Variation in Brood Sex Ratios of Texas Rio Grande Wild Turkeys

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ABSTRACT We evaluated brood sex ratio (BSR) variation in Rio Grande wild turkeys (RGWT; *Meleagris gallopavo intermedia*) in the Edwards Plateau and South Texas Plains of Texas, USA, during 2005–2006. Offspring sex was determined from DNA extracted from tissue biopsies of embryos from unhatched eggs or vascular tissue from eggshells of hatched and depredated eggs. Sex ratio across all eggs was 56.3% male (135/240; $\chi^2_1 = 3.75$, $P = 0.053$). We found that mean population growth rate based on a population simulation with BSR at unity averaged 1.02 (range = 0.924–1.058), whereas it declined to 0.978 (range = 0.816–1.037) using BSR estimates from our study. Although our statistical analyses did not detect BSRs different from unity in BSR, our simulation modeling demonstrated that BSR variation caused biologically significant differences in mean population growth rates. Even though the biological mechanism controlling primary sex ratio remains unknown, our estimates of BSR should allow managers to more reliably predict population dynamics insuring viable RGWT populations across Texas. (JOURNAL OF WILDLIFE MANAGEMENT 71(6):1793–1799; 2007)

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Efficient management of wildlife populations requires knowledge of how interactions among abundance, production, recruitment, and survival influence population trends. To evaluate intricate relationships between population processes and population trajectory, managers typically estimate demographic parameters (White and Burnham 1999) and construct predictive population models (Lande et al. 2003, Phillips and White 2003). Sex ratios are one such key demographic parameter that has interested wildlife ecologists and managers for nearly a century (Cole and Kirkpatrick 1915, Haldane 1922, Clutton-Brock 1986, Clutton-Brock and Iason 1986). Natural selection favors those parents that modify investment in offspring when fitness differs between sexes (Fisher 1930, Trivers and Willard 1973, Clutton-Brock 1986); thus, deviations from parity (1:1 sex ratio) are frequent in many avian species (Hardy 1997), although the mechanisms controlling sex-ratio variation are still controversial (Palmer 2000). Critical evaluations of sex-ratio data are unavailable for most avian species, slowing progress in linking population demographic parameters to population trajectories. Because individual variation in survival, production, and recruitment causes demographic stochasticity (Engen et al. 1998, Lande et al. 2003), understanding sex-based variation, and its relationship to population demography, is essential for maintaining viable wildlife populations.

Rio Grande wild turkey (RGWT; *Meleagris gallopavo intermedia*) populations have exhibited various abundance trajectories in Texas since the 1970s (Beasom and Wilson 1992, Collier et al. 2007). Knowledge of RGWT demography in the Edwards Plateau (EP) and South Texas Plains of Texas, USA, (STP; Gould 1975) is limited (Dominquez et al. 2006, Collier et al. 2007). Recent modeling exercises demonstrated that for small populations (<100 individuals), shifts in sex ratio could have significant influence on trends in abundance (Engen et al. 2003). Thus, knowledge of sex-specific recruitment becomes increasingly important in small, noncontiguous populations, such as those frequently found for RGWT (Glazener 1967). We found no estimates of brood sex ratios (BSR) in North American galliforms, leaving relationships between primary (prehatch), secondary (recruitment), and population sex ratio unknown (but see Göth and Booth 2005).

We used genomic information contained within eggs from successful and unsuccessful nests to evaluate BSR (at hatching) for RGWT in Texas. Specifically, our objectives were to 1) determine whether BSR in RGWT differed from parity, 2) determine whether differences from parity were related to nesting female age, study region, or year, and 3) use stochastic simulation modeling to evaluate whether

