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Polygyny and Female Breeding Failure Reduce Effective Population Size in the Lekking Gunnison Sage-Grouse

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Abstract

Populations with small effective sizes are at risk for inbreeding depression and loss of adaptive potential. Variance in reproductive success is one of several factors reducing effective population size (N_e) below the actual population size (N). Here, we investigate the effects of polygynous (skewed) mating and variation in female breeding success on the effective size of a small population of the Gunnison sage-grouse (*Centrocercus minimus*), a ground nesting bird with a lek mating system. During a two-year field study, we recorded attendance of marked birds at leks, male mating success, the reproductive success of radio-tagged females, and annual survival. We developed simulations to estimate the distribution of male reproductive success. Using these data, we estimated population size (N) and effective population size N_e for the study population. We also simulated the effects of population size, skewed vs. random mating, and female breeding failure on N_e . In our study population, the standardized variance in seasonal reproductive success was almost as high in females as in males, primarily due to a high rate of nest failure (73%). Estimated N_e (42) was 19% of N in our population, below the level at which inbreeding depression is observed in captive breeding studies. A high hatching failure rate (28%) was also consistent with ongoing inbreeding depression. In the simulations, N_e was reduced by skewed male mating success, especially at larger population sizes, and by female breeding failure. Extrapolation of our results suggests that six of the seven extant populations of this species may have effective sizes low enough to induce inbreeding depression and hence that translocations may be needed to supplement genetic diversity.

Keywords: Lek, Reproductive success, Variance, Mating system, *Centrocercus*

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1. Introduction

Effective population size (N_e) is an important parameter in conservation biology (Lande and Barrowclough, 1987; Frankham et al., 2002). It is defined as the size of an idealized population of breeding adults that would experience the same (1) loss of heterozygosity, (2) change in the average inbreeding coefficient, or (3) change in variance in allele frequency through genetic drift as the actual population (Futuyma, 1998; Frankham et al., 2002). As effective population size decreases, the rate of loss of allelic diversity via genetic drift increases. Two consequences of this loss of genetic diversity, reduced fitness through inbreeding depression and reduced response to sustained directional selection ("adaptive rate of potential"), are thought to elevate extinction risk (Frankham et al., 2002; Frankham, 2005). Captive breeding studies suggest N_e should exceed 50–100 to avoid inbreeding depression. Mathe-

matical models suggest that N_e should be at least 500 to retain adaptive potential, though some estimates are as high as 5,000 (Frankham et al., 2002). Estimating N_e could therefore indicate whether a population might be at risk of from either consequence.

The effective size of a population is often much less than its actual size (N). Fluctuating population size, variance in reproductive success, and unequal sex ratios all reduce N_e (Wright, 1938; Frankham, 1995). Fluctuating population size has the largest effect and unequal sex ratios the least. We focus here on the effect of variable reproductive success.

In a population of constant size, increasing the variance in reproductive success in either sex will reduce N_e (Hill, 1972; Nunney, 1993, 1996; Hedrick, 2005). Mechanisms that elevate variance in reproductive success will often differ between the sexes. For males, the mating system will be the primary determinant of vari-

ance (Shuster and Wade, 2003). Polygyny is expected to produce higher variance in male reproductive success than alternative mating systems because variance will increase as fewer males monopolize more mates. The effect of polygyny on N_e has been examined both theoretically (Nunney, 1993; Engen et al., 2007) and in multiple empirical studies with a focus on mammals (Nunney and Elam, 1994; Storz et al., 2001, 2002). Except in polyandrous mating systems, variance in female reproductive success may depend more on the proportion of females that reproduce and the variance in offspring produced per successful female than on the numbers of mates (Nunney, 1993; Frankham et al., 2002). However, few empirical studies have investigated the extent to which variation in female reproductive success affects N_e (Turner et al., 1999; Kelly, 2001).

The Gunnison sage-grouse (*Centrocercus minimus*) is a recently described bird species existing in seven small populations in southwestern Colorado and southeastern Utah (Young et al., 2000; Gunnison Sage-grouse Rangewide Steering Committee, 2005). In 2005, population size estimates ranged from 40 birds in the smallest populations to approximately 2,500 in the largest. Most populations are geographically isolated from each other and exhibit low genetic diversity (Oyler-McCance et al., 2005). In addition to any effects of population fragmentation, effective population size might be relatively low in Gunnison sage-grouse for at least three reasons.

