Demographic Response to Experimental Genetic Management in Bighorn Sheep Herds in Oregon

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Abstract: Steens Mountain and Leslie Gulch populations of bighorn sheep (*Ovis canadensis*) in Oregon were experimentally augmented in 2000 and 2001, respectively, with ewes from the Santa Rosa Mountains population of Nevada, a herd with higher genetic diversity. The intent of these augmentations was to reverse declining trends in herd productivity through increases in genetic diversity. In this research we investigated the demographic response of the Steens Mountain, the larger Steens metapopulation, and Leslie Gulch California bighorn sheep herds to experimental genetic management. We evaluated pre- and post-augmentation demographic trends using several metrics derived from yearly herd inventory data. Our results suggest that both the Steens Mountain and Leslie Gulch herds exhibited demographic changes after augmentation. Steens Mountain changed from strongly declining in numbers to a more stable pattern whereas the Leslie Gulch population metrics increased substantially over the full course of our study. The responses we observed indicated that inbreeding depression potentially played a role in previous downward trends of our study populations, but further research will be necessary to assess this hypothesis.

KEY WORDS bighorn sheep, genetic management, genetic rescue, population dynamics

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Genetic management, defined as management action intended to increase genetic variability, of wild populations has been called the "…greatest unmet genetic challenge in conservation biology" (Frankham et al. 2002, p. 362). However, there are strikingly few examples of genetic management in the literature and even fewer reports of genetic management resulting in the genetic rescue (i.e., increased genetic diversity and a response in some demographic parameter; Thrall et al. 1998) of wild populations. Madsen et al. (1999) reported the rescue of a population of adders (*Vipera berus*) in Spain after the addition of 20 individuals from more genetically-diverse stock and Westemeier et al. (1998) reported increased reproductive fitness in a remnant population of greater prairie chickens (*Typmanuchus cupido pinnatus*) after augmentation with individuals from several large, more genetically diverse populations. The results of the genetic management of the Florida panther (*Puma concolor coryi*) also has received much attention, with some authors pointing to evidence portraying the management action as a success (Pimm et al. 2006) while others have expressed doubts about some (Creel 2006) or most of that evidence (Maehr et al. 2006). In the most comprehensive record of a population's response to augmentation, Hogg et al. (2006) documented genetic rescue in a long-term study of Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) in Montana, USA.

Although an ample body of theoretical work suggests that restoring gene flow to small, isolated populations via genetic augmentation has benefits in terms of the maintenance of genetic diversity and the avoidance of inbreeding depression (e.g., Whitlock et al. 2000, Ingvarsson and Whitlock 2000), empirical examples of such outcomes are few and generally have not accounted for the effects of unmeasured variables by studying replicate populations (Ball et al. 2000, Keller et al. 2001, Saccheri and Brakefield 2002, Schönhuth et al. 2003, Vilà et al. 2003). That is, successful genetic management resulting in the genetic rescue of a wild population has not been demonstrated in an experimental framework. This is surprising given the widespread use of translocation as a tool in wildlife management (Fischer and Lindenmayer 2000) and the numerous opportunities that exist to experimentally evaluate genetic and demographic responses to augmentation within managed wildlife populations resulting from this type of translocation (e.g., Mock et al. 2004).

Whittaker et al. (2004) describe such an experimental framework using bighorn sheep (*O. c. canadensis*; formerly recognized as California bighorn sheep *O. c. californiana*) in Oregon. After documenting poor productivity (<20 lambs:100 ewes) and population-specific numerical declines along with no indication of disease related die-offs, Oregon Department of Fish and Wildlife (ODFW) conducted a genetic analysis of some of that state's bighorn sheep herds (Whittaker et al. 2004). They evaluated measures of genetic diversity among 5 herds in Oregon (Hart Mountain, Aldrich Mountain, Lower John Day River, Steens Mountain, and Leslie Gulch; Figure 1) and those of the Santa Rosa Mountains herd of Nevada to determine if the observed declines could be due to inbreeding depression (Whittaker et al. 2004). This research revealed that the Oregon herds exhibited significantly lower levels of genetic diversity when compared to that of the Santa Rosa Mountains herd of Nevada. Inbreeding depression was suspected as the causal mechanism behind the decline in productivity of the Oregon herds because most have a lineage tracing back to the original translocation of 20 sheep to Hart Mountain, Oregon in 1954 (Coggins et al. 1996). As a consequence of this research, experimental augmentations of the Steens Mountain (N = 16 in 2000) and Leslie Gulch (N = 15 in 2001) populations of bighorn sheep in Oregon were carried out using sheep from the more genetically-diverse Santa Rosa Mountains herd (Whittaker et al. 2004).