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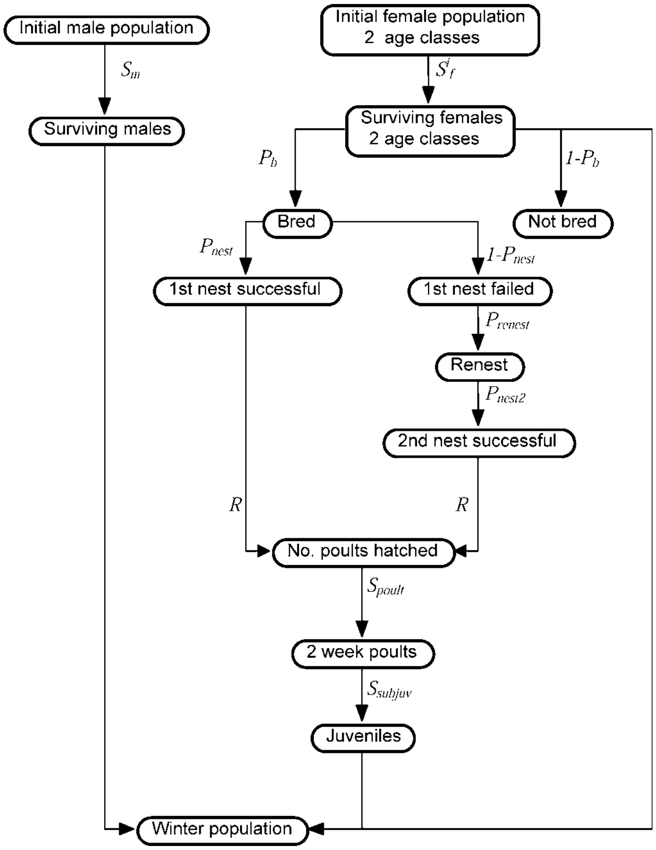

Figure 1. Basic structure of the conceptual model used to model the response of Rio Grande wild turkey population dynamics to variation in brood sex ratio using data on survival and production collected during 2001–2006 on the Edwards Plateau and South Texas Plain of Texas, USA.

variable BSRs influenced population growth rates and trajectory.

STUDY AREA

We conducted our study on sites in Bandera, Kerr, Medina, and Real counties in the EP, and sites in Kleberg, Kenedy, Nueces, and Brooks counties in the STP. The climate of the EP ranged from semi-arid to temperate with mild winters and hot, humid summers. The EP study sites were characteristic of the region's topography, with rolling divides characterized by limestone bedrock and outcrops with rocky soils (Gould 1975). This region previously was a fire-evolved grassland savannah interspersed with live oaks (*Quercus virginiana*) and mesquite (*Prosopis glandulosa*), with Ashe juniper (*Juniperus ashei*) along sheltered outcroppings (Taylor and Smeins 1994). Fire suppression and grazing concomitant with settlement gradually converted the area to brushland and open woodland consisting primarily of live oak mottes and Ashe juniper thickets. The climate of the eastern STP ranged from semi-arid to subtropical with mild winters and hot, humid summers (Gould 1975). Soils ranged from deep sands to fine sandy loams to sandy clay loams and native vegetation consisted of coastal prairie, live oak woodland, mesquite savanna, and Tamaulipan thornscrub. Several exotic grasses, such as bufflegrass (*Pennisetum ciliare*), and King Ranch bluestem (*Bothriochloa ischaemum*) have established in the area.

METHODS

Sex Ratio Data

We conducted our research during the breeding season (Apr–Jul) of 2005 and 2006. We captured juvenile and adult RGWT at each study site between December and March using rocket-nets, drop-nets, and walk-in funnel traps (Davis 1994, Schemnitz 1994, Peterson et al. 2003) baited with cracked corn and milo. We sexed, aged, and measured physiological and morphological characteristics of each captured bird. We equipped both juvenile (<8 months) and adult RGWT with backpack-style radiotransmitters weighing 69.0–95.0 g (Kenward 1987; Advanced Telemetry Systems, Isanti, MN) and located all radiotagged individuals ≥3 times weekly between December and July; we located females daily during the nesting season using ground triangulation or homing (White and Garrott 1990).

