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BALANCED SEX RATIO AT HATCH IN A GREATER SAGE-GROUSE (*CENTROCERCUS UROPHASIANUS*) POPULATION

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Abstract—Only one estimate of sex ratio at hatch exists for Greater Sage-Grouse (*Centrocercus urophasianus*). Managers typically assume a ratio at the population level of approximately 2:1 (female:male), primarily on the basis of sex ratio in the harvest. We determined the sex of newly hatched young and unhatched Greater Sage-Grouse by amplifying a portion of the sex-linked CHD gene. Sex ratio for Greater Sage-Grouse in east-central Nevada was 0.51 ± 0.03 (SE; $n = 272$). We found no substantial difference in size between eggs that produced male chicks and those that produced females (44.5 ± 0.2 mm^3 vs. 44.3 ± 0.3 mm^3) or between the masses of male and female chicks (25.8 ± 0.3 g vs. 26.3 ± 0.3 g), which suggests that energetic cost investments by females were similar between offspring of different sexes. We also found no effect of female condition on differential investment in male versus female offspring. Given that adult survival does not differ substantially between the sexes in our study population (J. S. Sedinger unpubl. data), we suggest that this population may not contain 2 adult females to 1 adult male and that any bias in adult sex ratio is likely attributable to differential survival from hatch to first breeding. *Received 10 February 2009, accepted 1 June 2009.*

Key words: *Centrocercus urophasianus*, CHD-gene, genetic sexing, Greater Sage-Grouse, parental investment, sex ratio.

Balance del Cociente de Sexos al Momento de la Eclosión en una Población de *Centrocercus urophasianus*

Resumen.—Sólo existe una estimación del cociente de sexos al momento de la eclosión para *Centrocercus urophasianus*. Los gestores ambientales típicamente suponen un cociente al nivel poblacional de aproximadamente 2:1 (hembra:macho), basados principalmente en el cociente de sexos en la cosecha. Determinamos el sexo de pichones recientemente eclosionados y de individuos no eclosionados mediante la amplificación de una porción del gen ligado al sexo CHD. El cociente de sexos de *C. urophasianus* en el centro este de Nevada fue 0.51 ± 0.03 (EE; $n = 272$). No encontramos una diferencia sustancial en el tamaño entre los huevos que generaron pichones macho y aquellos que generaron hembras (44.5 ± 0.2 mm^3 vs. 44.3 ± 0.3 mm^3) o entre los pesos de los pichones macho y hembra (25.8 ± 0.3 g vs. 26.3 ± 0.3 g), lo que sugiere que las inversiones de costo energético por parte de las hembras fueron similares entre las crías de sexos diferentes. Tampoco encontramos un efecto de la condición de la hembra sobre inversiones diferenciales en crías macho versus hembra. Dado que la supervivencia del adulto no difiere sustancialmente entre sexos en nuestra población de estudio (J. S. Sedinger, datos no publicados), sugerimos que esta población puede no contener dos hembras adultas por cada macho adulto y que cualquier sesgo en el cociente de sexos de los adultos puede atribuirse probablemente a una supervivencia diferencial desde el momento de la eclosión hasta el primer período de cría.

In most animals, the numbers of male and female offspring produced are approximately equal. Darwin was unable to explain how this 1:1 sex ratio of offspring was maintained via natural selection and so left "its solution for the future" (Darwin 1874:399). Fisher (1930) showed that equal investment in each sex is the result of frequency-dependent selection, because any overproduction of one sex would be counterbalanced by a competitive advantage for the other, thereby producing a return to unity. Since then, several modifications of Fisher's equal-allocation hypothesis have described scenarios under which sex ratios may deviate from equality (Hamilton 1967, Trivers and Willard 1973, Clark 1978, Charnov 1982).

Before the development of molecular sexing techniques, there were few reliable assessments of primary sex ratio (Clutton-Brock 1986) or differential investment in offspring of different sexes, because of the difficulty of visually determining the sex of avian hatchlings. Griffiths and Tiwari's (1995) discovery of the chromobox-helicase-DNA-binding (CHD) gene on the W and Z chromosomes, and the subsequent development of a technique based on rapid polymerase chain reaction (PCR) that was able to

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identify sex in almost all bird species tested, has led to a resurgence in studies of avian sex ratios. Since then, biased sex ratios have been reported in species from half of the avian orders (Pike and Petrie 2003, Alonso-Alvarez 2006).

Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter "sage-grouse") are a highly dimorphic lek-breeding species in which adult males are, on average, 1.5× heavier than adult females (Patterson 1952, Connelly et al. 2004). As in most lek-breeding species, the mating success of male sage-grouse is highly skewed toward the dominant males on a lek (Scott 1942, Gibson et al. 1991, Höglund and Alatalo 1995). Thus, Trivers and Willard's (1973) maternal-condition hypothesis predicts that female sage-grouse in good condition should bias their investment in favor of males, thus producing high-quality males that have a higher probability of attaining dominant status on a lek. Similarly, females in poor condition should favor female offspring that have a high probability of breeding if they survive to their first breeding season.

With the decline in sage-grouse populations and their possible listing as threatened or endangered, it is important to have accurate estimates of key population parameters, including sex ratio. Sex ratio is a fundamental attribute of population structure because it may govern potential reproductive output (Becker et al. 2008) and variation in reproductive success, especially for males when females are the limiting sex (e.g., Rohwer and Anderson 1988). For example, in ducks, incubating females are vulnerable to predation, which is believed to reduce annual survival of females, producing a male-biased sex ratio (Johnson and Sargeant 1977, Sargeant et al. 1984, Richkus et al. 2005). By contrast, male sage-grouse could be vulnerable to predation while displaying on leks (Bradbury et al. 1989) or because they are larger or more conspicuous (Swenson 1986), which could produce a female-biased sex ratio.

Although the adult sex ratio in sage-grouse is frequently assumed to be 1:2 (male:female) on the basis of hunter returns, there have been few studies on sex ratios in sage-grouse. Swenson (1986) used juvenile sex ratios to test the hypothesis that juvenile males in dimorphic species suffer higher mortality under poor forage conditions because of the higher growth rates they are required to sustain (e.g., Wegge 1980, Cooch et al. 1997). Swenson used hunter kill data from 1965–1985, collected from all 56 counties in Montana, to calculate juvenile sex ratios. Swenson (1986) found that the sex ratio was (1) consistently skewed in favor of females (39.2–46.6% males) and (2) more heavily skewed toward females in years and areas with low-quality habitat, thus supporting the hypothesis of increased male mortality. An important limitation of Swenson's (1986) study was that he assumed that sex ratio and vulnerability of the sexes to harvest were the same and constant across years and areas.

To date, only one study (Bush 2005) has specifically examined sex ratio at hatch in sage-grouse and related it to maternal condition. Bush (2005) found that the overall population sex ratio (across years and leks) was significantly female biased (57%) and that sex ratio at hatch within 5 individual leks and across 5 years (1999–2003) of the study were female biased, though not significantly so. The effect of female quality and environmental variables on brood sex ratios was weak; the top model including female quality explained only 16% of the variation (Bush 2005).

In an ongoing study initiated in 2003 in east-central Nevada, we have radiotagged female sage-grouse annually on leks and monitored their nesting activities to assess impacts of a recently constructed electrical transmission line. We used these females in the breeding seasons of 2005 and 2006 to locate nests, obtain measurements of maternal condition, collect blood and tissue samples for sex identification, and obtain measurements of maternal investment (in eggs and hatchlings). In precocial birds, egg size and hatchling mass are good indicators of resources invested in individual chicks, because these species produce relatively large eggs that influence early growth and survival (Lack 1968, Moss et al. 1981, Martin 1987). Additionally, it is thought that parental care after egg formation (i.e., incubation, antipredatory behavior, leading of young, etc.) benefits all offspring, regardless of sex, and thus is not a functional means of biasing individual resource investment (Maxson and Oring 1980, Winkler and Walters 1983, Cooch et al. 1997).

Our specific objectives were to (1) examine the local population's sex ratio at hatch and brood sex ratios for deviation from a binomial distribution to determine whether the frequently assumed female-biased adult sex ratio in sage-grouse is attributable to a biased sex ratio at hatch and (2) assess variation in egg volume and mass of chicks just after hatching (i.e., allocation of resources) to assess whether greater investment was made in male than in female young. We also predicted that investment in male young would be condition dependent: females in good condition would allocate more resources to male young, thus producing larger male eggs, larger male chicks at hatch, or both. Sex ratios are expressed as the proportion of males in a brood unless we state otherwise.