Our investigation centers on these augmentations as examples of attempted genetic management in the wild. Using annual herd inventory data (e.g., counts, population size estimates, and lamb/ewe ratios) collected subsequent to and after the experimental augmentations were performed, the goal of this research was to evaluate whether there was a demographic response by these herds after experimental genetic management. Specifically, our objective was to determine if a genetic rescue effect could have occurred as a result of our experiment by comparing and contrasting population trends within the Steens Mountain and Leslie Gulch bighorn sheep herds before and after their respective augmentation events.

METHODS

Study Area

Steens Mountain, located in Harney County, Oregon, is a fault-block upheaval

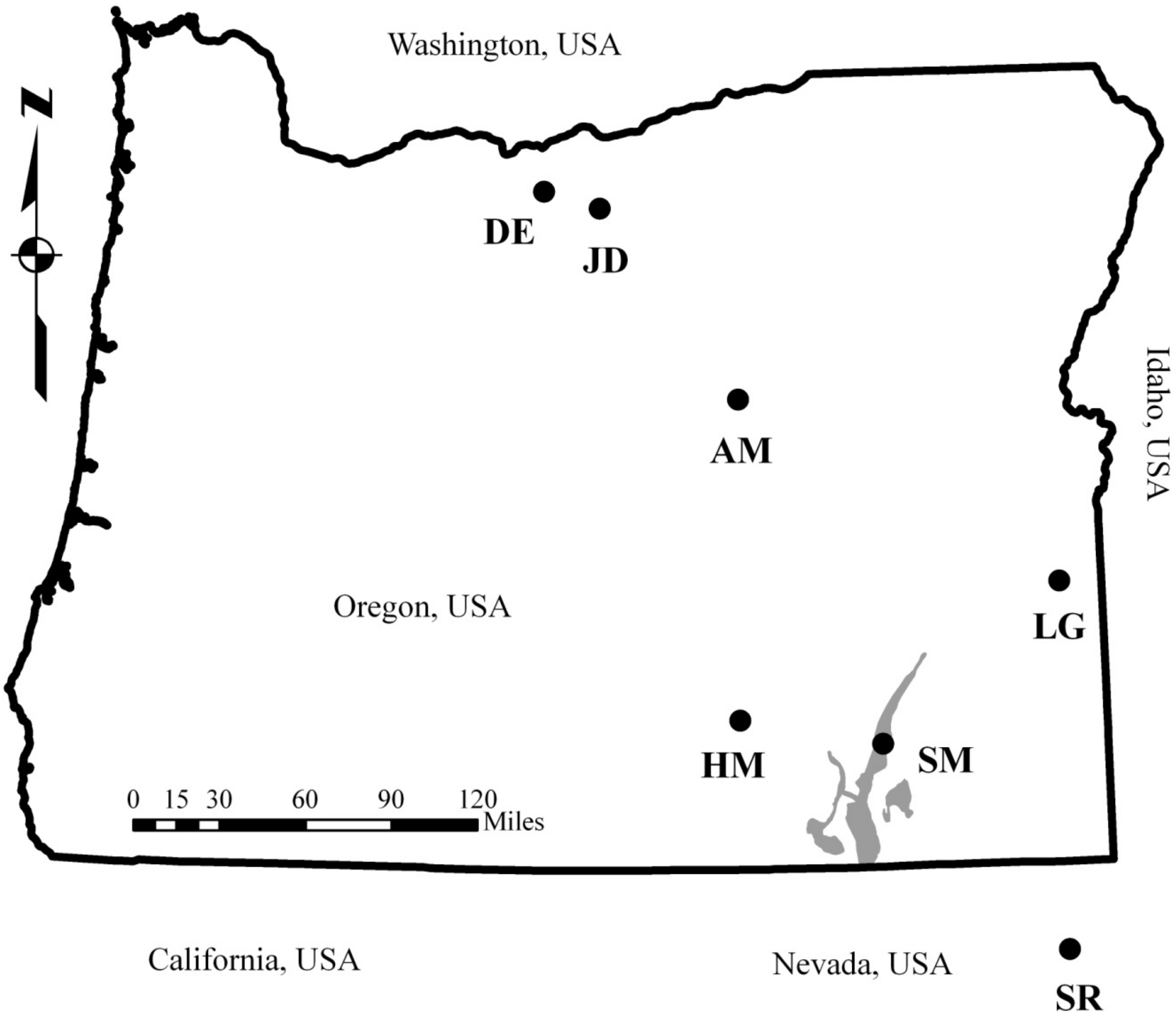

Figure 1. Bighorn sheep populations sampled as part of our larger genetics study. Oregon populations were Aldrich Mountain (AM), Deschutes River (DE), Hart Mountain (HM), Lower John Day River (JD), Leslie Gulch (LG), and Steens Mountain (SM). The Nevada population was Santa Rosa Mountains (SR). The shaded area surrounding Steens Mountain bounds the larger Steens metapopulation.

that rises nearly a vertical mile from the surrounding landscape (Whittaker et al. 2004; Figure 1). Bighorn sheep primarily occupy the more-vertical, east face of the mountain. The herd was established from two translocations of 4 and 7 bighorn sheep from Hart Mountain in 1960 and 1961, respectively (Coggins et al. 1996). By 1985 the Steens Mountain herd had reached numbers large enough to permit its use a source herd for reintroductions and augmentations elsewhere in Oregon (ODFW 2003). Subsequent natural range expansion and additional ODFW translocations (Coggins et al. 1996) around the mountain proper have resulted in a metapopulation-like configuration of herds around Steens Mountain (larger Steens metapopulation; Figure 1). Peripheral populations currently include: Andrews Rim, Alvord Peaks, Heath Rim, Lone Mountain, Mickey Butte, North and South Catlow Rims, Palamino Canyon, Pueblo Mountains, Squaw Creek, and Stonehouse Canyon (Table 1). In 2000, 16 additional bighorn females were translocated to Steens Mountain proper from the Santa Rosa Mountains of Nevada in an attempt to increase genetic diversity in the Steens Mountain herd (Whittaker et al. 2004).

