Role of Patch Size, Disease, and Movement in Rapid Extinction of Bighorn Sheep

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Abstract: *The controversy (Berger 1990, 1999; Wehausen 1999) over rapid extinction in bighorn sheep (*Ovis canadensis*) has focused on population size alone as a correlate to persistence time. We report on the persistence and population performance of 24 translocated populations of bighorn sheep. Persistence in these sheep was strongly correlated with larger patch sizes, greater distance to domestic sheep, higher population growth rates, and migratory movements, as well as to larger population sizes. Persistence was also positively correlated with larger average home-range size (p = 0.058, n = 10 translocated populations) and home-range size of rams (p = 0.087, n = 8 translocated populations). Greater home-range size and dispersal rates of bighorn sheep were positively correlated to larger patches. We conclude that patch size and thus habitat carrying capacity, not population size per se, is the primary correlate to both population performance and persistence. Because habitat carrying capacity defines the upper limit to population size, clearly the amount of suitable habitat in a patch is ultimately linked to population size. Larger populations (250+ animals) were more likely to recover rapidly to their pre-epizootic survey number following an epizootic (p = 0.019), although the proportion of the population dying in the epizootic also influenced the probability of recovery (p = 0.001). Expensive management efforts to restore or increase bighorn sheep populations should focus on large habitat patches located ≥23 km from domestic sheep, and less effort should be expended on populations in isolated, small patches of habitat.*

El Papel del Tamaño del Parche, Enfermedades y Movimientos en la Rápida Extinción del Borrego Cimarrón

Resumen: *La controversia (Berger 1990, 1999, Wehausen 1999) sobre extinciones rápidas del borrego cimarrón (*Ovis canadiensis*) se ha enfocado solo en los tamaños poblacionales como una correlación con los tiempos de persistencia. Reportamos la persistencia y adaptabilidad de 24 poblaciones translocadas de cimarrones. La persistencia de estos borregos cimarrones estuvo fuertemente correlacionada con parches de tamaño grande, distancias grandes con los borregos domésticos, tasas de crecimiento poblacional elevadas, movimientos migratorios, y con tamaños poblacionales grandes. La persistencia también estuvo positivamente correlacionada con un tamaño de rango de hogar promedio grande (p = 0.058, n = 10 poblaciones translocadas) y el tamaño del rango de hogar de los cimarrones (p = 0.087, n = 8 poblaciones translocadas). Un mayor tamaño en el rango de hogar y mayores tasas de dispersión estuvieron positivamente correlacionadas con parches grandes. Por lo tanto concluimos que el tamaño del parche y la capacidad de carga del hábitat, pero no el tamaño poblacional, en sí, es la correlación principal tanto para la adaptabilidad como para la persistencia de la población. Debido a que la capacidad de carga del hábitat define los límites superiores del tamaño poblacional, es claro que la cantidad de hábitat propicio en un parche está en última instancia ligada al tamaño poblacional. Las poblaciones más grandes (250+ animales) tuvieron más factibilidad de recuperación de sus* n *muestreados pre-epizoóticos después de una epizootia (p = 0.019), aunque la proporción de la población que estaba falleciendo durante el evento epizoótico también influenció la probabilidad de recuperación (p = 0.001). Los costosos esfuerzos de restauración o incremento de poblaciones de bor-*

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rego cimarrón deberían ser canalizados hacia parches grandes que se encuentran a más de 23 km de las ovejas domésticas, y se deberían canalizar menos esfuerzos hacia poblaciones que se encuentren en parches de hábitat aislados y pequeños.

Introduction

The rapid extinction of small populations of bighorn sheep (*Ovis canadensis*) has been described by Berger (1990). He proposed a general model of extinction as a function of population size based on extinction rates of 122 bighorn sheep populations in California, Colorado, Nevada, Texas, and New Mexico. He estimated that all populations of ≤50 sheep would be extinct within 50 years, approximately 50% of populations of 51–100 animals would survive 50 years, and all populations of ≥100 would persist for 50 years. Berger (1990:93) concluded that "native populations below a threshold size (n = 50) are unable to resist rapid extinction." Several exceptions of small populations that persisted were later reported by Krausman et al. (1993, 1996) for Arizona and by Goodson (1994) for Colorado. Wehausen (1999) reported more exceptions and questioned the validity and the general applicability of Berger's model. Berger (1999) later countered that Wehausen's (1999) reinterpreted data set demonstrated the same approximate high extinction rate (42%) for all populations as did Berger's (1990) original paper, but simply with less steep trajectories.