Methods

Study site.—The study took place on an area of ~6,500 km^2, encompassing 12 leks, in Eureka County, Nevada (Fig. 1). It was bounded by the Cortez and Simpson Park mountains to the west and the Diamond and Sulphur Spring mountains to the east. Elevation ranged from 1,400 to 3,100 m, with mean annual rainfall of 23 cm and snowfall of 37.2 cm (National Climatic Data Center, Asheville, North Carolina). Vegetation was dominated by shrubs, with a generally sparse understory of grasses and forbs (Atamian 2007).

Field methods.—The study was conducted during 2005 and 2006 as part of a larger study initiated in 2003. We trapped females on leks before nest initiation. Peak female lek attendance was around 1 April, with most nests initiated 1–2 weeks later and hatching 35–38 days later. A fall trap coordinated with the Nevada Department of Wildlife was conducted on brood-rearing areas in 2005. Females were captured using large, long-handled dip nets and night-lighting with the use of binoculars to increase the distance at which birds were detected (Giesen et al. 1982, Wakkinen et al. 1992, Connelly et al. 2003). We used small-diameter (1–2 cm) mesh or rubber netting to avoid entangling the birds.

All females were fitted with a 22-g radio necklace (A4060; Advanced Telemetry Systems, Isanti, Minnesota) and received size-14 metal bands (National Band and Tag, Newport, Kentucky). We determined age (see below for criteria), weighed individuals (±0.05 kg), and measured the length of the 1st primary (±0.1 cm), 5th primary (±0.1 cm), wing chord (±0.1 cm), tarsus (±0.01 cm), and foot (±0.1 cm) (Eng 1955, Dalke et al. 1963). We placed females into two age-categories, yearling or adult, based on the shape of