Table 1. Year established or first inventoried, and release size for subpopulations comprising the larger Steens metapopulation of California bighorn sheep.

Population	Year	N	Source Population
Steens Mountain	1960	4	Hart Mountain
	1961	7	Hart Mountain
Andrews Rim	1998		Range expansion
Alvord Peaks	1991		Range expansion
Heath Rim	1996		Range expansion
Lone Mountain	1992	15	Hart Mountain
Mickey Butte	1995		Range expansion
N & S Catlow Rims	1989	17	Hart Mountain
Palamino Canyon	2004		Range expansion
Pueblo Mountains	1976	16	Hart Mountain
	1980	7	Hart Mountain
	1983	17	Hart Mountain
Squaw Creek	1993	17	Hart Mountain
Stonehouse Canyon	1996	18	Lower John Day[1]

[1] Bighorns in the Lower John Day herd originate from 2 translocations: 1989 from Hart Mountain and 1990 from Williams Lake, B.C., (the source herd for Hart Mountain).

Leslie Gulch is a rocky gorge that connects to the larger Lower Owyhee River canyon and is located in Malheur County of eastern Oregon (Figure 1; Whittaker et al. 2004). Bighorn sheep were established in Leslie Gulch with a translocation of 17 sheep from Hart Mountain in 1965 (Coggins et al. 1996). Similar to Steens Mountain, Leslie Gulch eventually contained enough sheep to be included as an additional source herd for bighorn sheep restoration efforts in Oregon (ODFW 2003). In 2001, the Leslie Gulch herd received an additional 15 bighorn females translocated from the Santa Rosa Mountains of Nevada in an attempt to increase genetic diversity (Whittaker et al. 2004).

Experimental Design

Three population-level metrics were available from yearly ODFW winter bighorn sheep herd inventories: 1) total number counted during classification surveys (i.e., minimum number alive), 2) population size estimates derived from ODFW population models (POP-II; Bartholow 1995), and 3) lambs:100 ewes defined as the number of lambs counted divided by the number of ewes counted multiplied by 100. Total number counted and population size estimates were intended to index population abundance whereas lambs:100 ewes was interpreted as an index of herd productivity. Inventories of Steens Mountain and the larger Steens metapopulation were based on counts from the ground, whereas data from Leslie Gulch were based on inventories conducted via helicopter (ODFW 2003).

