpations and recolonizations.

bighorn sheep would obviously result in a slower natural recovery, since dispersal would not occur until the entire available habitat was occupied.

Bighorn sheep translocations are very expensive. The founder animals are subjected to stress and risk of death during capture and transplant, sources are limited, and intra- and inter-state transports are logistically cumbersome. The typical translocation of about 28 bighorn sheep costs about $20,000–40,000.

Much habitat remains unoccupied for potential restoration. Our Geographic Information System (GIS) analysis in a six-state area near national park lands indicated only 38% of the entire potential suitable habitat was occupied (Singer et al. 2000*b*). Dispersal is considered important to wildlife species because it leads to the discovery and occupation of new patches (Stenseth 1983), it contributes to the persistence of populations (Brown & Kodric-Brown 1977; Beier & Noss 1998), and it may contribute to the avoidance of inbreeding (Geist 1971; Dobson 1982).

Thus, managers need to know what procedures they can follow that will promote natural dispersal and subsequent colonizations of unoccupied habitat rather than translocations into each patch. The purpose of our study was to determine those factors correlated with dispersal and colonization of unoccupied habitat patches by 31 translocated populations of bighorn sheep that occurred in or near 15 National Park Service (NPS) units in the western United States. Our objectives were to analyze those factors that could be modified or altered by managers during restoration (e.g., selection of patches near versus distant to domestic sheep; selection of larger versus smaller patch sizes for releases; selection of areas for restoration with certain corridor features; total size of founder groups; and adult sex ratios in founder groups) that might increase the likelihood of successful natural colonizations of additional patches by translocated groups.

Considerable marking of animals (n = 679 marked animals), 527 population-years of post-release monitoring, and extensive GIS analysis of suitable habitat in the patches (39,117 km^2 of potential habitat were assessed) were available in this large data set.

Study Areas

Sheep were released into 31 study areas in five states from 1946–1991 (Table 1). The study areas, state, released populations, total size of release, number of years of data collection, type of data, estimated potential N_e of the released group, the source nearby unoccupied patches, and size of the habitat patches are all detailed in Table 1. Dispersal and colonizations were closely monitored in nine of the released populations by university graduate students, and by full-time resource agency technicians or biologists in 11 others. There were also regular aerial radio locations and periodic helicopter surveys of 28 populations in all occupied and unoccupied patches (Table 1).

Methods

Dispersal of Translocated Populations

We documented population dispersal from the release patch through observations of the occupied range of all marked and unmarked animals. Colonizations were determined by the first presence of marked or unmarked animals of both sexes and the production of young in previously unoccupied patches of habitat. Each management agency (NPS, Bureau of Land Management [BLM], Colorado Division of Wildlife, Utah Wildlife Resources, U.S. Forest Service, our own U.S. Geological Survey crews, and university graduate students) closely monitored any colonizations of new patches and pioneering movements by radiocollared or marked animals dispersing from the released populations (detailed in Singer & Gudorf 1999).

In 12 of the translocated populations monitored most intensively by our NPS and USGS crews, we monitored all dispersal events and movements of radiocollared animals by aircraft and from the ground at least weekly (n = 143 radiocollared animals). Less intensive radiotelemetry studies were conducted in another 16 populations (n = 28 total radiomonitored populations; n = 412 additional radiocollared animals; 18 ± 3 radiocollars per translocated founder group) by state and federal agencies along with periodic helicopter surveys to determine the status of occupied and unoccupied habitat. Marking collars on another 124 bighorn sheep, along with national park observation recording systems, provided extensive information for another three populations (n = 31 marked populations). All national park units encourage employees who travel in the backcountry in the park to record any sightings of the released bighorns on Wildlife Observation Cards. These sightings represent thousands of km of backcountry travel by human observers within each park unit. We used bighorn sheep locations from helicopter and ground sightings within each park, combined with locations of radiocollared animals, and estimated the approximate largest area occupied by connecting the outermost observations (Mohr 1947; White & Garrott 1990). To obtain an approximate rate of spread by the released populations, we estimated the largest area occupied by released bighorn sheep within the release patch and divided by years since release.

We concluded no successful colonizations went undetected. Nevertheless, some short-term transient exploratory movements and return to the first patch by unmarked or marked individuals might have gone undetected.