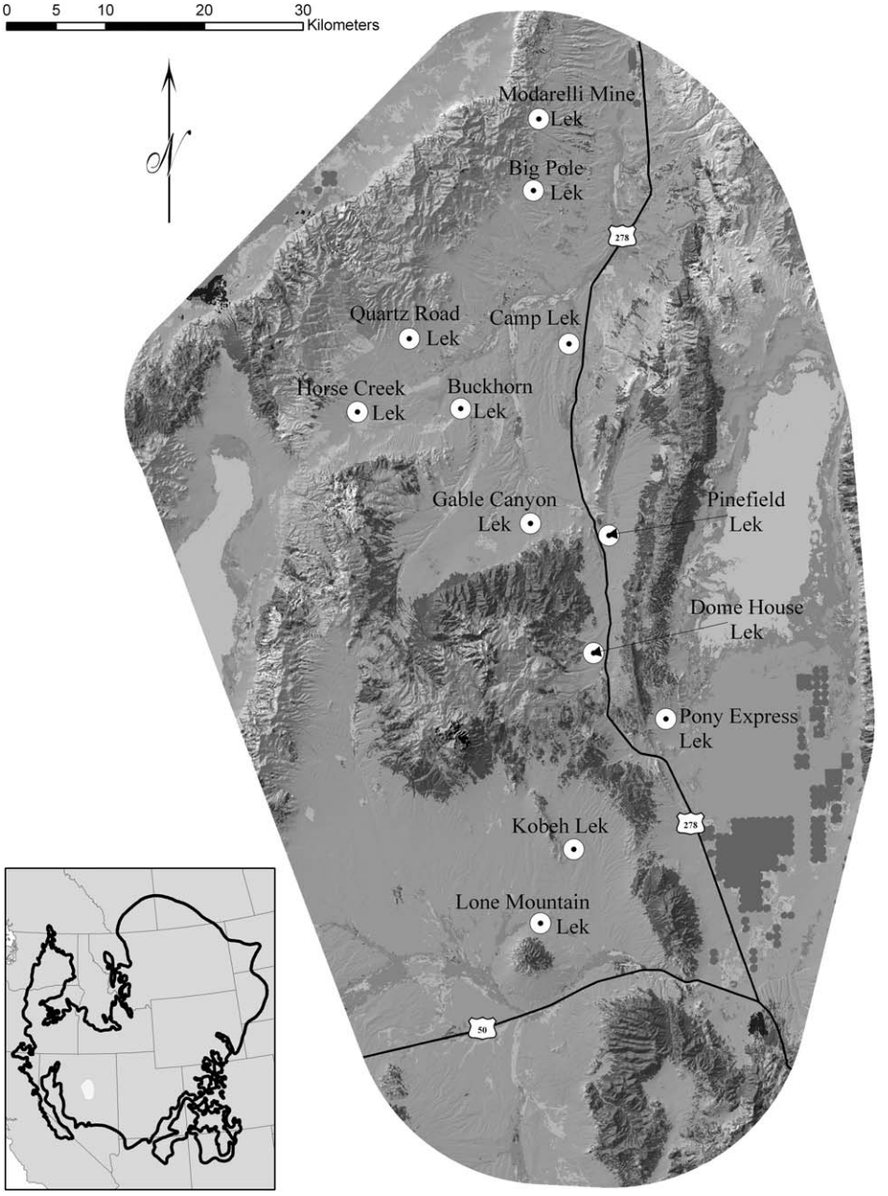

Fig. 1. Historical range of Greater Sage-Grouse, with the study area enlarged to show locations of the 12 study leks. The base layer is generalized cover types with a 30-m-resolution hillshade beneath.

the 9th and 10th primaries (Eng 1955, Dalke et al. 1963). In addition, we collected whole blood samples from all females and a subset of males during the lekking season to provide positive controls for genetic sexing. Blood was drawn from the brachial vein and frozen until genetic testing.

We attempted to locate females twice weekly during the breeding season. Upon locating a nesting female, we marked a visual checkpoint ≥20 m away and, if there was no adverse weather and no predators in sight, approached and moved the female off the nest. Each egg was marked with a letter, measured (length and width, ±0.01 cm), and floated to estimate stage of incubation. Within 24 h, we checked the nest again from a distance to confirm that the female had returned. The nest was then monitored from a distance twice weekly (with daily visits begun 3 days before predicted hatch based on 28 days of incubation) until either the eggs hatched or the nest failed, at which time we collected the eggs or egg remains and froze them for later sexing. Clutch size was the number of eggs present when the nest was found, except for 2 nests in which unmarked eggs were found after the initial visit, where clutch size was the number of eggs found during the first visit plus

the number of unmarked eggs found in each nest after completion (1 and 3 eggs, respectively). We estimated hatch date of successful nests as the midpoint of the interval between the time at which the clutch was found to have hatched and the previous nest check (precise to within ±0.3 day of actual hatch). We extrapolated the hatch date of failed nests after determining their stage of incubation by floating the eggs.

Broods were located within 3 days of hatching via the radiocollared female and were trapped and processed. Females were still brooding their young during the hours before dawn within 2–3 days of hatch, which is similar to what Gregg (2006) found. Females were flushed and the young gathered by hand and placed in a cloth sack, which was then placed inside a researcher's jacket to maintain chick body temperature. We weighed each chick (±0.5 g). In addition, we collected 2 blood quills from each individual and stored them dry in Ziploc bags for use in genetic sex identification. Once processing was completed, the entire brood was released together and researchers moved away from the brood in the direction opposite to where the female was last heard or seen. We remained in the area to confirm reassociation of the female and chicks.

Genetic sexing methods.—Genetic samples consisted of blood quill samples taken from chicks during brood trapping, vascular membranes from hatched or depredated eggs, embryos from abandoned eggs, and blood samples from adults. Sex of 18 embryos was determined genetically by K. Bush (University of Alberta, Edmonton) as part of a study examining mutation rates in unhatched sage-grouse chicks. We determined sex of the remaining samples by amplifying a portion of the sex-linked CHD gene using PCR and microsatellite primers P2 and P8 (Griffiths et al. 1998). In birds, females are the heterogametic sex (ZW) and males are homogametic (ZZ). The P2 and P8 primers amplify the Z-linked CHD fragment in both sexes and the W-linked CHD fragment in females only, producing 1 peak or band for males and 2 peaks or bands for females.