Our goal was to evaluate factors that may influence the persistence or extinction of small bighorn sheep populations consistent with the declining population paradigm of Caughley (1994). Recent analyses by Berger and Wehausen emphasize the role of small size (i.e., the small population paradigm of Caughley 1994), rather than identifying limiting factors or mechanisms that might account for the extinction of small populations. Caughley (1994) has described the limitations of the small population paradigm, wherein the effect (i.e., smallness) is treated as if it were the cause of extinction. We suspect that carrying capacity—the upper limit to population size—and other factors are more critical than is small population size per se. We inspected all the factors that might contribute to the rapid decline (smallness) and extinction of a number of translocated populations of bighorn sheep. We address other limiting factors to shed light on why some populations go extinct and others do not. We propose that a blending of the two paradigms may help explain the rapid extinction of some bighorn sheep populations.

We present an analysis of the persistence of 24 translocated populations of bighorn sheep as an independent and better-documented replicate of the indigenous populations analyzed by Wehausen (1999) and Berger (1990). Independent replication is always desirable where there is a conflict of interpretation. In our sample, the release date is known and persistence can be compared to time since release for all populations. Also, there is less confusion over movements between herds because all releases occurred in areas devoid of other sheep and many released animals were radiocollared. The translocations were roughly comparable at the time of release because all occurred in areas of historic range. All release areas possessed some suitable habitat. We analyzed populations in only one state (Colorado) analyzed by Berger (1990) and none of those analyzed by Wehausen (1999). Our information was more recent (translocations occurred 1946–1986, median year of release 1975), and the techniques (use of helicopter, radiocollars, mark-recapture, sightability models) were more modern and quantitative (Neal et al. 1993; Bodie et al. 1995; Krausman et al. 1996) than some of the survey techniques in the data sets of Berger (1990) and Wehausen (1999). Finally, the observation period was sufficient based on population performance under optimal conditions (e.g., North and South San Rafael Swell, Utah; Moody Canyon) for any of the populations to grow to several hundred animals.

We predicted that persistence of translocated populations of bighorn sheep would be positively correlated with patch size and negatively correlated with ratio of patch perimeter to area. In many taxa, persistence of animal populations has been positively correlated with patch size (Fritz 1979; Schoener & Spiller 1987; Thomas 1990; Fahrig & Merriman 1992; Kindvall & Ahlen 1992; Hanski 1994) because larger patches typically support larger populations that are more resistant to catastrophe and chance extinction (Gilpin & Soulé 1986). Larger patches are also likely to contain more habitat diversity, will create less edge effect because of a lower ratio of perimeter to area, and should permit greater genetic heterozygosity in populations (Saunders et al. 1991).

We also predicted that the presence of domestic sheep would be negatively associated with persistence. Bighorn sheep are vulnerable to epizootics and large die-offs, most of which are caused by bronchopneumonia typically traced to *Pasteurella* (Spraker & Hibler 1982). Active epizootics in bighorn sheep have been associated with close physical contact with livestock, especially domestic sheep (Buechner 1960; Lange et al. 1980; Foreyt & Jessup 1982; Goodson 1982; Sandoval 1988).

We also hypothesized that sedentariness in bighorn sheep populations would be negatively correlated with persistence. Sedentariness (Risenhoover et al. 1988) is the nonmigratory tendency and overconcentration typical of many static or declining bighorn sheep herds. The

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sedentariness may be related to increasing habitat isolation from human development and to encroaching tall shrub and conifer cover due to fire suppression (Risenhoover et al. 1988; Etchberger et al. 1990). Sedentariness may be the single largest problem facing modern bighorn sheep populations (Risenhoover et al. 1988). The overconcentration of bighorn sheep in small areas makes them more vulnerable to predators and may increase parasite loads. Additionally, forages are used by nonmigratory herds at higher rates and on a year-round basis, likely causing poorer animal body condition (Risenhoover et al. 1988).