First, N_e could be depressed because the species' polygynous lek mating system, in which a relatively small proportion of males on leks perform most copulations (Wiley, 1973; Young et al., 2000), elevates the variance in male reproductive success. The potential for mating skew to decrease N_e in lekking grouse has been recognized previously (Bellinger et al., 2003; Johnson et al., 2003, 2004; Bouzat and Johnson, 2004), but the magnitude of the effect has not been studied. Additionally, studies of other lekking birds suggest that the effect of mating skew is likely to be a function of population size because mean lek size increases with population size (Bradbury et al., 1989) and the distribution of matings within a lek becomes less skewed as lek size increases (Alatalo et al., 1992; Widemo and Owens, 1995, 1999).

Second, effective population size might be reduced by nest predation because this increases the variance in female reproductive success. There have been few studies of nest success in Gunnison sage-grouse (Young, 1994), but in the closely related greater sage-grouse (*C. urophasianus*) nest success rates average 47% (range 14–86%; Schroeder et al., 1999). This range of values suggests that variance in reproductive success could sometimes be high in females as well as males. Finally, if this species exhibits similar demography to the

greater sage-grouse, N_e may be lowered by a strongly female-biased sex ratio among breeding individuals. The bias arises from both a female-biased population sex ratio (Schroeder et al., 1999) and sexual bimaturism, in which most males do not compete reproductively until in their second year of life while females nest in their first year (Wiley, 1974).

In this paper, we estimate both the population size (N) and effective population size (N_e) of a small population of Gunnison sage-grouse. We use a mark-resight method to estimate population size (Walsh et al., 2004). We combine demographic parameter estimates derived from both field data and simulations of male reproductive success distributions to estimate N_e using a demographic method derived by Nunney (1993, 1996). Additionally, we use simulations to investigate how N_e is affected by: (1) the potential interaction between lek mating and population size, (2) the skewed lek mating system versus a null hypothesis of random mating, and (3) variance in female reproductive success caused by female breeding failure.

2. Methods

2.1. Study area

We studied the second largest population of Gunnison sage-grouse, located in the San Miguel Basin, Montrose and San Miguel counties, Colorado, United States (38°N 108°W), from 2003 to 2004. Elevations in the study area range from 1,900 to 2,800 m. Below 2,300 m, Gunnison sage-grouse habitat is characterized by sagebrush (*Artemisia* spp.), greasewood (*Sarcobatus* spp.) and salt brush (*Atriplex* spp.). At higher elevations the habitat is characterized by sagebrush and Gambel oak (*Quercus gambelii*). Eight leks were active in the population at the start of the study.

2.2. Field methods

In both years, we captured birds in winter flocks, prior to April 1, with spotlights and nets (Giesen et al., 1982; Wakkinen et al., 1992). We captured additional birds within 1.5 km of leks during late April and early May 2003. We classified birds by age (yearling vs. adult) and gender using size and primary feather molt (Crunden, 1963). Males were fitted with 3.2 g tail-mounted radio transmitters while females were fitted with 14 g neck-lace-mounted transmitters (Holohil Systems, Inc.). All birds were marked with a unique color band combination. Over both years we marked 34 males (15 adults, 19 yearlings) and 39 females (29 adults, 10 yearlings). Five males and seven females surviving from a previous study were also included. Sample sizes for most analyses are less than these totals, due to contextual restrictions on sample composition.

Each year we monitored six of the eight active leks, excluding two inaccessible high elevation leks. We

monitored leks daily following previously described methods (Gibson et al., 1991) from late March to early May. Observations started one hour before sunrise and continued until the last bird left the lek or the birds stopped displaying. These observations provided data on male mating success and lek attendance by marked and unmarked birds of both sexes.

Following the morning display, we triangulated the locations of all radio-tagged birds to detect mortality, and to determine whether a female's movements indicated she had localized to a possible nesting location (Gibson and Bachman, 1992). Approximately two weeks after a female restricted her movements, we located her visually to confirm incubation and recorded nest location with a global positioning system, taking care not to flush her from the nest. We did not return to a nest until either the female was triangulated away from it for three consecutive days or her predicted hatching date approached (based on a 27 d incubation period; Schroeder et al., 1999). Once a female left a nest, we determined whether it was successful (at least one egg had hatched), abandoned, or destroyed by a predator. We counted eggshells (if present), examined them for presence of an embryonic membrane as evidence of hatching, and also opened any unhatched eggs to determine fertility. We checked egg-based estimates of chick numbers hatched by locating females and counting their broods within 48 h of hatching. In every case the number of chicks matched the number of hatched eggs.