We investigated the characteristics of 79 suitable, but

Table 1. Translocated released populations, characteristics of the release and the release patch, and number of colonizations by the released bighorn sheep population.

Name	State	Year of Release	Founder N	Potential N_e of Founder	Number of Founder Sources	Population Growth Pattern[a]	Size of Release Patch (km^2)[b]	1994 Census N	Migratory Tendency[d]	Number Unoccupied Patches Colonized[f]
Moody Canyon[e,g,h]	UT	1975	23	18	3	1	466[c]	395	3	1
Red Slide[e,g,h]	UT	1984	22	22	2	1	466[c]	145	3	1
Mesa Verde[i]	CO	1946	14	12	1	2	4.9	10	1	0
Dillon[f,g,h,i]	CO	1974	44	21	2	2	264	7	1	1
Lake Fork[f,g,h]	CO	1975	16	14	1	2	28.3	8	1	0
Black Canyon[g,h]	CO	1986	83	51	4	2	25	30	1	0
Colorado Monument[e,f,g,h,i]	CO	1979	39	27	3	1	312	138	2	1
Beaver Creek[f,g,h]	CO	1983	21	18	1	2	18.5	9[j]	1	1
Bear Mountain[e,f,g,h]	UT	1983	36	27	2	1	120	36	3	1
Sheep Creek[f,g,h]	UT	1989	21	16	1	1	1,000[c]	45	3	2
Hole-in-Rock[g,h]	UT	1989	22	17	1	1	1,000	60	1	2
Cross Mountain[g,h,i]	CO	1977	19	15	1	2	49	10	1	0
Ladore Canyon[e,h,i]	CO	1952	32	24	1	3	136	130	1	1
Pool Creek[f,g,h,i]	CO	1984	19	11	2	1	333	70	1	1
Arches[e,f,g,h,i]	UT	1985	23	15	2	1	224	93	1	2
Maze[g,h,i]	UT	1982	25	24	2	1	1,145	90	3	0
Bighorn Canyon[e,f,g,h,i]	MT	1975	13	12	2	1	736	195	3	2
Badlands North[f,g,h,i]	SD	1967	14	12	1	1	161	163	1	2
Theodore Roosevelt[h,i]	ND	1966	20	15	1	2	8.1	0	3	0
Island Sky[e,f,g,h,i]	UT	1966	60	45	1	1	442	225	3	2
Potash[f,g,h,i]	UT	1975	10	9	1	1	449	160	3	2
Lockhart[f,g,h,i]	UT	1980	7	6	1	2	1,416[c]	35	3	0
Needles[f,g,h,i]	UT	1965	15	12	1	2	1,416	30	1	0
BLM[e,g,h]	ND	1991	28	21	2	1	30	30	1	1
Lone Buttes[g,h]	ND	1985	18	15	1	1	10.8	33	1	0
Magpie Creek[g,h]	ND	1959	20	15	1	2	3	18	1	0
Wanagan[g,h]	ND	1970	10	9	1	1	3.9	20	1	0
Chateau[g,h]	ND	1970	15	12	1	1	4.2	40	1	0
Moody[g,h]	ND	1970	10	9	1	1	15	25	1	1
North Bullion[g,h]	ND	1989	9	9	1	1	10	20	1	0
South Bullion[g,h]	ND	1974	20	15	1	1	5	50	1	0

[a]1 = steadily increasing to stable; 2 = initially increased but then declined to extirpation or remnant; 3 = declined to <30, but then increased.
[b]Suitable habitat where translocated animals were released based on GIS habitat model of Smith et al. (1991) modified by Johnson & Swift (2000).
[c]Two translocated populations joined, and their suitable habitat areas were pooled.
[d]Migratory tendency: 1 = nonmigratory; 2 = only segments of the population migratory; 3 = fully migratory.
Dispersal and colonization of released group monitored by:
[e]university graduate student; [f]full-time resources agency technicians or biologists; [g]regular aerial radiotelemetry flights; [h]periodic helicopter surveys of the unoccupied habitat; [i]park observation system; [j]this herd was later depopulated in 1997.