Thus, we predicted that population size and growth rate would be positively related to greater movement and dispersal, including seasonal migration, larger home-range size, and greater numbers of forays. Greater movement, in turn should be positively correlated with increasing patch size. We hypothesized that the recovery and subsequent persistence of any populations of bighorn sheep subjected to epizootics would be correlated with larger population sizes (sensu Berger 1990).

Methods

Persistence, Population Growth, and Patch Size

We determined population size in 1997 (the most recent year of data for all herds) from 24 translocated populations of bighorn sheep (Table 1). We estimated population sizes from annual helicopter counts, corrected for animals missed by means of either (1) mark-recapture (Neal et al. 1993), (2) population reconstruction, or (3) Idaho sightability corrections (Bodie et al. 1995; Singer & Gudorf 1999; Singer et al. 2000*a*, 2000*b*). We calculated average lambda (λ) for the most recent 10 years for each population with the formula $\lambda = N_{t+1}/N_t$, where t is time in years and N is population size. We categorized each population as migratory when $\geq$75% of the population used two or more distinct seasonal ranges that did not overlap, partially migratory when 25–74% of the population used two or more ranges, and nonmigratory when <25% of the population used seasonal ranges (Table 1).

We calculated area of suitable habitat within each occupied habitat patch using a habitat evaluation procedure for Rocky Mountain bighorn sheep developed by Smith et al. (1991), with modifications made by Johnson and Swift (2000). Six habitat criteria were integrated in a geographic information system (GIS) to determine areas of habitat suitable for viable populations of bighorn sheep. Bighorn sheep are habitat specialists that prefer open, steep slopes or open, flat areas located adjacent to these steep slopes. Bighorn sheep confine nearly 95% of their activities to open areas of escape terrain or to areas within 300 m of escape terrain (Smith & Flinders 1991). We defined occupiable habitat as all escape terrain on slopes of 27–85° (averaged across 30-m^2 pixels and identified from standard U.S. Geological Survey digital elevation models) and all adjacent habitat located within 300–500 m of escape terrain. We used five additional criteria to evaluate habitat suitability for bighorn sheep: (1) distance to perennial water sources; (2) presence of human-made and natural barriers to routine bighorn movement; (3) adequate horizontal visibility (measurement of visibility of 55% through vegetation; Johnson & Swift 2000); (4) presence of urban or developed areas; and (5) presence of livestock grazing allotments. These criteria are described in greater detail by Zeigenfuss et al. (2000).

We evaluated current population size and population growth rate (λ) as a function of habitat and population variables through general linear models. Independent variables tested included (1) our GIS estimate of suitable habitat area, (2) migratory tendency, (3) perimeter-to-area ratio of modeled suitable habitat (an indication of patchiness of the habitat), (4) distance to domestic sheep, (5) founder size, (6) population growth rate, and (7) years since release. We investigated all combinations of two, three, or four of these variables to select the most parsimonious or "best" biological model, defined, following Burnham and Anderson (1991), as a trade-off between the number of parameters, model bias, and variance of the estimate. We used Akaike's information criteria (AIC) and forward and backward stepwise regression to select the best model (McQuarrie & Tsai 1998). We also ran univariate models for each variable.

We gathered information on movements of radiocollared individuals for 10 of the populations from more than 5000 radiotelemetry locations of 99 individual sheep. Study-site home ranges were estimated by the 95% convex polygon estimation method, which removes the observation farthest from the arithmetic center, calculates a new center, and then repeats the procedure until 5% of the observations are excluded (Ackerman et al. 1990). By defining a probabilistic measure of home-range size, this method removes outliers and increases the objectivity of the estimate. These adjustments allow for comparison across populations with different sample sizes (White & Garrott 1990).

We defined a dispersal foray as any short-term movement of a radiocollared animal from and back to an established home range. Rate of foray was determined for each herd by totaling the number of forays for all radiocollared individuals and dividing by the total number of years of individual's radiocollar data. We also recorded the number of colonizations by both sexes of adjacent unoccupied patches. We conducted univariate analyses of the 10 populations with information on sheep movements (the sample was insufficient for multivariate analysis) with general linear models as described above.