We used inventory data from 1992-2009 for Steens Mountain and 1994-2009 for Leslie Gulch (Table 2). Separately, we combined data from Steens Mountain proper and its peripheral populations within years from 1992-2009 to represent the larger Steens metapopulation (Table 2). Peripheral populations were included in analyses if population metrics were available for ≥1 year before and after augmentation (i.e., the population was well established). Of the 11 peripheral populations evaluated in the larger Steens metapopulation, 8 met this criterion: Andrews Rim, Alvord Peaks, Lone Mountain, Mickey Butte, North and South Catlow Rims, Squaw Creek, and Stonehouse Canyon. It should be noted that these data sets are imperfect; they were collected by ODFW personnel when and where time and funds allowed. Consequently, the data set contained many missing values, and to minimize bias associated with incomplete counts, population size estimates were

Table 2. Oregon Department of Fish and Wildlife (ODFW) inventory data for the Steens Mountain, Steens Metapopulation, and Leslie Gulch herds. Total count = number counted during classification surveys; N-hat = population estimate derived from ODFW population models; Lambs:100 = (number of lambs counted)/(number of ewes counted)* 100. Total count and N-hat were summed for all sub-populations in the Steens Metapopulation whereas Lambs:100 is the mean across sub-populations. Pre- and Post- indicate data available for pre- and post-augmentation series.

	Steens Mountain						Steens Metapopulation[a]						Leslie Gulch					
	Total Count		N-hat		Lambs:100		Total Count[b]		N-hat[b]		Lambs:100[b]		Total Count		N-hat		Lambs:100	
Year	Pre-	Post-	Pre-	Post-	Pre-	Post-	Pre-	Post-	Pre-	Post-	Pre-	Post-	Pre-	Post-	Pre-	Post-	Pre-	Post-
1992	168				25		79.5 (4)				40.0 (4)							
1993	167		250		19		86.5 (4)		128.8 (4)		36.4 (4)							
1994																		
1995	61		225		16		46.5 (6)		90.8 (6)		32.3 (6)		137		160		17	
1996	56		225		11		29.7 (7)		95.8 (6)		22.8 (7)		116		150		19	
1997	132		200		27		53.7 (7)		85.0 (8)		45.8 (7)		92		125		7	
1998	132		185		26		61.0 (9)		80.9 (9)		43.1 (9)		92		125		24	
1999	129		185		22		56.3 (9)		87.2 (9)		37.2 (9)		107		125		24	
2000	137		185		17		50.8 (9)		86.1 (9)		34.6 (9)		105		125		33	
2001		97		185		40		57.8 (4)		130.0 (4)		36.8 (4)	132		160		21	
2002		143		195		21		53.1 (7)		83.1 (8)		20.9 (7)						
2003		122		195		31		64.1 (7)		106.7 (9)		35.7 (7)						
2004		135				23		66.0 (9)				24.1 (9)		194				38
2005		91				32		59.0 (8)		135.0 (2)		26.1 (8)		232				42
2006		84				30		55.0 (7)		135.0 (2)		32.6 (7)		170		250		40
2007		62		175		27		58.6 (8)		145.0 (7)		39.6 (8)		235				24
2008		66				23		45.3 (7)				29.8 (7)		224				21
2009		59				35		51.3 (8)		100.1 (7)		32.8 (8)		197				47

excluded from our analyses if they were equal to the total number counted in that year.

Data Analysis

Population-level metrics were analyzed separately for Steens Mountain, the larger Steens metapopulation, and Leslie Gulch. We used simple linear regression to calculate the slopes of our estimates of total count, population size, and lambs:100 ewes through time (i.e., years) using the procedures outlined in Robbins et al. (1986). Balanced (total number of years) pre- and post-genetic augmentation time series were regressed separately for each study area (Robbins et al. 1989). For example, data from Steens Mountain proper were split into two, 9-year data series: before (1992-2000) and after (2001-2009) augmentation. Likewise, the data from Leslie Gulch were analyzed separately as data series before (1994-2001) and after (2002-2009) augmentation. Because not all populations in the larger Steens metapopulation were inventoried every year, annual estimates of each of the demographic variables for this herd complex were corrected by taking the sum of population estimates divided by the number of populations inventoried within each year. We used simple linear regression on the 3 corrected population metrics in balanced pre- (1992-2000) and post- (2001-2009) augmentation series as described previously for Steens Mountain proper.

