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# Persistence of Different-sized Populations: An Empirical Assessment of Rapid Extinctions in Bighorn Sheep

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**Abstract:** *Theory and simulation models suggest that small populations are more susceptible to extinction than large populations, yet assessment of this idea has been hampered by lack of an empirical base. I address the problem by asking how long different-sized populations persist and present demographic and weather data spanning up to 70 years for 122 bighorn sheep (*Ovis canadensis*) populations in southwestern North America. Analyses reveal that: (1) 100 percent of the populations with fewer than 50 individuals went extinct within 50 years; (2) populations with greater than 100 individuals persisted for up to 70 years; and (3) the rapid loss of populations was not likely to be caused by food shortages, severe weather, predation, or interspecific competition. These data suggest that population size is a marker of persistence trajectories, and they indicate that local extinction cannot be overcome because 50 individuals, even in the short term, are not a minimum viable population size for bighorn sheep.*

**Resumen:** *La teoría y los modelos de simulación sugieren que las poblaciones pequeñas son más susceptibles a la extinción que las poblaciones grandes, pero la evaluación de esto se ha visto obstaculizada por falta de una base empírica. Me refiero a este problema aquí, preguntando por cuánto tiempo persisten las poblaciones de diferentes tamaños y presentando datos demográficos y climáticos de un período que alcanza hasta 70 años para 122 poblaciones de ovejas Bighorn (*Ovis canadensis*) en el sudoeste de Norte América. Los análisis revelan que: 1) 100% de la poblaciones con menos de 50 individuos se extinguieron en 50 años. 2) Poblaciones con más de 100 individuos persistieron hasta los 70 años. 3) La rápida pérdida de poblaciones probablemente se ha debido a falta de alimento, clima severo, predación, o competencia interespecífica. Estos datos proponen que el tamaño de una población es un marcador de trayectorias de persistencia, e indican que una extinción a nivel local no puede ser impedida, ya que 50 individuos no representan un tamaño de población mínima viable para las ovejas bighorn, aún en el corto plazo.*

## Introduction

Concern about the long-term persistence of populations (Smith 1974; Geist 1975; Shaffer & Sampson 1985; Goodman 1987; Newmark 1987) has led to questions about the size a population should be to minimize its chances of extinction (Gilpin & Diamond 1980; Wilcox & Murphy 1985). Until now, only evidence from simulation models (Soulé et al. 1979; Diamond 1984; Harris et al. 1987; Iwasa & Mochizuki 1988), from avian turnover rates (Pimm et al. 1988), and of the historical loss of species of unknown population sizes (Brown 1971; Patterson 1984) has been available to suggest how long isolated mammalian populations persist, and it has not been possible to assess the generality of the models or conservation tactics (Lande 1988). Such assessments are important because, as ecosystems continue to be fragmented, questions arise about the spatial requisites needed to assure the sustenance of many species, and empirical data are necessary to judge the validity of extinction and viability models. Historical data offer a promising approach to refining knowledge in this area. Prior use of such data was helpful in forming and testing island biogeographic theory, but the data have not been amenable to projections of persistence by population size since they usually exist in the form of records of species' or populations' occurrences where data on population size are unavailable.

Here, I use existing data on multiple, small, insular bighorn sheep populations, primarily in the deserts of southwestern North America, to examine how long local extinctions may be resisted. Although Soulé (1987) suggested that small populations are more vulnerable to extinction than large ones, neither the time frame of persistence in relation to population size nor the effects of various factors are well known for mammals. Native sheep in xeric environments are well suited for examination of such issues for two principal reasons. First, they occur in small, isolated populations and in larger metapopulations (Geist 1971) inhabiting almost continuous mountain chains from which historical data on population size are available. And, although "population" is defined in terms of scale and dimensionality (Soulé 1987), bighorn biologists use the word to refer to sheep confined naturally to a discrete mountainous area (which may vary from several km<sup>2</sup> to more than 1,000 km<sup>2</sup>); I adopt this usage here. Second, food abundance and its changes over time can be estimated for each population because plant primary productivity is predicted by rainfall (Rosenzweig 1968; Coe et al. 1976). By using historical information it is possible to generate the data set needed to examine how long different-sized populations persist and possible causes of extinction.