2.3. Estimation of population size (\hat{N})

For each year we made separate estimates of male and female numbers based on peak daily counts of marked and unmarked birds seen at monitored leks. Following Walsh et al. (2004), we generated estimates using Bowden and Kufeld's (1995) mark-resight method implemented in NOREMARK software (White, 1996). Population size (\hat{N}) was computed as the sum of male and female estimates. We estimated population size for a focal area in which birds were trapped and leks extensively monitored, excluding the two high elevation leks. We included sightings of all marked birds captured prior to and alive as of April 1, except for those (two females and a male in 2003, and a female in 2004) that could not have been observed because they moved to the unmonitored high elevation area. To avoid overestimating the attendance of radio-tagged birds, marked sighting records excluded individuals whose radio signals were detected during lek observations but that were not also visually identified on the lek. We used daily lek observations collected between April 1 and April 20, excluding four days each year when heavy snow made individual identification impossible. After April 20 grass had grown too high to

allow reliable identification of color bands.

We also computed an adjusted population size estimate for the entire San Miguel population, by adding a component for the high elevation leks based on seasonal high count data collected by the Colorado Division of Wildlife (unpublished). A seasonal high count is the highest of four daily counts made during the breeding season. High counts underestimate male population size because not all males attend leks daily (Walsh et al., 2004) and do not include females. A simulated high count sampling procedure applied to data from our focal study area indicated that high counts represent an average of 58% of our mark-resight male population estimate. Therefore we estimated the size of the entire San Miguel Basin as focal area mark resight estimate + (1 + females per male) * high elevation leks high count/0.58. We computed females per male from the sex-specific mark resight population estimates (Section 3.1.1).

2.4. Estimation of effective population size

To estimate N_e we used Nunney (1993) equation A2:

$$N_e = [4r(1-r)N_{\text{breeders}}T] / \{A_m(1-r) + A_f r\} - (2r/b_f) + [I_{b_m}(1-r) + I_{b_f} r] + A_m I_{A_m}(1-r) + A_f I_{A_f} r\}$$

where r is the sex ratio among potential breeders expressed as the proportion of males, N_{breeders} is the number of potentially breeding individuals, T is the generation time averaged across both sexes, A_f and A_m are the reproductive lifespans of females and males, b_f is mean seasonal female reproductive success, I_{b_f} and I_{b_m} are the standardized variances (variance/mean²) in seasonal reproductive success of females and males, and I_{A_f} and I_{A_m} are the standardized variances in lifespan of females and males. The estimation of each parameter is described below and summarized in Table 1.

2.4.1. N_{breeders} and sex ratio (r)

We computed these parameters from our sex-specific estimates of population size (Section 2.3). We defined N_{breeders} as the total number of birds in the population that had reached the age of reproductive maturity, which is the first year of life for females and the second year for males (Wiley, 1974). N_{breeders} was therefore all females plus adult males while r was adult males divided by all females. To obtain the number of adult males, we multiplied the male population size estimate by an estimate of the proportion of adults, thereby excluding the yearling population segment. We estimated the proportion of adults by projecting annual survival estimates (Section 2.4.2) into a life table. Our estimate of 58% adults is close to the proportion of adults among captured males (53%). Effective population size

Table 1 – Input parameters for estimation of N_e using Nunney's (1993) equation A2

Parameter	Definition	Derivation	Estimate
N_{breeders}	Number of potential breeders	Adult males + all females	145
r	Proportion of males among potential breeders	Adult males: N_{breeders}	0.21
A_f	Female reproductive lifespan	$A_f = 1/(1v_f)$	1.82
A_m	Male reproductive lifespan	$A_m = 1/(1v_m)$	1.38
T_f	Female generation time	$T_f = M_f - 1 + A_f$	1.82
T_m	Male generation time	$T_m = M_m - 1 + A_m$	2.38
T	Average generation time	$(T_f + T_m)/2$	2.10
b_f	Mean female reproductive success (brood size)	Field data	0.90
I_{b_f}	Standardized variance in female reproductive success	Field data	4.70
I_{b_m}	Standardized variance in male reproductive success	Simulations	5.10
I_{A_f}	Standardized variance in female reproductive lifespan	v_f	0.45
I_{A_m}	Standardized variance in male reproductive lifespan	v_m	0.273

The calculation derivations are from Nunney and Elam (1994). M_f and M_m are ages at maturity for females and males ($M_f = 1$, $M_m = 2$); v_f and v_m are annual survival of females and males (values in Section 3.1.3).

estimates obtained using these two values differed by less than 1 individual or 2%.

2.4.2. Annual survival and derived parameters

Annual survival estimates of potential breeders of both sexes (v_f and v_m) were necessary to calculate generation time (T), sex specific reproductive lifespans (A_f and A_m) and standardized variances in sex specific reproductive lifespan (I_{A_f} and I_{A_m}) as described in Table 1. We calculated annual survival as the proportion of marked birds alive on April 1, 2003 that survived to March 31, 2004. Survival of radio-tagged females was monitored by radiotracking. During the field season (March-June), we also radiotracked males to monitor mortality. Because males shed their tail-mounted transmitters during the summer molt, subsequent survival was based on recapture or visual identification at leks in 2004. Reliance on resighting could lower detection probability and might therefore bias male survival estimates downwards. However, this is unlikely to have affected our results substantially because seven of eight males died while the transmitters were still attached. In order to compute population age structure (Section 2.4.1), we made a similar estimate of yearling male survival (J.R. Stiver, unpublished data).