We used Student's t-tests to evaluate the null hypothesis of no difference in slope coefficients between pre- and post-augmentation regressions (Zar 1999, p. 360) of each of the 3 population metrics independently for Steens Mountain proper, the larger Steens metapopulation, and Leslie Gulch. If regression slopes for any population metric did not differ between pre- and post-augmentation series, we also used Student's t-tests to evaluate the null hypothesis of no difference between pre- and post- regression elevations (i.e., we tested for vertical separation of the regression series) for that metric following Zar (1999; p. 364).

Further, in order to evaluate trends for each demographic metric over each full time series, we constructed regression models using the entire data sets for each herd (i.e., 1992-2009 for Steens Mountain proper and the larger Steens metapopulation and 1994-2009 for Leslie Gulch) using total counts, population size estimates, and lambs:100 ewes in separate models. All regression models were constructed using lm in R (R Development Core Team 2008) and the raw data for each regression we conducted were plotted using SigmaPlot version 10.0 (Systat Software, Point Richmond, CA, USA). We used $\alpha = 0.05$ as our level of statistical significance for all analyses.

RESULTS

Overall, only 3 of the 17 pre- and post-augmentation regressions (one regression was not conducted due to insufficient data) exhibited slope coefficients that were significantly different from zero (Table 3; Figure 2). In addition, we detected only 1 significant difference between pre- and post-augmentation regression slope coefficients across the 8 comparisons evaluated (Table 3). Population size estimates for Steens Mountain proper decreased less severely after genetic augmentation than was the trend prior to augmentation ($P=0.04$; Table 3, Figure 2). The explanatory power of the pre and post-augmentation models we evaluated ranged from >91% to <0.001% of the total variance explained by the models (Table 3). In particular, our regressions of numbers of lambs:100 ewes over years had exceptionally low explanatory power, with an overall average R^2 value across all pre- and post- time series combined of less than 0.07 (Table 3). Therefore, plots of the relationships between total counts and estimated population sizes relative to time are provided for all three data sets (Steens Mountain proper, the larger Steens metapopulation, and Leslie Gulch; Figure 2) while those involving lambs:100 ewes were excluded. We detected no significant differences in the regression elevations for any of the pre- and post-augmentation comparisons evaluated (Table 2).

Seven of the 9 models conducted using data from the full time series exhibited significant trends (i.e., slope coefficients $\neq 0$; Table 3). The sheep population on Steens Mountain proper decreased in both total count and population size estimates over the period from 1992-2009, although lambs:100 ewes increased slightly over the same time period. All three population metrics (total counts, population size estimates, and lambs:100 ewes) increased significantly in the Leslie Gulch herd during approximately the same time period (1994-2009; Table 3, Figure 2). However, only the data for total counts exhibited a significant temporal trend in the larger Steens metapopulation: decreasing over time after the data were standardized to account for the number of populations inventoried in each year (Table 3; Figure 2).

DISCUSSION

Both the Steens Mountain and Leslie Gulch populations of bighorn sheep appeared to exhibit changes in some demographic parameters after augmentation, but the form of these potential responses to experimental genetic management differed between the populations. At Steens Mountain, we detected a change from a strong declining trend in population size estimates prior to augmentation to a relatively stable population size after augmentation. The standardized data from the larger Steens metapopulation followed a pattern similar to that of Steens Mountain, but, unlike the herd on the mountain proper, we were unable to assign statistical significance to the

Table 3. Population metrics for the Steens Mountain, Steens Mountain metapopulation and Leslie Gulch bighorn sheep herds in Oregon pre- and post- genetic augmentation. Total Counted = number counted during classification surveys; N-hat = ODFW modeled population estimates; lambs:100 = Lambs per 100 ewes. For Steens metapopulation, we calculated the average value among all populations for which the metric was reported in each year. To calculate full trends we combined pre- and post- data. The different slopes column contains p-values indicating a difference between pre- and post-augmentation trends. The different elevations column contains a p-value from secondary hypotheses tests indicating differences in regression elevations if regression trends did not differ. Our α for all tests was 0.05. Significant values are in bold.