## Methods, Sources of Data, and Limitations

I collated information on 129 native populations from five states — California, Colorado, Nevada, New Mexico, and Texas (Table 1). Excluded were states where sheep now occur solely because of reintroductions by humans (Oregon and Washington), states that did not respond to my queries (Arizona), and states whose data span less than two decades (Utah). Also excluded were populations for which only one size estimate was available. Populations were included only when estimates were published or provided by respective management agencies or university biologists who had made multiple ground or aerial censuses. Since the focus of my analyses was on persistence of native populations, I did not include extant native populations for time periods after sheep had been reintroduced to them; only two Nevada populations and one New Mexico population were in this category. The sources I used were Bear & Jones (1973), Berbach (1987), Buechner (1960), Campbell (1984), Davis & Taylor (1939), Deforge et al. (1981), Dunaway (1970), Goodson (1982), Gross (1960), Jones (1950), Lenarz (1979), McQuivey (1978), Moser (1962), Ober (1931), Sands (1964), Weaver (1972), Weaver (unpublished), Weaver & Mensch (unpublished), Wehausen (1980, 1985), Welles & Welles (1961), California Fish and Game (unpublished), Colorado Division of Wildlife (unpublished), National Park Service (Death Valley), Nevada Department of Wildlife (unpublished), and New Mexico Fish and Game (unpublished).

To be conservative, I omitted data from an additional 94 populations since past estimates of population size were not available, even though it was known that these populations had undergone recent extinctions (Wehausen et al. 1987b). Because my goal was to estimate persistence by population size, I relied on data sources that provided actual estimates rather than those that merely noted the presence or absence of sheep. Persistence was estimated for each decade up to 70 years, the maximum period for which data were available. To minimize the confounding influence of sampling intervals, only the latest annual census per decade was used. I considered a population to be extinct only after two or more censuses failed to provide evidence of its existence.

To estimate primary plant productivity, I used precipitation records from *Climatology of the United States* and based estimates on the stations closest to each bighorn population. Data were unavailable for 7 of the 129 populations. For each of the remaining 122 sites, rank-related correlations were used to examine the relationships between precipitation and time (years) (Table 1).

Extinction frequencies for five classes of population sizes ( $S_i$ ) ( $i = 1-5$ : of 1-15, 16-30, 31-50, 51-100;

100+) were estimated by asking whether each population was present (P) or extinct (E) at and over time ( $T_j$ ) where  $j = 1-7$  and refers to decades of possible persistence. Put simply, the probability of persistence was calculated by categorizing the presence or absence (= extinctions) of populations by size and time as follows. If  $S = 0 @ T_j$  and  $@ T_j + 1$ , then  $SP_{ij} = SP_{ij} + 1$  and  $SE_i = SE_{ij} + 1$ . However, if  $S = 0 @ T$  or  $T + 1$ , then  $SE_{ij} = SE_{ij} + 1$ .  $SP_{ij}$  refers to the frequency of populations present, and  $SE_{ij}$  to the frequency of extinctions for size  $i$  and time  $j$ . This procedure applied to  $N$  populations yields a binomial for incremental periods (in this case 10 years), but because of uneven censusing by management agencies or researchers, sample sizes differed among decades. For example, if hypothetical population  $X$  consisted of 20 animals in 1938 and was extinct in 1958 when recensused twice, then a maximum persistence time of 20 years was assigned.