Population Size versus Recovery from Epizootics

We analyzed data from an additional 41 bighorn sheep populations that had experienced epizootics (Feuerstein

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Table 1. Demographic and habitat characteristics of 24 translocated populations of bighorn sheep in the western United States.

Site[a]	*State*	*Year of release*	*Founder* n	*Population growth pattern*[b]	*Size of release patch* (km^2)[c]	*Perimeter of release patch (km)*	*1997 population size*	*Migratory tendency*[d]	*Population growth rate* (λ)	*Distance to domestic sheep (km)*	*Home range* (km^2)	*Average ewe home range* (km^2)	*Average ram home range* (km^2)	*Foray rate*[e]	*Colonizations of unoccupied patches*
Moody Canyon (1,3,4)	Utah	1975	23	1	466[f]	3200	324	3	1.17	45	17.6	11.4	30.1	0.23	1
Red Slide (1,3,4)	Utah	1984	22	1	466	3200	145	3	1.17	24					1
Mesa Verde (5)	Colorado	1946	14	2	4.9	26	5	1	0.96	8					0
Dillon (2,3,4,5)	Colorado	1974	44	2	264	8000	35	1	0.90	1	19.5	30.6	14.0	0	1
Lake Fork (2,3,4)	Colorado	1975	16	2	28.3	1000	20	1	0.74	0					0
Black Canyon (3,4)	Colorado	1986	83	2	25	760	40	1	0.85	1					0
Colorado Monument (1,2,3,4,5)	Colorado	1979	39	1	312	630	150	2	1.18	10	35.3	35.3		0.04	1
Beaver Creek (2,3,4,6)	Colorado	1983	21	2	18.5	23	0	1	0.52	1.8				0.13	1
Ladore Canyon (1,4,5)	Colorado	1952	32	3	136	700	130	1	0.89	3					1
Pool Creek (2,3,4,5)	Colorado	1984	19	1	333	1500	70	1	1.26	3	29.0	3.2	54.7		1
Arches (1,2,3,4,5)	Utah	1985	23	1	224	580	125	1	1.21	15	11.5	12.5	9.8	0	2
Maze (3,4,5)	Utah	1982	25	1	1145	2000	90	3	1.13	45				0.15	0
Bighorn Canyon (1,2,3,4,5)	Montana	1975	13	1	736	2800	90	3	1.13	10	19.6	15.7	24.2		2
Badlands north (2,3,4,5)	South Dakota	1967	14	1	161	610	111	1	1.18	4	6.1	6.1		0.16	2
Badlands south (2,3,4,5)	South Dakota	1981	6	1	253	870	45	1	1.00	8.5				0.21	
Theodore Roosevelt (4,5)	North Dakota	1966	20	2	8.1	400	0	3	0.27	3					0
Island in the Sky (1,2,3,4,5)	Utah	1966	60	1	442	790	225	3	1.13	52	21.2	11	31.5	0.05	2
Potash (2,3,4,5)	Utah	1975	10	1	449	1180	160	3	1.15	31					2
Lockhart (2,3,4,5)	Utah	1980	7	2	1416[f]	2350	45	3	1.20	6					0
Needles (2,3,4,5)	Utah	1965	15	2	1416	2350	30	1	1.17	24	9.4	8.6	14.7	0	0
Lone Buttes (3,4)	North Dakota	1985	18	1	10.8	34	33	1	1.08	2					0
Magpie Creek (3,4)	North Dakota	1959	20	2	3	31	28	1	1.00	10					0
Wanagan (3,4)	North Dakota	1970	10	1	3.9	30	20	1	1.05	16					0
Chateau (3,4)	North Dakota	1970	15	1	4.2	35	40	1	1.08	16					0