	Total Counted										
	Pre-			Post-			Full				
Study Site	Slope	R^2	p-value	Slope	R^2	p-value	Slope	R^2	p-value	Diff. Slopes	Diff. Elev.
Steens Mountain	-2.676	0.031	0.675	**-9.233**	**0.639**	**0.010**	**-3.898**	**0.280**	**0.029**	0.347	0.388
Steens Metapopulation	-3.463	0.291	0.168	-1.190	0.260	0.161	**-3.055**	**0.233**	**0.050**	0.356	0.885
Leslie Gulch	-0.786	0.009	0.839	1.600	0.014	0.827	**9.581**	**0.717**	**< 0.001**	0.771	0.168

	N-Hat										
	Pre-			Post-			Full				
	Slope	R^2	p-value	Slope	R^2	p-value	Slope	R^2	p-value	Diff. Slopes	Diff. Elev.
Steens Mountain	**-10.25**	**0.916**	**< 0.001**	-2.530	0.483	0.305	**-4.641**	**0.646**	**0.003**	**0.044**	-
Steens Metapopulation	**-5.321**	**0.623**	**0.035**	1.644	0.043	0.656	2.011	0.173	0.138	0.127	0.453
Leslie Gulch	-1.786	0.050	0.630	-	-	-	**8.690**	**0.502**	**0.049**	-	0.167

	Lambs:100										
	Pre-			Post-			Full				
	Slope	R^2	p-value	Slope	R^2	p-value	Slope	R^2	p-value	Diff. Slopes	Diff. Elev.
Steens Mountain	-0.014	< 0.001	0.987	-0.250	0.012	0.779	**0.700**	**0.253**	**0.040**	0.846	0.159
Steens Metapopulation	0.134	0.003	0.900	0.450	0.039	0.610	-0.393	0.085	0.255	0.817	0.342
Leslie Gulch	2.036	0.307	0.196	-0.971	0.030	0.741	**1.583**	**0.434**	**0.014**	0.372	0.304

difference of estimated population size trends from sharply decreasing pre-augmentation to a more neutral pattern after augmentation. Over the course of our full time series, both Steens Mountain and the larger Steens metapopulation trended downward in the total number of sheep counted and the average number of sheep counted per herd during inventories, respectively. A slightly different pattern emerged in the full time series of population size estimates: Steens Mountain again trended downward overall, but average population size estimates for the larger Steens metapopulation were statistically stable over time. In fact, though both of our abundance metrics decreased over the full course of the study, the metapopulation maintained a large number of bighorn sheep overall ($\widehat{N}$ = 701 in 2009).

The spatial dispersion of mountain sheep populations is defined by the patchy distribution of the rugged habitat on which they depend (Geist 1971). These disjunct populations are subject to relatively common extinctions (Berger 1990, Torres et al. 1994), but individual movements between local populations also are common (Schwartz et al. 1986, Bleich et al. 1996). Steens Mountain contains the most sheep of any herd in the larger Steens metapopulation, and, while we would not have expected a metapopulation level response to the augmentation of one population to emerge within the time frame of our study, a continued decline of inventory metrics for the mountain proper may have presaged the natural extinction and recolonization profile symptomatic of true metapopulations (Hanski and Gilpin