When dealing with census data from different management agencies and techniques that vary among years and habitats, it is difficult to remove potential biases and to standardize data sets. Clearly, methods used four or five decades ago will be less precise than those used today, and there is no straightforward way to deal with this problem. Therefore, I must assume that larger populations were more detectable than smaller ones and that any biases reported in the overestimation of populations of large size should be cancelled by the effects of underestimation of populations of smaller sizes. However, it is also possible to contrast data on persistence in relation to population size at different time periods. Assuming that the persistence trajectories of different-sized populations are real, then analyses based on recent and older population estimates should not differ. If this were the case, it would bolster support for the idea that population estimates, while being biased to an unknown extent, do not alter the interpretations since patterns detected from the more recent data would be consistent with those found during censusing periods from decades ago.

### Persistence and Population Size

Populations of 100+ sheep persisted for up to 70 years; those with fewer than 50 individuals went extinct in less than 50 years, while those with between 51–100 sheep existed for about 60 years (Fig. 1). Because, at year 60, the sample is so small (of two historic populations, none persisted), it is not possible to ascertain whether sheep in the 51–100 category fit closer to the persistence trajectories of the smaller or larger populations.

The extinctions were related to initial population size and the number of years over which data were available (three-dimensional contingency analysis:  $X^2 = 134.87$ ;  $df = 46$ ;  $p < 0.001$ ), but except for populations of

100+, initial population size was not independent of year ( $X^2 = 22.10$ ;  $df = 16$ ; NS). It is also possible to test further for partial dependence (Zar 1984), not by relying on the entire data set, but by using only those data for the last two decades, the time frame when census methods have presumably become more refined. While time period (in this case, two decades;  $T_j = 2$ ) had only a slight effect on persistence ( $X^2 = 20.48$ ;  $df = 12$ ;  $0.05 < p < 0.10$ ), extinctions were not independent of initial population size ( $X^2 = 39.87$ ;  $df = 4$ ;  $p < 0.001$ ), reaffirming that population size by itself is a reasonable marker of persistence. When data over all time periods are considered, a positive relationship between population size and persistence time existed (Fig. 1;  $r_s = +0.54$ ;  $p < 0.0005$ ). Hence, these data offer the strongest evidence yet that native populations below a threshold size ( $N = 50$ ) are unable to resist rapid extinction.

### Tests of Potential Causes of Rapid Population Losses

To what extent do the persistence times reflect recolonization rather than extinction? Undoubtedly, precision is lost by lack of knowledge of recolonization frequency. However, the persistence estimates are conservative and underestimate population losses because any recolonization would result in increased persistence rather than local extinction. Furthermore, the available data indicate that extinction has far outstripped recolonization, 34 to 2 (one-tailed binomial test;  $p < 0.001$ ), although recolonizations often go undetected (Bleich et al. 1990).

Four variables that may mediate the rapid demise of these small populations may be examined: (1) climatic severity, (2) food shortages, (3) predation, and (4) interspecific competition. None of these appears to be causally related to the rapid extinctions. If the demises were a consequence of severe weather, then populations in areas of extreme conditions should be in greater jeopardy than those where conditions are more benign. I examined this possibility by contrasting environmental severity (as measured by the mean number of annual days in which mean maximum daily temperature was below or above  $0^\circ\text{C}$ ) between populations greater and less than 50 sheep. Since 10 percent ( $N = 50$ ) of the small populations occupied areas where temperatures fell below  $0^\circ\text{C}$  for more than one month on average (in contrast to 44 percent [ $N = 62$ ] of the larger populations:  $Z = 3.97$ ;  $p < 0.0001$ ), it is unlikely that climatic factors were the primary reason for the rapid loss of small populations.