We extracted DNA from samples using a Qiagen DNeasy Tissue Kit (Qiagen, Valencia, California). After extraction, DNA was quantified using a fluorescent nucleic acid stain (Quant-iT PicoGreen, Invitrogen, Carlsbad, California) and read on a Labsystems Fluoroskan Ascent fluorescence plate reader (Nevada Genomics Center, University of Nevada, Reno). All samples were diluted to 5 ng μL^{-1}. We used 50 ng of template DNA in 15-µL PCR reactions using 1 unit of Titanium Taq DNA polymerase (Clontech, Mountain View, California), 1×Titanium Taq buffer (40 mM Tricine-KOH, 16 mM KCl, 3.75 µg mL^{-1} BSA, 3.5 mM $MgCl_2$, pH 8.0), 0.25 mM dNTPs (Applied Biosystems, Foster City, California), and 0.2 mM of microsatellite primers P2 and P8 (Griffiths et al. 1998). The PCR reactions were performed in a MultiBlock System Satellite 0.2G Thermal Cycler. The amplification profile consisted of an initial denaturing step of 94°C for 1 min followed by 35 cycles of denaturing at 94°C for 30 s, annealing at 53°C for 45 s, and extension at 72°C for 45 s, followed by a final extension step at 72°C for 30 min.

The PCR products were diluted and then processed through an ABI Prism 3730 DNA analyzer with an internal reference ladder (Nevada Genomics Center). We analyzed chromatograms in GeneMapper, version 3.7 (Applied Biosystems). The 21 blood samples obtained from adults of known sex were used as positive controls. If fragment-analysis results were unclear, we reran the PCR and fragment analysis.

Statistical analysis.—We tested the local population for departures from a 1:1 sex ratio at hatch in 2005, 2006, and both years combined using a binomial test (Wilson and Hardy 2002). We used a goodness-of-fit test to assess brood sex ratios (proportion of males to total brood) for departure from the binomial distribution. We ran a logistic regression using a null model (no explanatory terms other than the intercept) for each year separately and for the 2 years combined and used a chi-square statistic applied to the deviance to assess goodness-of-fit (Wilson and Hardy 2002, Crawley 2005). Lack of fit of the null model to the data would indicate departure from the binomial distribution (i.e., significant variation in sex ratio) among broods.

To test our prediction that allocation of resources was biased in relation to chick sex and female condition, we used linear mixed models to examine maternal resource investment (egg volume and chick mass) in relation to chick sex and measures of maternal condition (relative hatch date, clutch size, female size, and age of female). Female size was defined as the first principal component (PC1) from a principal component analysis (PCA) that included length of the 1st primary, 5th primary, wing chord, tarsus, and foot (Rising and Somers 1989). Controlling for clutch size also allowed us to assess the potential for tradeoffs between egg size and clutch size in the context of differential investment in male versus female offspring. We controlled for interdependence in egg size among eggs or chicks from the same brood by including "female" as a random effect in all analyses. Chick age (days) was included as a covariate in analyses of chick mass to control for differences in age (1–3 days) among broods at time of capture. We estimated egg volume (V, cm^3) from Flint and Sedinger's (1992) equation: $V = 8.22 + (0.4636LB^2)/1{,}000$, where L was length (mm) and B was breadth (mm).

We assessed model performance and strength of evidence for individual variables using Akaike's information criterion (AIC; Burnham and Anderson 2002). All analyses were conducted using SAS, version 9.1 (SAS Institute 2000). We report parameter estimates ± SE.

RESULTS

We determined the sex of 272 chicks from 38 broods produced by 33 females (5 females produced broods in both 2005 and 2006). These 38 broods were complete clutches (i.e., we obtained a genetic sample from every egg or chick). The local population's sex ratio at hatch in each year and for the study as a whole was not significantly biased (Table 1); males represented 51% (±3% SE) of the 272 chicks we sampled. Brood sex ratios did not show any significant departure from binomial expectation in 2005 ($\chi^2 = 0.98$, df = 13, $P = 0.47$), 2006 ($\chi^2 = 1.09$, df = 23, $P = 0.34$), or in both years combined ($\chi^2 = 1.03$, df = 37, $P = 0.41$).