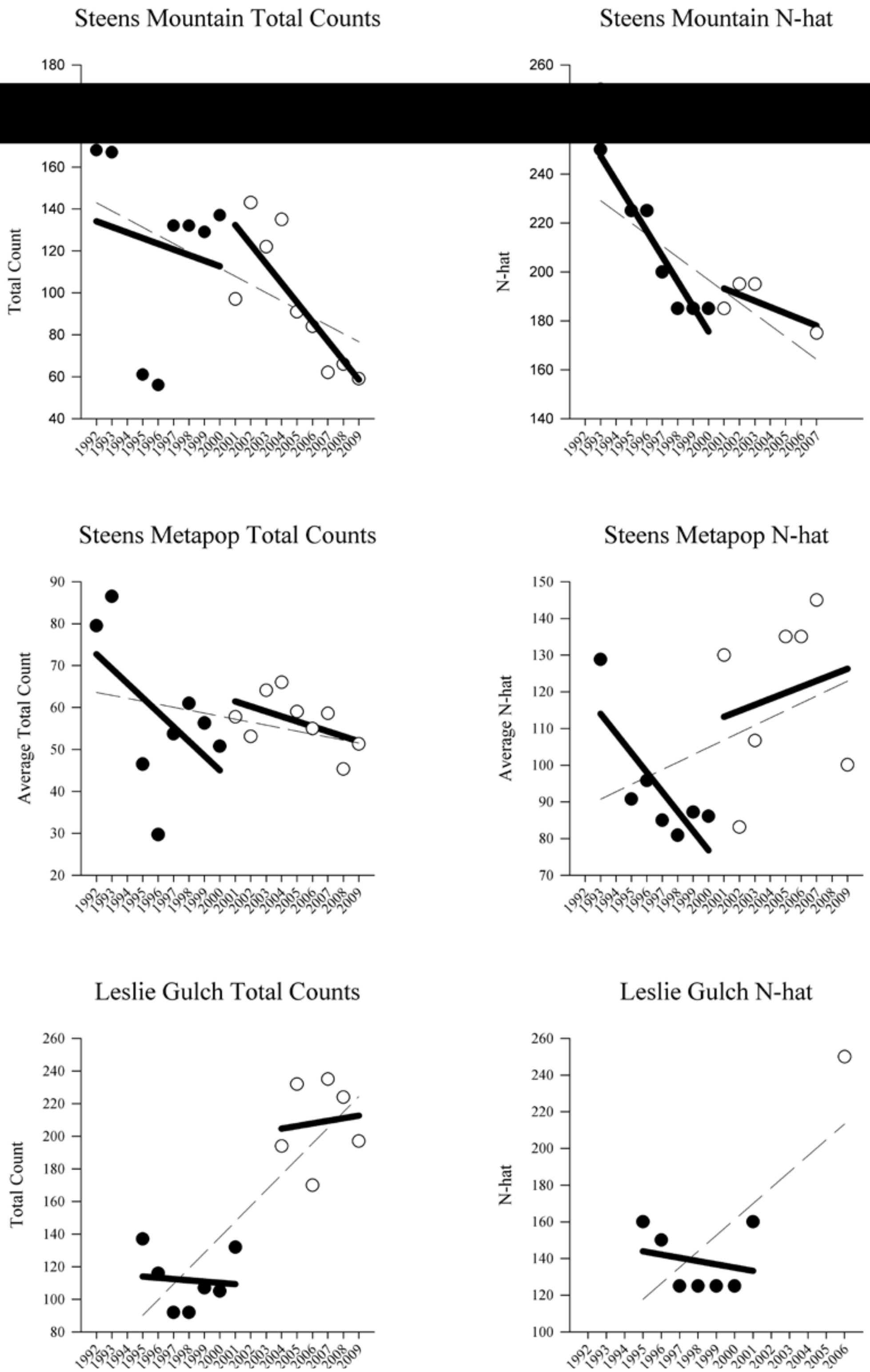

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Figure 2. Trends in total count and population size (n-hat) for the Steens Mountain, Steens metapopulation, and Leslie Gulch bighorn herds pre- and post- genetic augmentation. Solid lines represent pre- and post-augmentation regressions whereas hashed lines represent regressions including the full time series.

1997). Alternatively, the change we documented from strongly declining population sizes to a more neutral trend at Steens Mountain suggests that the genetic augmentation could have stabilized the population. This demographic change was possibly aided by the increasing trend in lamb production we observed over the full course of the study. However, understanding how a response by one herd will influence population trends in the metapopulation as a whole will require much longer time series of herd inventory data.

In contrast to the neutral trend exhibited by the Steens Mountain herd after augmentation, all available population metrics for the Leslie Gulch herd (total counts, populations estimates, and lambs:100 ewes) exhibited significant positive trends over the full time series (1994 to 2008; Fig. 2), indicating strong recruitment after experimental genetic management in this herd. Although none of the pre- and post-augmentation data series exhibited significant trends or different elevations, we suspect this was the result of a lack of power due to the small number of data points available for each of these models. The extent of the change exhibited by the Leslie Gulch herd after experimental genetic management was evident in the series of population size estimates: the most recent estimate ($\widehat{N}$ = 250), from 2006, was 56% larger than the last estimate prior to augmentation ($\widehat{N}$= 160 in 2001). While it is probable that other unmeasured variables were also involved in this increase, we expect that the augmentation played at least some role in driving the increased abundance of bighorn sheep in Leslie Gulch. In fact, genetic analyses revealed strong integration of augmented genotypes into both Steens Mountain and Leslie Gulch herds approximately one generation post-augmentation (Z. Olson, unpublished data), which indicates successful breeding among augmented ewes and survival of the resulting offspring. Thus, the changes exhibited by our study populations after their respective augmentations, although manifesting differently in Steens Mountain and Leslie Gulch, potentially were affected by the experimental genetic management.