Perhaps declining food supplies were responsible, especially because evidence from one desert population indicates that few lambs are recruited when precipitation is low (Douglas & Leslie 1986). If this were the case

**Table 1. Summary of location, year of first population census, and number of years of precipitation data (N),  $r_s$  values, and probability that precipitation changes over time were significant; NS = not significant; \* $p < 0.05$ ; \*\* $p < 0.02$ ; \*\*\* $p < 0.001$ .**

Site	Year	N	$r_s$	P	Site	Year	N	$r_s$	P
California									
1 Argus Ra	1957	24	-.02	NS	62 Santa Rosa	1957	0	—	
2 Avawatz Ra	1957	26	+.30	NS	63 Shadow Mts	1938	20	+.43	*
3 Baxter Cr	1915	40	+.01	NS	64 Sheep Hole	1957	30	+.34	NS
4 Big Maria Mts	1946	23	+.05	NS	65 Slate Ra	1957	14	-.11	NS
5 Birch Mtn	1911	50	-.21	NS	66 Stepladder	1957	13	-.20	NS
6 Black Mts	1957	26	+.18	NS	67 Taboose Cr	1948	24	-.02	NS
7 Bristol Mts	1957	30	+.34	NS	68 Tierra Blnc	1957	0	—	
8 Bullion Mts	1957	30	+.34	NS	69 Turtle Mts	1957	24	+.29	NS
9 Cache Pk	1933	16	-.11	NS	70 Vallecito	1957	30	+.42	*
10 Cady Mts	1957	23	+.13	NS	71 Wheeler Ri	1921	20	-.09	NS
11 Castle Pk	1957	27	+.40	**	72 Whipple Mts	1946	41	+.29	NS
12 Chemehuevi Mt	1957	30	+.37	*	73 White Mts	1970	17	+.35	NS
13 Chocolate Mts	1957	30	+.42	*	74 Woods Mtn	1974	12	+.31	NS
14 Chuckwalla Mt	1957	30	+.21	NS	Colorado				
15 Clark Mts	1957	29	+.17	NS	1 Arkansas R	1954	30	-.01	NS
16 Clipper Mts	1957	29	+.37	*	2 Battlement	1956	31	+.23	NS
17 Coso Ra	1957	24	-.02	NS	3 Black Cyn	1953	29	-.06	NS
18 Cottonwood Mt	1957	26	+.18	NS	4 Brush Cr	1947	21	+.50	*
19 Coxcomb Mts	1974	12	+.37	NS	5 Buffalo Pks	1956	24	+.16	NS
20 Dead Mts	1957	30	+.37	*	6 Cimarron Pk	1956	31	+.23	NS
21 Deep Springs	1946	35	+.04	NS	7 Clinetop	1955	30	+.51	***
22 Eagle Crags	1957	24	-.02	NS	8 Elkshhead Mt	1955	0	—	
23 Eagle Mts	1974	12	+.39	NS	9 Gore Ra	1955	24	+.16	NS
24 Funeral Mts	1957	26	+.18	NS	10 Lake City	1969	17	+.33	NS
25 Granite Mts	1957	22	+.28	NS	11 Mt Zirkel	1956	15	-.03	NS