[a] *Dispersal and colonization of released group monitored by 1, university graduate student; 2, full-time resources-agency technicians or biologists; 3, regular aerial radiotelemetry flights; 4, periodic helicopter surveys of the unoccupied habitat; 5, park observation system. 6, herd depopulated in 1997.*
[b] *1, steadily increasing to stable; 2, initially increased but then declined to extirpation or remnant; 3, declined to <30 but then increased.*
[c] *Suitable habitat in release patch based on geographic information system habitat model of Smith et al. (1991), modified by Johnson (2000).*
[d] *Migratory tendency: 1, nonmigratory; 2, only segments of the population migratory; 3, fully migratory.*
[e] *Number of forays (departure and return to normal home range) per radiocollared animal per year.*
[f] *Two translocated populations joined; their suitable habitat areas were pooled.*

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et al. 1980; Lange et al. 1980; Jessup 1981; Foreyt & Jessup 1982; Onderka & Wishart 1984; Bailey 1986, 1990; Festa-Bianchet 1988; Coggins & Matthews 1992; Meagher et al. 1992; Singer et al. 2000*b*). We included only those populations with data on pre-epizootic population size, percent population decline as a result of the disease outbreak, number of years to full recovery (defined as recovery to pre-epizootic size for those that recovered), whether the epizootic resulted in extirpation or quasi-extirpation, and most recent population size of the herd. We defined quasi-extirpation as a decline to ≤29 animals, a size from which we believed the population was unlikely to recover. Only one population from a sample of 100 populations (Singer et al. 2000*a*) ever declined to this small size and later grew beyond 30. We categorized a recovery rate as rapid (≤10 years) or slow (>10 years or no recovery at all). We then compared (1) extirpation and (2) recovery rate to pre-epizootic population size using logistic regression.

Table 2. Comparison of significant values for variables that correlated with population performance of bighorn sheep.*

Dependent variable	*Independent variable*	p (n = 24)	F
Current population size	suitable habitat	0.3948	0.75
	distance to domestic sheep	0.0002	20.53
	migratory tendency	0.0245	4.45
	population growth rate	0.0166	6.72
	years since release	0.6559	0.20
	preimeter: area of habitat	0.1531	2.19
	size of founder group	0.3255	1.01
Population growth rate (λ)	suitable habitat	0.0255	5.74
	distance to domestic sheep	0.0451	4.69
	migratory tendency	0.4080	0.94
	years since release	0.4772	0.52
	perimeter: area of habitat	0.0184	6.49
	size of founder group	0.5744	0.32

**Tests based on univariate models.*

Results

We found that (1) larger patch sizes, (2) a migratory tendency, (3) population growth rate, and (4) the absence of domestic sheep were correlated to 1997 population size (AIC = 9.25). We selected this "best model" using both stepwise regression and AIC criteria. Univariate analyses showed that translocated bighorn sheep populations grew to a large size when they were farther from domestic sheep ($p < 0.001$), when population growth rates were higher ($p = 0.035$), and when the animals were migratory ($p = 0.005$; Table 2). Although univariate analysis did not show a significant correlation of 1997 population size with patch size (Fig. 1a), this variable was an element of the best multivariate model for predicting population size. Growth rates (λ) were higher in those translocated populations that were released in larger patches ($p = 0.039$; Fig. 1b), where the patch possessed a smaller perimeter-to-area ratio ($p = 0.002$), and where distances to domestic sheep were larger ($p = 0.067$; Table 2).

Greater movements by bighorn sheep also contributed to the success of translocated populations. Bighorn sheep in larger populations had larger average home-range sizes ($p = 0.032$) and larger ram home-range sizes ($p = 0.079$; Fig. 2). The rate of colonization of nearby unoccupied patches was also correlated to patch size for the original release ($p < 0.004$). Bighorns released into smaller patches of suitable habitat—small patches averaged 81.5 ± 34.4 km^2 (x ± SE)—were less likely to colonize nearby patches, whereas animals released into larger patches of x = 158.7 ± 60.3 km^2 colonized, on average, one nearby patch. Those animals released into patches of suitable habitat of 573.1 ± 130.5 km^2 successfully colonized two adjacent patches on the average.