2.4.3. Female reproductive success

This was measured as brood size, the number of chicks found with a female within 48 h of hatching. Females whose nests failed were assigned zero chicks. We used brood size to estimate mean annual female reproductive success (b_f) and its standardized variance (I_{b_f}). To ensure consistency between census and effective population size estimates, the sample included all marked females alive on April 1 of each year. We pooled data from yearling and adult females to estimate female reproductive parameters because preliminary analyses revealed no statistically significant age differences. We also made separate estimates of two components of female reproductive success: the proportion of marked

females reproducing, i.e. hatching at least one chick, and mean brood size per successful female. These values were used when generating simulated distributions of reproductive success (Sections 2.4.4 and 2.5.1). Finally, for successful nests we computed hatching failure rate as the number of unhatched eggs present in the nest after brood departure divided by the total number of hatched and unhatched eggs.

2.4.4. Variance in male reproductive success (I_{b_m})

We estimated this parameter by a simulation procedure using data on (i) the distribution of males and females among leks, (ii) the distribution of matings among males within leks, and (iii) variation in female reproductive success (Section 2.4.3). The simulation was performed using PopTools v2.6.6 (Hood, 2005). It started with the input of male and female population sizes and involved the following steps:

- We first determined how many leks would typically form in a population of the simulated size from a linear regression of lek numbers on male population size. We generated the regression using four years of lek count data (2001-2004) from the six smaller Gunnison sage-grouse populations (Gunnison Sage-grouse Rangewide Steering Committee, 2005). These data report male numbers as seasonal high counts which represent 58% of the

Table 2 Uncorrected proportions of males on leks of different size rank, sorted from largest (1) to smallest (further details in text Section 2.4.4)

Lek rank	Uncorrected proportion of males
1	$0.826 - 0.247\ln(l)$, $p = 0.0001$, $n = 25$
2	$0.382 - 0.074\ln(l)$, $p = 0.03$, $n = 24$
3	0.145 ± 0.019 , $n = 19$
4	0.095 ± 0.011 , $n = 13$
5	0.082 ± 0.014 , $n = 8$
6	0.064 ± 0.094 , $n = 6$
7	0.039 ± 0.072 , $n = 5$
8	0.032 ± 0.008 , $n = 4$

Table 3 – Sample sizes, sighting records, and annual mark-resight population estimates (\hat{N}) for the monitored portion of the San Miguel Basin Gunnison sage-grouse population, 2003–4

Population segment	Marked individuals		Marked bird sightings		Unmarked bird sightings		\hat{N} (95%CI)	
	2003	2004	2003	2004	2003	2004	2003	2004
Males	13	14	89	72	263	235	50 (34-73)	57 (37-89)
Females	20	22	22	16	109	86	105 (55-202)	123 (64-238)

Numbers of marked individuals refer to birds alive on April 1 of each year that contributed to the population estimate.

population estimated by our mark resight method (Section 2.3). Therefore, we converted high counts to male population size by dividing by 0.58. The fitted regression, which was forced through 1, 1 so that a population with one male had one lek, was lek number = $0.93 + 0.07 \times \text{male population size}$ ($F_{1,22} = 28.6, p < 0.0001$).

- ii. Males were next assigned to leks. We estimated the proportional distribution of males among leks from the dataset used to estimate lek number. For each population and year we first computed the proportion of males in each lek, sorted from largest to smallest. We then pooled the data and, for each lek rank, regressed the proportion of males on the number of leks in the population. For the first and second largest leks, this proportion decreased significantly in populations with more leks (Table 2). For the lower ranked leks, this relationship was not significant and we therefore computed a mean proportion for each lek rank (Table 2). Finally, the “uncorrected” proportions from Table 2 were normalized by dividing the value for each lek rank by the sum of uncorrected proportions for the number of leks in the simulation. Once males had been settled, females were distributed in proportion to the number of males assigned to each lek, reflecting a pattern documented at greater sage-grouse leks (Gibson, 1996).
- iii. Within each lek females (matings) were assigned to adult males based on Kokko and Lindström (1997) mating skew model:

$$E[p_{\text{rank}}] = \frac{\lambda(1 - \lambda)^{\text{rank}-1}}{1 - (1 - \lambda)^n}$$

where $E[p_{\text{rank}}]$ is the expected proportion of matings obtained by male of a given rank (the most successful male has rank of one), n is the number of males on the lek, and λ is a mating skew parameter that varies with lek size. Lambda (λ) can take values from zero (random mating) to one (all matings monopolized by one male). We estimated the relationship between λ and lek size (n) using data from five leks with sufficient data from this study and eight greater sage-grouse leks (Gibson et al., 1991; Semple et al., 2001). We computed λ for each dataset using Skew Calcula-

tor software (Nonacs, 2003) and then fitted Kokko and Lindström's (1997) function

$$1 = \frac{1}{1 + an^b}$$

using least squares. Fitted parameter estimates were $a = 0.093$ and $b = 0.875$.