26 Granite Mts	1946	20	+.43	NS	12 Pikes Peak	1954	30	-.01	NS
27 Grapevine Mts	1957	26	+.18	NS	13 Pole Mtn	1941	37	+.33	*
28 Hackberry Ra	1969	16	+.58	**	14 Redstone	1962	18	+.07	NS
29 Inkopah	1974	13	+.35	NS	15 Roan Plateau	1954	17	+.32	NS
30 Inyo Mts	1957	29	+.04	NS	16 Rocky Mtn NP	1955	30	+.11	NS
31 Iron Mts	1957	29	+.34	NS	17 San Luis Peak	1970	17	-.10	NS
32 Ivanpah	1974	12	+.31	NS	18 Sangre d Crst	1956	31	+.23	NS
33 Kelso Ra	1957	26	+.30	NS	19 Sheep Mtn	1961	26	-.04	NS
34 Kingston Ra	1957	26	+.30	NS	20 Snowmass	1955	24	+.16	NS
35 Laguna Mts	1957	18	-.33	NS	21 St. Vrain	1958	13	-.02	NS
36 Last Chance	1957	29	+.04	NS	22 Vallecito	1968	19	-.38	NS
37 Little Maria	1946	23	+.05	NS	23 Waterton Cyn	1956	0	—	
38 Little San B	1974	12	+.37	NS	24 West Elk Mts	1958	25	+.12	NS
39 McCoy Mts	1946	23	+.05	NS	Nevada				
40 Mt Langley	1947	32	+.04	NS	1 Black Mts	1976	10	-.08	NS
41 Mt Tom	1920	21	-.24	NS	2 Delamar Ra	1976	10	-.32	NS
42 Mt Williamson	1947	40	+.01	NS	3 Desert Ra	1976	10	-.32	NS
43 New York Mts	1957	27	+.40	**	4 East Desert	1976	10	-.32	NS
44 Nopah Ra	1957	29	+.17	NS	5 El Dorado Ra	1976	10	-.08	NS
45 Olancha Pk	1926	14	+.10	NS	6 Grant Ra	1960	26	+.53	**
46 Old Dad Mts	1957	30	+.34	NS	7 Highland Ra	1976	10	-.08	NS
47 Old Women	1957	30	+.34	NS	8 Lone Mtn	1976	10	-.20	NS
48 Orcopia Mts	1957	30	+.21	NS	9 Las Vegas Ra	1976	10	-.32	NS
49 Owlshead Mt	1957	23	+.13	NS	10 McCullough Ra	1976	10	-.08	NS
50 Palen Mts	1946	40	+.38	**	11 Meadow Valley	1976	10	-.32	NS
51 Panamint Ra	1957	26	+.18	NS	12 Monte Carlo	1976	10	-.20	NS
52 Pichacho Mt	1957	17	-.33	NS	13 Mormon Mts	1974	12	-.12	NS
53 Pinto Ra	1974	12	+.37	NS	14 Muddy Mts	1976	10	-.32	NS
54 Piute Ra	1957	27	+.40	**	15 Newberry Ra	1976	10	-.32	NS
55 Providence	1957	30	+.37	*	16 Pintwater Ra	1976	10	-.32	NS
56 Quail Mts	1957	18	-.12	NS	17 Silver Peak	1955	30	+.62	***
57 Queen Mts	1974	0	—		18 Spring Ra	1976	10	-.32	NS
58 Sacramento	1957	29	+.01	NS	19 Toiyabe Ra	1958	26	+.53	**
59 San Brnadno	1957	30	+.34	NS					
60 San Gabriel	1957	0	—						
61 San Ysidro	1957	30	+.42	*					