unoccupied, patches of habitat and also in release patches for the 31 translocated populations of bighorn sheep. GIS procedures were used to quantify the amount of suitable habitat in both the release and unoccupied patches. Suitable habitat was calculated following a step-by-step elimination of unsuitable areas using successive GIS map overlays (Smith et al. 1991; Johnson & Swift 2000). First, all areas of occupiable escape terrain (slopes 27°–85°) averaged across 30×30 m grids, adjacent flat areas <300 m from that escape terrain, and flat areas <500 m to either side when located between escape terrain on two sides were mapped as potentially suitable (Buechner 1960; Van Dyke et al. 1983; Hurley & Irwin 1986; Bentz & Woodard 1988). All areas were first defined as occupiable in step one, but the areas with dense vegetation (defined as <55% visibility) (Risenhoover & Bailey 1985) were removed. Vegetation maps of tree density were ground checked in all the study areas during the summers of 1995–1997. In successive steps, areas with natural and manmade barriers, areas developed by humans, and areas with excessive snowpacks were also removed from the estimate of potentially suitable habitat (Smith et al. 1991). We differentiated other unoccupied patches from the initial release patch as those areas separated by either potential barriers (such as rivers, highways, low flat lands, rolling flat lands, densely forested areas) or other unsuitable habitat from the release patch. In some instances, limited and scattered pieces of escape terrain existed in the movement corridor. We defined corridors as those areas >3 km

across patches and with <1 km^2 total of suitable escape habitat. Only new patches <40 km from translocated populations and with >5 years since release were considered to have potential for colonization and were included in the analysis ($\bar{x}$ = 17 years ± 12 SE) since release, range 5–47 years.

Population size in 1994, total founder size, N_e of founders, average rate of population growth (λ, averaged) of the released population from time of release until 1994, years since release, and distance to the nearest domestic sheep (km) were recorded for each released population during the study period. The sex ratio of males: females is often low during translocations because adult rams may be more difficult to capture or transport, which reduces the relative potential N_e of the founding group. To investigate the role of sex ratio as a potential correlate to success, we calculated the largest potential N_e of the founding group using the formula, $N_e = 4\ NmNf/Nm + Nf$, assuming that 100% of adult females (Nf) were potential breeders, and about 40% of the adult males were potential breeders (Nm) (Fitzsimmons et al. 1995). We assumed that, on average, 59% of any female or male lambs would survive to potentially produce young at age 2.5 (Festa-Bianchet 1988; Jorgenson et al. 1997).

For those 28 populations that contained radiocollared individuals, we could determine with certainty the released translocated population responsible for colonization. For the remaining five populations, we assumed colonization occurred from the closest release population, although colonization could potentially have come from other, more distant populations. If so, this represents a potential source of error. We measured corridor distances as the shortest straight line (km) distance between all 79 unoccupied patches and the release patch, although not all dispersing animals may have traveled in a straight line. We rated water barriers to movements across corridors as follows: (1) no water barriers or small streams; (2) small river(s) present; (3) medium river(s) present; or (4) large river(s), reservoir(s), or large steep-sided canal(s) present. We rated resistance to movements caused by vegetative cover (Risenhoover & Bailey 1985; Hurley & Irwin 1986; Risenhoover et al. 1988) from low to high resistance to movement across corridors as follows: (1) open, low substrates (grasses, bare soil, low shrubs); (2) areas of tall shrubs or scattered trees; (3) tall shrubs and patches of mature trees; or (4) dense, continuous coniferous forest. Escape terrain within the corridors was rated from low to high resistance to movement as follows: (1) continuous or extensive broken terrain with small cliffs; (2) scattered escape terrain; and (3) large, flat expanses (Bailey 1980; Risenhoover & Bailey 1985; Hurley & Irwin 1986; Bentz & Woodard 1988; Risenhoover et al. 1988; Woodard & VanNest 1990).

Those factors that were potentially correlated to colonizations of new patches, rates of spread in the release patch, and population growth rates of released translocated populations were analyzed with logistic regression. We pooled the continuous variables of λ, population size in 1994, and years since release into categories that provided the best fit. We investigated all combinations of two, three, and four variables to select the most parsimonious or best biological model, as a trade-off between the number of variables, model bias, and variance of the estimate following guidelines of Burnham & Anderson (1991). We used the lowest AIC (Akaike Information Criteria) value for the best model selection (Sakamoto et al. 1986). Acceptance level was $p < 0.10$.