- iv. To convert matings to offspring sired, each female was randomly assigned a nesting success

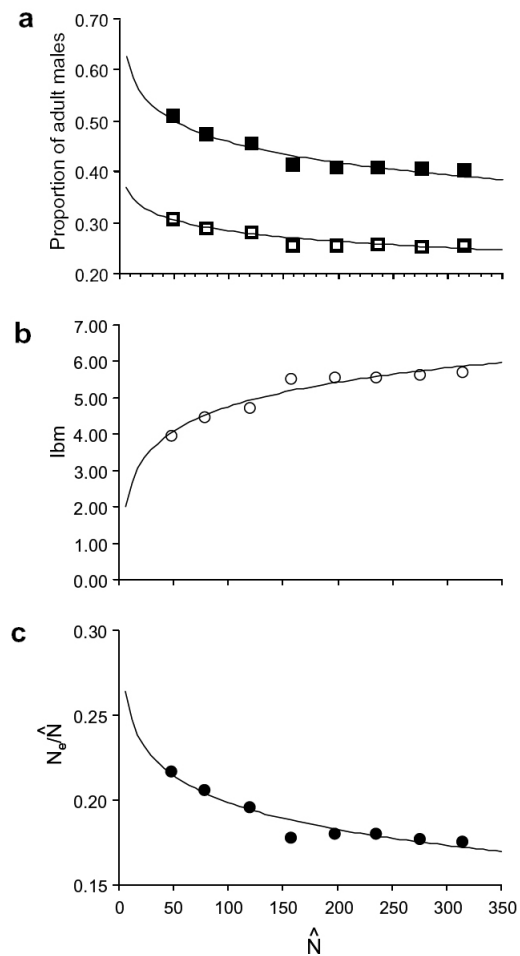


Figure 1 - Effects of population size (\hat{N}) on (a) the proportion of males mating (solid squares; $y = 0.6 - 0.05\ln(x)$; $p = 0.0001$) and reproducing (open squares; $y = 0.3 - 0.02\ln(x)$; $p = 0.0002$), (b) the standard deviation in male reproductive success (lbm; $y = 0.4 + 1.0\ln(x)$; $p < 0.0001$), and (c) N_e/\hat{N} ($y = 0.4 - 0.03\ln(x)$; $p < 0.0001$).

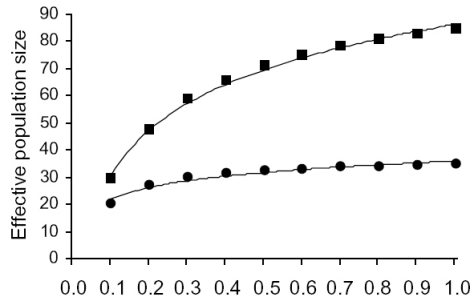


Figure 2 - Effective population size plotted as a function of the proportion of females hatching chicks under simulated lek mating (circles) and random mating (squares). Simulations are based on a census population size of 147.

value (0 or 1) based on the observed proportion of marked females that reproduced (Section 2.4.3). Successful females were then assigned a number of chicks drawn randomly from a normal distribution with the observed mean and variance in brood size per successful female. Chicks sired by each male were then summed over his assigned females.

- v. After step (iv), we computed the mean, variance and standardized variance (I_{b_m}) in male reproductive success (chicks sired per male), and the percentages of males mating and reproducing. Means of these values were computed after 1,000 simulations.

2.5. Simulated effects on effective population size

Besides estimating N_e for our study population, we simulated the effects on N_e of variation in (i) population size, (ii) mating system and (iii) female breeding failure. These analyses followed the methods described in Section 2.4, with the following changes.

2.5.1. Female reproductive success

For all simulations, empirical estimates of b_f and I_{b_f} (Section 2.4.3) were replaced by values based on simulated data. We randomly assigned a nest success value (0 or 1) to each female based on a specified probability that a female successfully reproduced. Successful females were then assigned a number of chicks drawn randomly from a normal distribution with the mean and variance in brood size per successful female observed in our study population. Using the observed proportion of females reproducing, this procedure produced estimates of b_f and I_{b_f} almost identical to the empirically derived values (Section 2.4.3) indicating that it accurately replicated the distribution of female reproductive success. The same values of nest success and brood size were used in the corresponding simulation of male reproductive success (I_{b_m} Section 2.4.4).