We used 146 eggs from 20 females in a linear mixed model analysis of egg volume to examine whether male- and female-bearing eggs differed in size. The average volume of male-bearing eggs was 44.5 ± 0.2 mm^3, versus 44.3 ± 0.3 mm^3 for female-bearing eggs. The best model included the effect of female size only, but the inclusion of female size did not significantly improve the performance of the model over that of the null model (ΔAIC = 1.44;

TABLE 1. Offspring sex and sex ratio at hatch (males/total ± SE) during a 2-year study of Greater Sage-Grouse, together with the results from the binomial test of the probability of observing the proportion of males by chance. Data were obtained from 38 complete broods collected in Eureka County, Nevada.

Year	Male	Female	Number of broods	Sex ratio	Binomial *P* value
2005	50	54	14	0.481 ± 0.049	0.77
2006	88	80	24	0.524 ± 0.039	0.59
2005–2006	138	134	38	0.507 ± 0.030	0.86

Table 2). All models that included chick sex performed more poorly than the null model, and although the model-averaged estimate (across all models) of the sex effect was negative (–0.07 ± 0.23), which means that female eggs were smaller than male eggs, it did not differ from zero. The interactions of chick sex with relative hatch date (0.15 ± 0.35) and clutch size (–0.05 ± 0.23), although not different from 0, were consistent with the hypothesis that females in better condition produced larger male eggs. Interactions between chick sex and female size (0.16 ± 0.31) and age of female (0.10 ± 0.86 and 0.37 ± 0.99 for adult and juvenile females, respectively) were inconsistent with this hypothesis.

In the linear mixed model analyses of chick mass, we used data from 145 chicks from 21 females. Male chick mass, controlling for age, averaged 25.8 ± 0.3 g, compared with an average female chick mass of 26.3 ± 0.3 g. In the analysis of chick mass, the best model contained all the variables additively (Table 3). The second- and third-ranked models, which were not competitive, contained clutch size, individually (ΔAIC = 7.46) and additively with chick sex (ΔAIC = 8.118). The first- and third-ranked models contained a chick sex effect, but the effect did not differ from zero in either model (0.30 ± 0.27 and 0.31 ± 0.27, respectively). The model-averaged estimate (across all models) of the parameter for the effect of chick sex on mass was positive (0.29 ± 0.49), which indicates that females were slightly heavier than males, the opposite of the trend in the other analysis. Model parameters for the interactions of chick sex with the relative hatch date (0.07 ± 0.28), clutch size (–0.14 ± 0.24), and female size (–0.15 ± 0.21) were small and their standard errors overlapped zero, which indicates only weak effects.

TABLE 2. Performance of linear mixed models relating maternal effects and chick sex to egg volume (n = 146 chicks) in Greater Sage-Grouse. Explanatory variables considered were relative hatch date (RH), clutch size (C), female size (size), age of female (age), and chick sex (sex) in two-way combinations (additive and interactive) with the maternal condition measurements (RH, C, age, and size). Sex of the 146 individuals was determined using genetic samples collected from eggs in Eureka County, Nevada, during the 2005 and 2006 field seasons.

Model	ΔAIC	AIC weight	Number of parameters	Deviance
Size	0.000	0.2803	4	580.363
Null	1.441	0.1364	3	583.804
Sex + size	1.499	0.1325	5	579.862
C	2.196	0.0935	4	582.559
RH	2.768	0.0702	4	583.131
Sex	2.860	0.0671	4	583.223
Sex*size	3.233	0.0557	6	579.596
Sex + C	3.608	0.0461	5	581.971
Sex + RH	4.214	0.0341	5	582.577
Age	4.551	0.0288	5	582.914
Sex*C	5.551	0.0175	6	581.914
Sex + age	6.034	0.0137	6	582.397
Sex*RH	6.035	0.0137	6	582.398
All variables	7.033	0.0083	9	577.396
Sex*age	9.852	0.0020	8	582.215

TABLE 3. Performance of linear mixed models relating maternal effects and chick sex to chick mass (n = 145 chicks) in Greater Sage-Grouse. Explanatory variables considered were relative hatch date (RH), clutch size (C), female size (size), age of female (age), and chick sex (sex) in two-way combinations (additive and interactive) with the maternal condition measurements (RH, C, age, and size). Sex of the 145 individuals was determined using genetic samples collected from eggs in Eureka County, Nevada, during the 2005 and 2006 field seasons.