There are a number of plausible mechanisms by which the change in demographic parameters exhibited by the Steens Mountain herd could have differed from that of the Leslie Gulch herd. For example, fewer transplanted ewes from the genetic augmentation could have integrated reproductively at Steens Mountain than in Leslie Gulch. Lower rates of reproductive integration could have occurred because of different reproductive success due to stress from the initial capture and release (e.g., Pelletier et al. 2004) or because of mortality after the transplant. However, the translocated ewes for both herds were subjected to similar capture conditions and radio-tracking after the augmentation indicated that no immediate mortality was evident for the augmented individuals of either herd (D. G. Whittaker, unpublished data). Nor were there obvious climatic differences (i.e., mean average temperature and precipitation) between pre- and post-augmentation periods for either Steens Mountain or Leslie Gulch (data not shown). In terms of resource availability, Leslie Gulch received 11 guzzlers designed to increase the availability of water in bighorn habitat since 1980, although the installation dates did not correspond with the augmentations in this study (i.e., two were installed in 1980 and the remaining nine were installed since 2004; S. Torland, unpublished data).

Different rates of predation between Steens Mountain and Leslie Gulch also could have led to different responses by the populations to augmentation. While it is unlikely that smaller predators such as coyotes (*Canis latrans*), golden eagles (*Aquila chrysaetos*), and bobcats (*Lynx rufus*) affect the growth of Oregon's bighorn sheep populations (Lawson and Johnson 1982), cougars are known to be efficient predators of bighorn sheep (ODFW 2003). This is particularly true where individual cougars have specialized in preying on bighorns (Festa-Bianchet et al. 2006). However, cause-specific mortality based on radiotelemetry from Steens Mountain and Leslie Gulch after augmentation has not indicated disparate levels of cougar predation between the herds (D. G. Whittaker, unpublished data). Further, we found no difference in the number of cougars killed (as a simple index of abundance) on Steens Mountain (N = 12) and in Leslie Gulch (N = 8) from 2005-2008 (ODFW 2009; $\chi^2 = 0.800$, df = 1, $P = 0.371$). These data suggest that cougar abundance and resultant predation are not likely the driving factors causing differing responses to augmentation by the bighorn sheep on Steens Mountain and in Leslie Gulch. While there can be little doubt that physical and environmental differences exist between the Steens Mountain and Leslie Gulch study areas, our study design was uniquely capable of documenting population level changes around a single, definite commonality between the populations: our experimental genetic augmentations.

Our results are not confirmatory, but we can infer from the demographic changes we observed in Steens Mountain and Leslie Gulch after experimental genetic management that inbreeding depression could have played a role in the declines reported previously for those herds (Whittaker et al. 2004). Inbreeding depression results from matings between related individuals which increases the chance that offspring from such matings will express deleterious traits and have reduced viability (or reduced fitness; Ralls et al. 1988, Keller and Waller 2002, Slate et al. 2004). In the case of wild populations, there was considerable debate as to whether inbreeding depression could have demonstrable impacts on populations (Lande 1988, Caro and Laurenson 1994). Nevertheless, more recent evidence from a variety of wild populations suggests that the effects of inbreeding may be more common in the wild than previously suspected (Keller and Waller 2002).

While demographic evidence of a response to genetic management may be indicative of a reduction in inbreeding depression due to the influx of new genetic diversity, further evidence is necessary to support this hypothesis before conclusions can be drawn about the success of experimental genetic management in 2 herds of bighorn sheep in Oregon. We are conducting further research using molecular markers to investigate the genetic contribution of the translocated females at Steens Mountain and in Leslie Gulch, and this should provide us with a more direct measure of reproductive integration. If the responses we observed were due to factors other than inbreeding depression, we would expect the demographic response to have come from some segment of the whole population, including at least some of those lineages present before the augmentation. Alternatively, if the response of bighorns in the Steens Mountain and Leslie Gulch herds was the result of a genetic rescue effect, we would expect the demographic response to be driven mostly by the progeny of the translocated individuals. Our forthcoming investigation should further elucidate the role that inbreeding depression played in the previous declines observed in the Steens Mountain and Leslie Gulch herds of bighorn sheep.

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