2.5.2. Effect of population size

In these simulations, changing population size affects the numbers and sizes of leks, which in turn affect the standardized variance in male reproductive success by altering the distribution of matings. We simulated eight population sizes ranging from 47 to 313 birds. The smallest population had 15 males and 32 females while the largest had 100 males and 213 females, thus maintaining the observed population sex ratio. We used the observed proportion of females reproducing when computing I_{b_f} and I_{b_m} .

2.5.3. Effects of skewed mating and female breeding failure

We simulated two mating scenarios: (i) skewed mating (described in Section 2.4.4) which mimics the pattern observed on leks, and (ii) random mating. The random mating scenario was implemented by setting the mating skew parameter λ (Section 2.4.4) to zero. We simulated each mating scenario at 10 levels of female breeding failure by varying the proportion of females reproducing from 0.1 to 1.0 at intervals of 0.1.

2.6. Statistical analyses

Unless otherwise indicated, we report summary statistics as mean \pm standard error. Statistical analyses were conducted in Statview v5.0 (SAS Inc., Cary, North Carolina).

3. Results

3.1. Empirical parameter estimates

3.1.1. Population size (\hat{N})

Table 3 gives sex-specific and total estimates of population size in each year with sample sizes and confidence intervals. Over both years, mean population size (\hat{N}) for the focal study area was 168 ± 13 ($n = 2$) with a population sex ratio of one male per 2.13 ± 0.03 females. After adjusting for omission of the two high elevation leks (Section 2.3), our population estimate for the entire San Miguel Basin was 216 ± 4 .

3.1.2. Survival (v_f and v_m)

Of marked individuals alive on April 1, 2003, 45% of 20 females and 27% of 11 adult males were still alive a year later. Seven of 11 female and seven of eight male deaths occurred prior to June 1, 2003. Table 1 lists additional demographic parameters computed from these survival estimates.

3.1.3. Female reproductive success

Mean reproductive success among females alive on April 1 was low ($b_f = 0.9 \pm 0.3$ chicks per female, $n = 39$) and the standardized variance in female reproductive success was correspondingly high ($I_{b_f} = 4.7$). Three factors contributed to this pattern. First, 10 fe-

males (26%) failed to hatch a brood because they died during the breeding season. Second, few nests (27%, summed over both first and second nesting attempts) were successful. Overall, only 21% of 39 females entering the breeding season, and 28% of 29 survivors, hatched any chicks. Finally, brood size among successful females was relatively low (4.3 ± 0.6 chicks per female, $n = 8$), due in part to low hatching success. Of 47 eggs found at seven successful nests after brood departure, 13 (28%) had failed to hatch. Five unhatched eggs contained partially developed embryos while eight appeared unfertilized. In this sample, hatching failure reduced brood size from 6.7 ± 0.4 , the sum of hatched and unhatched eggs, to 4.9 ± 0.7 (paired $t_6 = 2.9$; $p = 0.03$).

3.2. Modeled parameter estimates

3.2.1. Standardized variance in annual male reproductive success

Simulations of male reproductive success yielded a mean I_{bm} value of 5.1 ± 0.05 among adult males. In the simulations, a mean of $43.8 \pm 0.2\%$ of adults copulated but after clutch losses only $27.2 \pm 0.2\%$ reproduced.

3.2.2. Effective population size (N_e)

Using input parameter values listed in Table 1, our N_e estimate for the study area was 33 with a N_e/\hat{N} ratio of 0.19. Multiplying this ratio by the adjusted population estimate for the entire San Miguel Basin gives a N_e value of 42 for the entire population.

3.3. Effective population size simulations

3.3.1. Effect of population size

Effective population size increased from 10 to 55 as population size increased from 47 to 313. However, the N_e/\hat{N} ratio decreased as population size increased (Figure 1c; $p = 0.0002$) due to an increase in the standardized variance in male reproductive success, I_{bm} (Figure 1b; $p < 0.0001$). This pattern is partially explained by a decrease in the proportion of males mating in larger populations (Figure 1a). To explore this pattern further, we examined the numerical distribution of matings on leks of different sizes (details not shown). Although the proportion of matings obtained by the top ranked male was higher on smaller leks, as specified by Kokko and Lindström (1997) skew model, the number of matings per top ranked male increased with lek size because more females mated at larger leks. In addition, a higher proportion of males mated on smaller leks. Both of these effects should increase the variance in reproductive male success in larger leks. Because mean lek size increases with population size, they explain why the standardized variance in male reproductive success also increased.