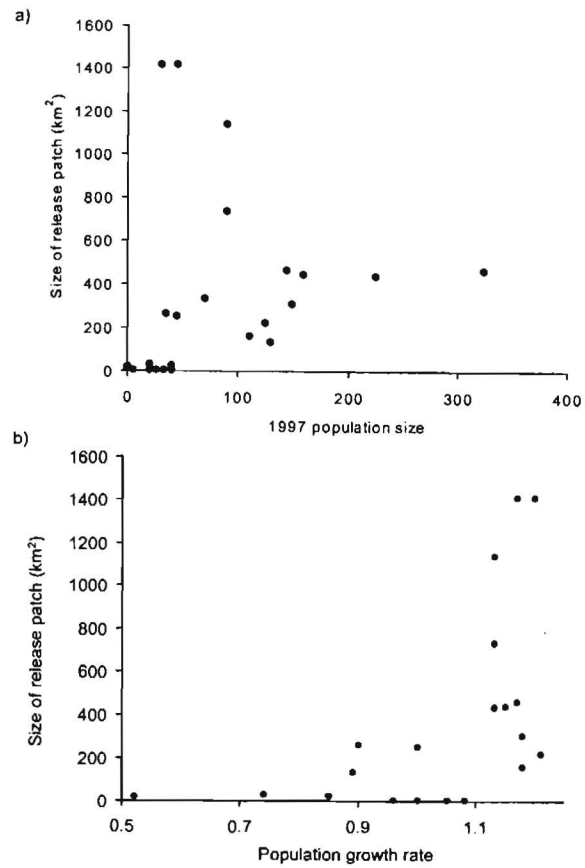

Figure 1. The relationship of size of release patch to 1997 (a) population size and (b) population growth rate (λ).

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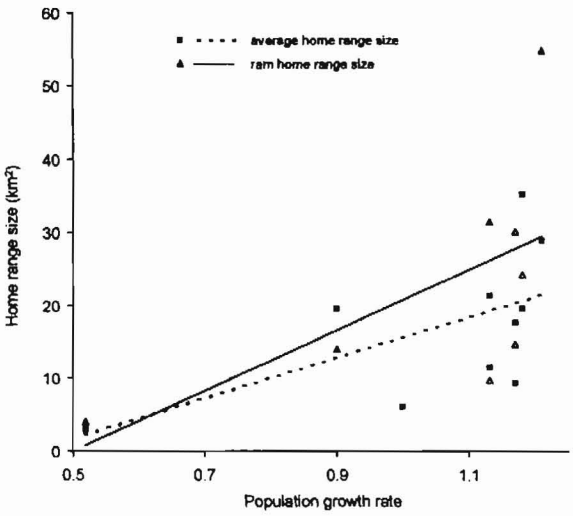

Figure 2. The relationship between population growth rates of 10 translocated bighorn sheep herds to average home-range size of both sexes and to home-range size of rams.

Pre-epizootic population size was correlated with extirpation or quasi-extirpation of the population. Following disease epizootics, smaller populations (49.2 ± 11.8 animals) were more likely to become extirpated or quasi-extirpated than larger populations (292.2 ± 82.4, $p = 0.019$). Small populations (67.6 ± 13.5 animals) were also slower to recover to their pre-epizootic number than were larger populations (371.0 ± 112.3, $p = 0.023$). Only 5% of herds with pre-epizootic population sizes of ≤50 were able to persist after a disease epizootic, whereas 75% of herds with populations of 51–100 and 83% of herds with populations of >100 individuals were able to recover and persist following an epizootic ($p = 0.001$).

Discussion

Consistent with findings for other vertebrates (Fritz 1979; Schoener & Spiller 1987; Fahrig & Merriman 1992; Kindvall & Ahlen 1992; Hanski 1994), patch size and ratio of the perimeter to area within the patch were positively correlated to growth rates (λ) of released populations of bighorn sheep. The growth of released populations to large sizes was best explained by larger patch size, longer distance to domestic sheep, higher population growth rates, and greater migratory and movement tendencies. Because population size is logically related to patch size, there appears to be a basis for a potential minimum threshold of population size for extinction, as Berger (1990, 1999) contends. But we concluded that patch size, not population size, is the parameter of concern. Thus, management actions that are justified for large patches of suitable habitat may be less justified for isolated small patches. Expensive management actions for bighorn sheep, such as habitat augmentation, creation of new water sources, prescribed burning, clearing, and corridor creation, should be conducted primarily in areas that meet minimum patch criteria, including minimum thresholds for patch size and ratio of perimeter to area and the absence of domestic sheep.