Model	ΔAIC	AIC weight	Number of parameters	Deviance
All variables	0.000	0.8824	10	567.958
C	7.457	0.0212	5	585.415
Sex + C	8.118	0.0152	6	584.076
Null	8.427	0.0131	4	588.385
RH	8.581	0.0121	5	586.539
Sex	8.905	0.0103	5	586.863
Sex + RH	8.958	0.0100	6	584.916
Size	9.045	0.0096	5	587.002
Sex + size	9.554	0.0074	6	585.512
Sex*C	9.777	0.0066	7	583.734
Sex*RH	10.895	0.0038	7	584.853
Sex*size	11.032	0.0035	7	584.990
Age	11.768	0.0025	6	587.725
Sex + age	12.270	0.0019	7	586.227
Sex*age	15.652	0.0004	9	585.610

DISCUSSION

We detected no bias in sex ratio at hatch in this population of Greater Sage-Grouse in either year of the study (48% and 52%) or both years combined (51%). These results contrast with the significant bias (57%, female) detected by Bush (2005) in the Alberta population of sage-grouse. Furthermore, the direction of the bias was not consistent between years in our study, whereas Bush (2005) found a consistent bias toward females in all 5 years (though not significant in each year). Although our overall sample size was smaller (272 vs. 507), we would have been able to detect a 6% deviation from parity in either direction. Our data suggest that the sex ratio at hatch in east-central Nevada is not biased.

The 1:1 sex ratio at hatch in our study differs markedly from the commonly assumed adult sex ratio of 1:2 (males:females), based on hunter returns, that is used in management of sage-grouse across their range. In 2005, the hunter-harvest wing-barrel data for eastern Nevada were 210 adult males to 313 adult females and 269 juvenile males to 333 juvenile females (Nevada

Department of Wildlife 2005, unpubl. data). Harvest data for 2006 were 256 to 299 adult males to females and 221 to 227 juvenile males to females (Nevada Department of Wildlife 2006, unpubl. data). We did not detect substantially different annual survival between our marked adult males (63%) and adult females (57%) (J. S. Sedinger unpubl. data). Therefore, if the assumed adult sex ratio is correct, males must have substantially lower survival from hatch to recruitment into the breeding population than females, as Swenson (1986) proposed. The 2005 harvest data are partially consistent with this hypothesis, although the 2006 harvest data are not. Alternatively, the assumed adult sex ratio may be incorrect, with the bias detected in hunter harvest data being attributable to differences in harvest vulnerability between the sexes that may result from differential habitat use, flock size (hens and broods form larger flocks), or association of females with less experienced juveniles. Future research examining the overall population sex ratio should focus on survival of juvenile sage-grouse. If wings from hunter kills are used to estimate adult sex ratios, investigators must control for potential differences in harvest vulnerability between the sexes.

We examined whether females invested more resources, overall, in male than in female offspring and found only weak support. Eggs containing males were not larger than eggs containing females. Likewise, body mass of male and female chicks at first capture did not differ. Atamian (2007) also failed to detect differences in structural size (PC1 score based on tarsus, wing chord, head, and foot) between male and female chicks. Our results contrast with the findings of Magrath et al. (2003) for Brown Songlark (*Cincloramphus cruralis*) and Anderson et al. (1997) for American Kestrel (*Falco sparverius*), both sexually size-dimorphic species. In both cases, the respective authors found that larger eggs contained the smaller of the sexes, females in Brown Songlarks and males in American Kestrels. The authors hypothesized that this may be an adaptation that lowers parental feeding costs in poor forage years (Magrath et al. 2003) or mitigates the competitive disadvantage of the smaller sex (Anderson et al. 1997). Even if this were correct for all size-dimorphic birds, sage-grouse would not necessarily be expected to follow this pattern, because they are precocial and accrue negligible parental cost in feeding young and there is little competition between young for food (except, possibly, in extremely poor forage years).

Our results indicate no differential investment in a particular sex in sage-grouse overall or as a function of female quality or condition. Thus, our results provide no support for the hypothesis of Trivers and Willard (1973) that females in good condition will invest more in male chicks. Additionally, at least in northeastern Nevada, sex ratio at hatch cannot explain the assumed female-biased sex ratio in sage-grouse populations. If such biased population sex ratios exist, they must result from differential juvenile or adult survival.

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