3.3.2. Effects of skewed mating and female breeding failure

Figure 2 plots simulated effective population size for random and skewed mating scenarios under different levels of female breeding failure. Effective population size was significantly lower under skewed than random mating (paired $t_9 = 8.7$; $p < 0.0001$). However, the level of reduction in N_e depended on the proportion of females reproducing. For example, skewed mating lowered N_e by 31% when only 10% of females reproduced, but by 59% when all females reproduced. Female breeding failure also lowered effective population size ($N_e = 35.8 + 6.0 * \ln(\text{proportion of females reproducing})$; $p < 0.0001$). For example, under skewed mating, N_e was reduced by 23% when we lowered the percentage of female reproducing from 100% to 20%, near the value observed in our population.

4. Discussion

Our empirically-based analyses suggest that the effective size of our study population was around 19% of its census size and that both sexes, rather than just males, exhibit high variance in seasonal reproductive success. The simulations additionally predict the extent to which N_e is lowered by both the skewed mating system and female breeding failure, and that mating skew will lower N_e/\hat{N} more in larger populations. These conclusions are subject to at least three caveats.

First, our estimates of demographic parameters are based on only two years of data and longer term study might lead to different conclusions if female reproductive success or annual survival rates were particularly low during the study period. Effective population size would increase if female reproductive success were higher. For example, Figure 2 illustrates how N_e responds to an increase in female nesting success. N_e

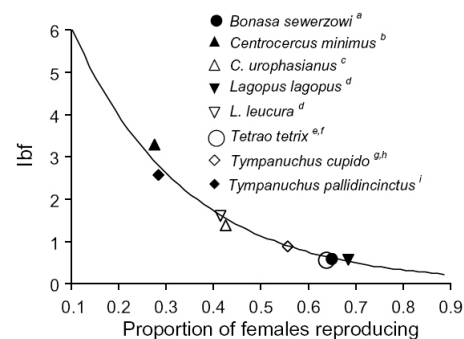


Figure 3 - Standardized variance in annual female reproductive success (I_{bf}) plotted as a function of the proportion of females reproducing for eight grouse species ($I_{bf} = 9.2e^{-4.2x}$; $p < 0.0001$). I_{bf} values were simulated using published estimates of female reproductive parameters. Cited references: ^aSun et al. (2003), ^bThis study, ^cSchroeder et al. (1999), ^dSandercock et al. (2005a), ^eWillebrand (1992), ^fCaizergues and Ellison (2000), ^gMcKee et al. (1998), ^hRyan et al. (1998), ⁱPitman et al. (2006a).

would also increase if annual survivorship were raised. For example, using formulas in Table 1 and Nunney's equation A2 (Section 2.4), a 20% increase in both male and female annual survival raises our N_e estimate for the focal study area from 33 to 40 and N_e/\bar{N} from 19% to 24%.

Second, we assumed that the mating system is adequately described by patterns of mating skew observed at leks. However, despite intensive lek monitoring we observed only 25–30% of females copulating annually (J.R. Stiver, unpublished data). Unseen matings could have occurred at leks during the evening display, on moonlight nights, or during the pre-dawn twilight when it was too dark to observe birds (Gibson et al., 1991). Additionally, some females might copulate away from leks entirely. Our results would be unaffected if those males observed mating on leks also monopolized unseen matings. However, if the males that were unsuccessful on leks performed relatively more unseen copulations, we would have overestimated the variance in male reproductive success and hence underestimated N_e .

Third, although a demographic estimate of N_e would ideally be based on the variance in lifetime reproductive success (Hill, 1972), the short-term nature of our study limited us to an approximate method that substitutes seasonal for lifetime variance (Nunney, 1993, 1996; Nunney and Elam, 1994). Nunney's method assumes that an individual's seasonal reproductive success is a random draw from the seasonal distribution and that annual survival is independent of reproductive success. These assumptions would be violated, causing systematic biases in N_e estimation, if reproductive success were age-dependent, individuals differed consistently in reproductive success across seasons, or seasonal reproductive success and survival were correlated. All of these patterns have been documented in long-term field studies of birds and mammals (Gibson and Guinness, 1980; Clutton-Brock, 1988; Newton, 1989; Stearns, 1992). Despite this, our use of Nunney's approach appears justified for two reasons. First, we found no difference in seasonal reproductive success between adult and yearling females in our study population (but see Aldridge and Brigham, 2001; Sandercock et al., 2005b) and we eliminated the major component of age-dependent reproductive success in males by considering only adult males as potential breeders (Gibson et al., 1991). Second, because only 27% of adult males and 45% of females survived from one year to the next (Table 1), there was limited scope for either individual differences in breeding success or correlations between success and survival to bias our N_e estimate.