Results

Population Growth Rates

Eighteen populations (55%) increased at a rate of $\lambda = 1.17 + 0.04\ \bar{x} \pm SE$ (range = 1.04–1.23). Only nine populations (29%) grew to a size >100 by 1994. For these increasing populations, there were no verified contacts and only one suspected contact with domestic sheep. The area of suitable bighorn habitat for the initial release was much larger for these increasing populations ($\bar{x}$ = 490 ± 90 km^2, range 35–1,145 km^2) than for populations that declined ($\bar{x}$ = 60 ± 30 km^2, range 5–350 km^2). Twelve populations (39%) went extinct or declined to a remnant status of <30 individuals that were not expected to recover or were unlikely to recover (size of remnant populations, $\bar{x}$ = 14.5 ± 12, range = 7–30). These populations initially grew (λ = 1.11 ± 0.03), before declining (λ = 0.77 ± 0.07 during declines). Only one population was observed to rebound from this remnant category (Ladore Canyon, Table 1).

Population growth rates of translocated populations were correlated with both N_e of founder group and early contact with a second translocated population in a nearby patch ($p = 0.08$). Population size reached in 1994 was correlated with potential N_e of founders, the number of source populations represented in the founder group, and early contact with a second translocated population ($p = 0.016$).

Rates of Spread Within the Release Patch

Approximate linear rates of spread through the first or release patch averaged 11.4 ± 0.2 km/year. Area rates of spread for populations during the increasing phase averaged 5.1 ± 0.9 km^2/year, but declining diseased populations lost 0.3 ± 0.2 linear km and 1.2 ± 0.8 km^2 of area range/year. Rate of spread through the first patch (km/year) was positively correlated with estimated potential N_e of founder group rate of increase in population size, number of source populations repre-

sented in the founder group, and early contact with a second translocated population ($p = 0.07$).

Colonizations of New Patches

We documented the colonization of 24 of 79 (30%) potential patches of unoccupied habitat. Many colonizations occurred during the first 15 years following the release (Fig. 2). A successful colonization occurred every 13.5 years for the increasing populations, or once every 22 years for all populations, both increasing and decreasing. Successful colonizations of new patches were positively correlated to rate of population increase in the release patch ($p = 0.0001$), number of years since release ($p = 0.02$), larger population size in the release patch in 1994 ($p = 0.05$), and seasonal migrations by the released population ($p = 0.004$; Table 1, Figs. 3–5). The number of successful colonizations was also correlated to patch size of the release habitat patch ($F = 18.7$; $r^2 = 0.64$, $p = 0.001$).

Fewer water barriers, more open vegetation, and more rugged, broken terrain in travel corridors were correlated with successful colonization (this model). The single, most parsimonious model explaining successful colonizations (lowest relative AIC value of 59.5) included: (1) high population growth rates ($p = 0.002$); (2) fewer water barriers ($p = 0.13$); (3) fewer vegetation barriers ($p = 0.02$); and (4) more rugged terrain ($p = 0.03$).

Distance did not explain colonizations in a linear fashion. Thus, we estimated colonization rates based on the distance between patches using Equation 1:

$$\textit{probability of colonization} = \tag{1}$$

$$a\left[\frac{1}{sd\sqrt{2\pi}\,e^{0.5}}\left[\frac{distance - 2\mu}{sd}\right]\right]$$

where $a = 0.973$, $\mu = 12.28$, and $sd = 5.17$. This function describes a normal distribution. The maximum probability of colonization versus distance (0.75 probability) was for patches 12.3 km from the release patch. Bighorn sheep apparently colonize patches at an intermediate distance more readily than patches that are nearby or distant. For example, 18 patches were separated by <5 km, but only 5 (28%) of those close patches were colonized, possibly because it was too easy for the animals to return to their original home ranges when <5 km away.

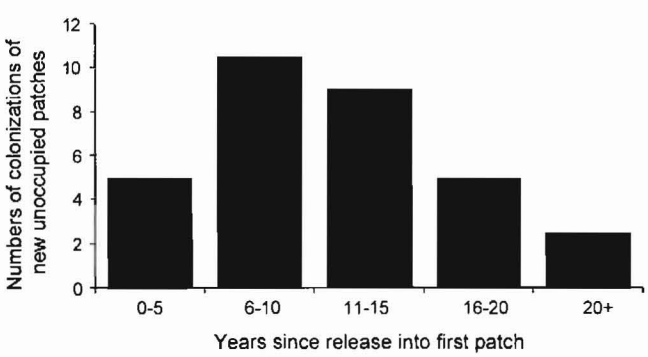

Figure 2. Probability of successful colonizations in relation to years since release in the first patch for 31 translocated populations of bighorn sheep released, 1947–1991.