Table 1. Continued.

Site	Year	N	$r_s$	P	Site	Year	N	$r_s$	P
Texas					8 Glass Mts	1937	21	+ .19	NS
1 Apache	1937	25	+ .08	NS	9 Guadalupe	1937	25	+ .08	NS
2 Baylor Mts	1937	25	+ .08	NS	10 Sierra Diab	1937	25	+ .08	NS
3 Beach Mts	1937	25	+ .08	NS	New Mexico				
4 Carrizo	1937	25	+ .08	NS	1 Big Hatchet	1953	28	+ .37	*
5 Chinatic	1937	21	+ .19	NS	2 San Andreas	1941	31	+ .47	**
6 Delaware	1937	25	+ .08	NS					
7 Eagle Mts	1937	25	+ .08	NS					

Weather stations used in the above were located at: (California) Baker, Barstow, Bishop, Bishop Creek, Blythe, Death Valley, El Centro, Lone Pine, Needles, Twentynine Palms; (Colorado) Alamosa, Aspen, Canon City, Delta, Estes Park, Grand Junction, Lake City, Montrose, Rifle; (Nevada) Austin, Las Vegas, Searchlight, Tonopah; (New Mexico) Jornada Experiment Station; (Texas) Pecos, Van Horn.

for the populations that I examined, then a negative relationship between food abundance at each site and time should be characteristic of populations experiencing extinctions. Also, larger populations should not be associated with declining food abundance because it is the smaller populations that are more susceptible to extinction (Fig. 1). Annual precipitation was used as an indicator of food abundance since it is a good predictor of primary productivity in xeric environments (Rosenzweig 1968; Coe et al. 1976), and data on precipitation were available as far back as 1915. At none of the 122 sites was the relationship between estimated primary productivity and time negative, suggesting that declining food was not responsible for the extinctions (Table 1). In contrast, 17 percent of the 122 sites had increasing estimated plant productivity and 5 (all with fewer than 50 sheep) experienced extinction (Table 2). No association occurred between the size of extinct populations and estimated plant productivity ( $G_{adj} = 0.12$ ;  $df = 1$ ; NS; Table 2). This nonsignificant relationship remains unaltered by exclusion of populations from Colorado where precipitation is often in the form of snow. While numerous factors may account for the demises of small populations, neither food nor weather appears to be among them.

The last two potential factors responsible for the rapid extinctions, predation and interspecific competition, appear to have played minor roles, if any. Though accounts of predation on sheep are available (Murie 1944; Geist 1971; Kelly 1980), carnivore densities are linked to prey biomass (Hornocker 1970; Sunquist & Sunquist 1989). Where sheep densities are low, as in the Mohave desert, and populations are declining, no evidence indicates that predation effectively reduces population size, especially because prey items vary with availability (Stephens & Krebs 1986). And, while mountain lions (*Felis concolor*) are thought to be more efficient predators of sheep than are coyotes (*Canis latrans*) (McCutchen 1982; Berger 1990), lions do not occur in many of the desert ranges where sheep are found (Smallwood & Fitzbugh 1987). Finally, if inter-

specific food competition were responsible for demises of native sheep, cattle or other herbivores should co-occupy sheep habitat and share the same food. Although cattle (and wild horses) prefer grasses, as do native sheep (Bailey 1980; Hanley & Hanley 1982), these species occupy different habitats, and interspecific effects on sheep population size have yet to be demonstrated (Berger 1986).

### Potential Genetic and Etiological Effects

In contrast to the negative evidence given above, some data suggest that both genetic (Schwartz et al. 1986)

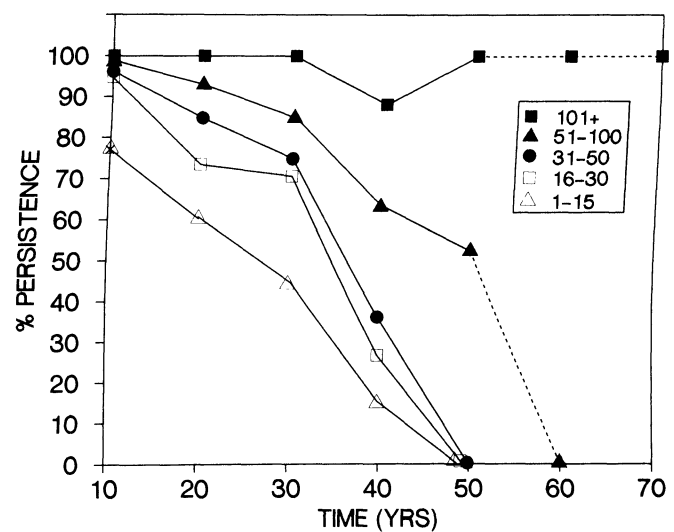


Figure 1. Relationships between time and the percentage of populations persisting according to five population size categories. Sample sizes for each category at 10-year intervals as follows: 1-15 individuals: 53, 54, 40, 19, 7, 4, 0; 16-30 individuals: 32, 30, 20, 8, 5, 4, 1; 31-50 individuals: 41, 34, 18, 14, 8, 4, 1; 51-100 individuals: 43, 26, 16, 8, 4, 2, 0; 100+ individuals: 67, 44, 20, 11, 2, 1, 1. Dotted lines reflect samples based on less than four populations.