Other authors have recognized the potential for skewed mating to decrease N_e by increasing the vari-

ance in male reproductive success in lek breeding grouse (Bellinger et al., 2003; Johnson et al., 2003, 2004; Bouzat and Johnson, 2004). In our simulations, skewed mating reduced N_e by 31–59% (depending on the proportion of females that reproduced) when compared to random mating. Random mating may be an overly conservative basis for comparison, however, because sexual selection presumably occurs in most animal populations (Shuster and Wade, 2003). Hence, this comparison on its own does not necessarily indicate that lek mating is associated with low N_e values. Two other comparisons bear on this question, though not conclusively. Using estimates based on the demographic method we employed, Nunney (2000) suggested that the ratio of N_e/N_{breeders} will usually lie between 0.25 and 0.75. For our data this ratio is 0.23 (33/145, computed for the study area). With higher female nesting success this figure would exceed 25%, but still remain towards the bottom of Nunney's proposed range. In contrast, our N_e/\bar{N} estimate of 0.19 exceeds the mean of many values, both demographic and genetic, synthesized by Frankham (1995) (0.11) and a genetic estimate of 0.10 for the lekking greater prairie chicken (Johnson et al., 2004). However, these comparisons are less informative because genetic estimates integrate all influences on N_e , including past population fluctuations, and should therefore yield lower values than demographic estimates, such as ours, that do not.

A novel prediction from the simulations is that N_e/\bar{N} should decline as population size increases. This effect arises because leks become larger as population size increases and, in larger leks, the variance in mating success is inflated because a smaller proportion of males mate and the number (though not the proportion) of matings by the most successful males increases. Although the predicted increase in the variance in male reproductive success with population size arises from a model of the dynamics of lek mating, this pattern has also been described in data from the polygynous, but non-lekking, red-winged blackbird (Weatherhead, 2005) and in flour beetles (Pray et al., 1996).

Reproductive success is often assumed to be more variable in males than females and consequently the relationship between male reproductive success and N_e has received considerable attention (Nunney, 1993; Storz et al., 2001, 2002). However, in our population, the standardized variance in seasonal reproductive success was almost as high in females (4.7) as in males (5.1). Our simulation results illustrate how increasing the rate of female breeding failure depresses N_e by elevating the variance in female reproductive success (Figure 3). As illustrated in Figure 3, the standardized variance in seasonal reproductive success is also negatively correlated with the proportion of females reproducing

across different species of grouse. This suggests that rates of female breeding failure should also be considered a potential influence on N_e in other grouse. In our analyses, we assessed the proportion of females reproducing immediately after hatching. However, some female grouse lose their entire broods after chicks leave the nest, but within 2 weeks of hatching (Aldridge and Brigham, 2001; Sandercock et al., 2005b; Pitman et al., 2006b; Tirpak et al., 2006). This would further elevate breeding failure, increasing the variance in female reproductive success and lowering N_e .

The estimated effective size of our study population (42) was below the level at which inbreeding depression occurs in captive breeding studies and well below the level at which adaptive potential is predicted to decline (see Section 1). Lowered hatching success is a well-documented correlate of inbreeding in wild bird populations (van Noordwijk and Scharloo, 1981; Keller et al., 2006). Our hatching failure rate of 28% is similar to values reported for a bottlenecked and inbred population of the greater prairie-chicken (*Tympanuchus cupido*; Westemeier et al., 1998). Similarly, Briskie and Mackintosh (2004) found that hatching failure rates averaged 25% for 11 bird populations which had passed through severe population bottlenecks, whereas outbred bird populations average 10% (Koenig, 1982). Hence, while we cannot rule out non-genetic causes of low hatchability, the hatching success data are consistent with current inbreeding depression.

If the San Miguel Basin Gunnison sage-grouse population is experiencing inbreeding depression, the other small populations could also be at risk. To explore this issue, we estimated effective sizes of the remaining Gunnison sage-grouse populations by converting 2004 lek high counts for each population (Gunnison Sage-grouse Rangewide Steering Committee, 2005) to \hat{N} as described in Section 2, and then calculating N_e for each population using the regression in Figure 1c. This procedure assumes that all populations exhibit similar demography to the San Miguel Basin, whereas fragmented bird populations may vary demographically (Engen et al., 2007). For the five smallest populations, extrapolated N_e values ranged from 3 to 31. If our regression were also valid for larger populations, N_e in the largest population, the Gunnison Basin, would be 329. This suggests that six of the seven Gunnison sage-grouse populations may have effective sizes low enough to induce inbreeding depression and all seven could be losing adaptive potential. If so, long term persistence of the six smaller populations would require translocations to supplement genetic diversity.

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