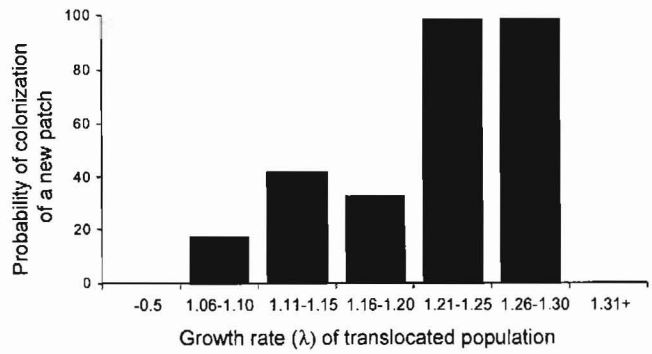

Figure 3. Probability of successful colonizations of new patches was correlated to population growth rates (λ) of the 31 translocated populations of bighorn sheep in the western United States, 1946–1997.

Rates of ram dispersal events were 100% greater than ewe dispersal events ($z = 4.5$; $p = 0.001$; $n = 295$ radio-collar-animal years). Rams typically pioneered habitat patches several years before ewes.

Discussion

We observed much higher rates of colonizations by bighorn sheep than prior researchers (Geist 1971, 1975; McQuivey 1978; Bailey 1986, 1990; Schwartz et al. 1986;

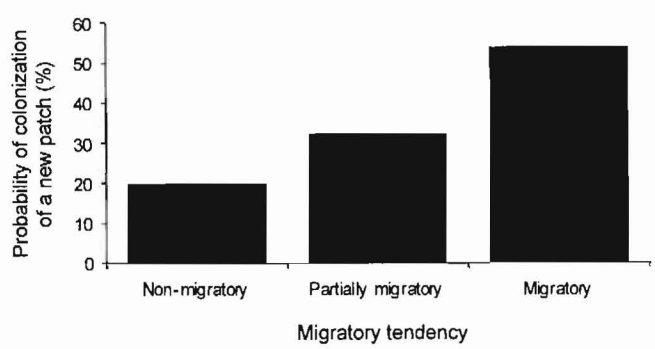

Figure 4. Probability of successful colonizations in relation to migratory tendency in the release patch for 31 translocated populations of bighorn sheep (migratory = >75% of the population uses distinct seasonal ranges; partially migratory = part of the population migrates; nonmigratory = year-round use of the same ranges).