Persistence of bighorn sheep populations was negatively correlated with the presence of domestic sheep. Evidence from controlled experiments (Onderka et al. 1988; Callan et al. 1991) and anecdotal field observations (Lange et al. 1980; Goodson 1982; Sandoval 1988) are in accordance with this correlation. We recommend that bighorn sheep be restored only to areas >23 km away from domestic sheep (Singer et al. 2000*a*).

We recommend that GIS evaluations of habitat patches be conducted prior to costly restoration or management interventions for small populations (see also Berger 1999). This is worth the effort considering the high cost of habitat manipulation, additional translocations or augmentations (Bleich 1990), and the scarcity of source stock of bighorn sheep (Leslie 1980).

We suspect that several mechanisms relate patch size to persistence. Larger patches tend to be more diverse in habitat and elevation, and, in larger patches, more-mobile bighorn sheep would have an opportunity to forage on a wider variety of phenological stages. Migration, which we found to increase with larger patch size, may be advantageous as a predator-avoidance strategy among ungulates (Bergerud 1984; Sinclair 1985), in particular due to the increased dispersion of vulnerable ungulates at birthing time (Bergerud & Page 1987). Migratory reproductive female ungulates also have larger body mass and thus potentially higher reproductive success than nonmigratory females. Larger patches should also result in less overcrowding and a higher per capita rate of food availability and thus improved body condition. The possibility of higher parasite loads and higher vulnerability to predators on overcrowded smaller patches also makes for interesting (Risenhoover et al. 1988), although as yet untested, hypotheses. Overcrowding on small patches may be associated with disease epizootics (Bailey 1986; Festa-Bianchet 1989). Larger populations that occupy larger patches should also possess higher genetic heterozygosity (Saunders et al. 1991; Fitzsimmons et al. 1995, 1997).

A larger pre-epizootic population size increased the likelihood of the persistence and rapid recovery of a population following disease outbreaks. Krausman et al. (1996) and Wehausen (1999) argue that populations of bighorn sheep with ≤50 animals have persisted, but our analysis suggests that such populations have only a 5% chance of surviving even a single epizootic. The opti-

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mum population size for recovery from epizootics determined by our analysis (292 ± 82 animals, $x \pm$ SE) was six times larger than the 50 animals that Wehausen (1999) argues is a persistence threshold. Of course, not all populations are subjected to epizootics, but no bighorn sheep population is ever completely without risk. Disease is so common in this species (Bailey 1990; Hobbs & Miller 1991; Gross et al. 1997, 2000) that we recommend populations be managed for sufficient size to survive epizootics.

We conclude that larger patch size, larger home-range size, greater migratory tendency, and the absence of domestic sheep are the most critical factors for population persistence in bighorn sheep. Small population size alone should not be treated as the cause of extinction (Caughley 1994). But because population size is ultimately a consequence of patch size, it may be sensible for management to identify some population thresholds for persistence. One advantage to managers of identifying a threshold population size is to identify the population size at which persistence and recovery are more likely following epizootics. Also, below some threshold population size, the average group size may be too small for efficient vigilance and predator detection. For example, Berger and Cunningham (1988) reported a group size of 6-10 bighorn sheep and Risenhoover and Bailey (1985) a group size of >10 animals for optimal vigilance behavior and foraging efficiency. In support of this relationship, three populations in our study numbering >100 possessed average group sizes of 9.8 ± 0.9 ($x \pm$ SE) animals, and three small populations of 25-30 animals possessed smaller group sizes of only 3.7 ± 0.4 animals. Thus, the smaller populations possessed average group sizes below the suggested optimum. We concur with Berger (1999) that some populations may be too small to justify expensive management, although not all small populations should be written off (Thomas 1990; Wehausen 1999). We recommend that resources be directed to those bighorn sheep populations that inhabit large, high-quality patches of habitat where potential contacts with domestic sheep are minimal.

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