**Table 2.** Summary of effects of significant ( $p < 0.05$ ) trends in estimated plant productivity (PP) over periods of demographic censuses for 122 bighorn sheep populations. Small < 50 sheep; large > 50 sheep. (See Table 1 for locations and relationships between estimated PP and time.)

	Percentage of total sample	Number of extinctions	
		Small	Large
PP increasing (N = 21)	17.2	5	0
PP decreasing (N = 0)	0	0	0
No relationship (N = 101)	82.8	24	5

$G_{adj} = .12$ ; NS, for comparison of population extinctions in relation to increasing PP versus all populations with no relationship to PP.

and etiological (Foreyt & Jessup 1982; Clark et al. 1985; Wehausen et al. 1987a) factors influence bighorn reproduction and survival, and, presumably, these affect persistence. In captivity, inbred bighorns suffer higher juvenile mortality than those from less inbred lines (Sausman 1984). Whether this occurs in field populations is unknown, but questions about population size and potential genetic effects can be examined because small founding populations are reintroduced (by wildlife managers) back into the same locations where native sheep become extinct (Leslie 1980; Gray 1986). If population size per se were responsible for the lack of persistence, then both native and reintroduced small populations should persist for similar time frames. I examined this prediction by contrasting minimum persistence times of 57 reintroduced populations (from California, Colorado, Nevada, Oregon, and South Dakota) with native ones matched for  $S_i$  of 8–15 and 16–30. Reintroduced populations succeeded better at 10 and 20 years ( $G = 16.79$ ;  $df = 3$ ;  $p < 0.05$  and  $5.03$ ;  $0.05 < p < 0.10$ ). These differences cannot be explained solely by habitat variation or by reintroduction of sheep into areas where cattle grazing is not permitted: in Nevada alone, 11 of 14 reintroductions into areas of historical bighorn occupation were successful despite cattle grazing during both population declines of native sheep and reintroductions. However, two unsuccessful transplants occurred in areas of domestic sheep use. Because founders are often from larger and presumably more heterozygous populations, genetic factors may indeed underlie the differences in success between populations founded by humans and declining native populations. If this view is correct, then greater genetic diversity may buffer against rapid extinction, a hypothesis that can only be tested rigorously when habitat conditions are controlled (Wakelyn 1987).

Evidence that indirectly implicates etiological factors is diverse, including examples of widespread extirpations when native sheep were exposed to domestic sheep (Goodson 1982; Foreyt & Jessup 1982) and to

avenues of viral infection promoted by cattle (Wehausen et al. 1987a). Unfortunately, such evidence remains indirect and in need of rigorous testing (but see Onderka & Wishart 1988; Onderka et al. 1988).

## Conclusions

The data presented here illustrate that population size can be used to gauge the persistence of populations, especially when factors such as inclement weather, food shortages, predation, or interspecific competition fail to exacerbate extirpation. Nevertheless, it is clear that small (and especially single) mammalian populations are in imminent need of enhanced management to maximize their persistence. Data for numerous species, including bighorn sheep and the sole deme of black-footed ferrets (*Mustela nigripes*) (Clark 1987; Thorne & Williams 1988), confirm that exposure to extrinsic factors, notably epizootics, precipitates sweeping localized and rapid extirpation.

If small, fragmented populations are to be conserved, then it no longer seems wise to await the accumulation of additional demises to determine whether such populations of other species become extinct as rapidly as native sheep. Nevertheless, it is important to recognize that species differing from sheep in body size, generation times, fecundity, trophic levels (Belovsky 1987), and perhaps economic status should differ in persistence times. Presently, data for other mammals are lacking, but historical approaches may prove to be one way to evaluate the generality of persistence models, perhaps through use of information on widely fluctuating population sizes in species such as voles, lagomorphs, and mice.

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