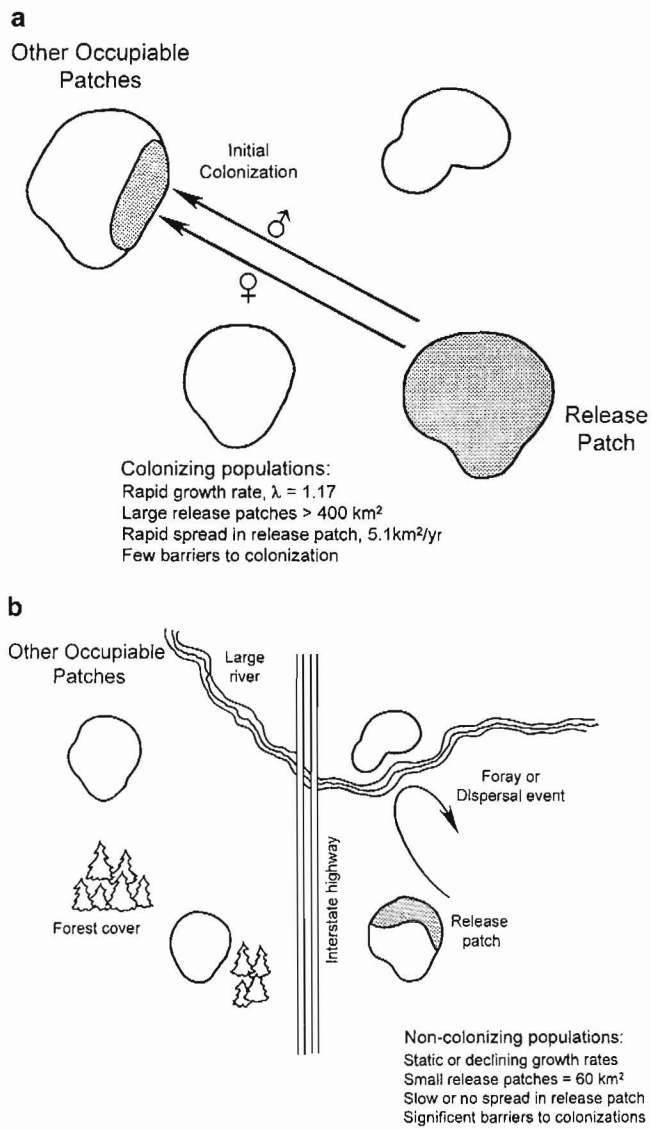

Figure 5. Schematic correlates for colonizations (a) versus no colonizations (b) of nearby unoccupied habitat patches by bighorn sheep following their release into a new patch.

Risenhoover et al. 1988; Bleich et al. 1990, 1996). We suspect this was because our study areas included large regions of unoccupied habitat with a greater probability of detecting colonizations by released animals than the other studies. We stress many of the colonizations we report are too recent to provide conclusions to their eventual long-term persistence.

As we originally predicted, large rivers, continuous conifer forest, and flat terrain constituted significant barriers to bighorn sheep dispersal. We also observed higher rates of dispersal from rapidly increasing populations that had not yet reached habitat saturation or ecological carrying capacity, i.e., we concluded the pre-saturation or increaser dispersal hypothesis (Lidicker 1976; Krebs 1978; Stenseth 1983) applied to bighorn sheep. Most colonizations of new patches occurred between 6 and 15 years post-release and during a time when released populations were growing fastest. Most colonizations were of patches 10–15 km distant. The rate of colonizations dropped off approximately linearly beyond 15 km, while fewer colonizations also occurred in patches <5 km distant.

We conclude that prior reports of low rates of dispersal from many bighorn sheep populations may be the result of poor prior restoration procedures. Many prior translocations consisted of small founder groups (typically <25 animals) released into small, isolated patches of habitat (Risenhoover et al. 1988). This may be a prescription for failure.

Sedentariness, or overconcentration, of translocated populations of bighorn sheep may be a large obstacle to restoration of bighorn sheep populations (Risenhoover et al. 1988). Sedentariness may result in higher transmission rates of lungworms, overcrowding on restricted habitats, and overuse of forages due to year-round grazing of the same ranges (Risenhoover et al. 1988). Potential N_e of founders was positively correlated with population increase and rate of spread; however, adult rams are harder to trap and managers are reluctant to transport many rams since they may injure others if not transported separately. Typically, only those few young rams caught with ewes are transported (which reduces N_e). Our study also emphasized the need to restore populations into large patches of suitable habitat, because dispersals will be more likely from these large patches.

Dispersal is potentially important to bighorn sheep for the successful recolonization of historic but currently unoccupied habitat patches, for gene flow between subpopulations, and for the discovery of newly-created suitable habitat due to fires or to the recent removal of livestock leases and grazing (Geist 1975; Goodson 1982; Stenseth 1983; Risenhoover et al. 1988; Bleich et al. 1990, 1996). Male-biased dispersal during the breeding season in bighorn sheep may decrease deleterious inbreeding by close relatives (Geist 1971, 1975; Wolff 1994). Survival of self-perpetuating metapopulations of bighorn sheep that do not require constant augmentations and restorations will depend upon at least moderate rates of dispersal. Caveats for increased dispersal might be greater exposure to predation while moving through unknown habitats and marginal escape terrain (Watts & Schemnitz 1985), or greater exposure to diseases. We conclude that colonizations by recovering populations of bighorn sheep can be increased, and thus the process of restoration expedited and made less expensive by the following practices: (1) increasing the size of N_e of founder groups; (2) mixing founders; (3) placing translocated groups into larger patches (>400 km^2 of suitable habitat); (4) placing

animals in patches with few barriers between patches; and (5) placing bighorn in patches with no domestic sheep.

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