We determined nest initiation and incubation using female movement patterns and visual observation, and we monitored each active nest daily until we determined nest fate (Metz et al. 2006). Because we knew egg numbers for nests, we did not collect egg fragments; instead, we focused collection on whole eggs or eggshell caps from each nest (whether hatched or depredated). This protocol ensured that cross-contamination or multiple evaluation of the same genomic material did not occur. We individually bagged and labeled samples so each egg was uniquely identifiable to both female and nesting attempt within a year (some F nested >1 time during the breeding season).

We determined offspring sex using molecular sexing techniques (Griffiths et al. 1996). We collected tissue biopsies from embryos in unhatched eggs and we removed vascular tissue from eggshells of hatched and depredated eggs. We extracted genomic DNA with a DNeasy kit (Qiagen, Valencia, CA) following the manufacture's protocol; however, we used twice the recommended amount of animal tissue lysis buffer and Proteinase K on tissue from eggshells. We used primers P8 and P2 with polymerase chain reaction (PCR) to amplify 2 conserved chromo-helicase-DNA-binding (CHD) genes that are located on the sex chromosomes of most birds (Griffiths et al. 1998). The CHD-W gene is unique to females and the CHD-Z gene occurs in both sexes. Thus, when we examined the PCR product on a gel, there was a single (CHD-Z) band for males and a distinctive second (CHD-W) band for females. To ensure we assigned correct sex, and to make certain that small size differences between CHD-Z and CHD-W were revealed (Dawson et al. 2001), we labeled the 5′-end of the forward primer with a fluorescent marker for genotyping on an ABI PRISM 377 automated DNA sequencer (Applied Biosystems, Foster City, CA). All PCR protocols we used are described in Griffiths et al. (1996). We diluted all PCR products (0.85 μl) in a mix of formamide and ROX 500 (Applied Biosystems) size standard, and we determined genotypes using Genotyper 2.5 (Applied Biosystems). We

Table 1. Range of population demographic estimates used to parameterize the stochastic population simulation model used to predict population response of Rio Grande wild turkeys on the Edwards Plateau of Texas for different values of brood sex ratio.

Abundance and sex-ratio estimates	Min.	Max.
Initial abundance	100	500
Initial sex ratio[a]	0.15	0.35
Brood sex ratio[a]	0.30	0.80
Recruitment estimates		
P of first nest successful: juv	0.19	0.47
P of first nest successful: ad	0.18	0.54
P of second nest successful: juv	0	0.20
P of second nest successful: ad	0.12	0.37
$\bar{x}$ clutch size	11	11
	Juv	**Ad**
Proportion of F breeding	0.62	0.76
P of renesting	0.47	0.47
Sub-juv survival	0.36	
Ad survival	0.66	

[a] Expressed as proportion M.

conducted all statistical analysis using R (R Development Core Team 2005).

Population Projections

We projected population dynamics using a stochastic age- and sex-structured simulation model written in R. Our model was represented mathematically in compartments, which tracked the population using 1-year time steps. Our model tracked both sexes. We separated females by age (juv, ad) due to differences in breeding biology, but we did not separate males as 1) previous research indicated no differences in male survival between juveniles and adults (Goodwin et al. 1991, Collier et al. 2007; although see Holdstock et al. 2006) and 2) we did not consider male contribution to breeding in the simulation model. We used model expressions following Phillips and White (2003), incorporating demographic variation using binomial random variates such that estimates of survival, recruitment, and sex ratio were stochastic within the simulation. Our model can be described by a life-cycle graph (Fig. 1) with nodes representing different states of the RGWT population, and transitions between nodes occurred at rates denoted by the associated parameters. Model parameters included survival rates for adults (S_f^a), juveniles (S_f^j), poults (S_{poult}), and subjuveniles (S_{subjuv}; poult to recruitment into the juv population); recruitment parameters representing the probability of breeding (P_b; no. F that initiated nesting), probability of having a successful nest on the first (P_{nest}) and second (P_{nest2}) nesting attempt, the probability of renesting (P_{renest}), and recruitment rate (R; clutch size of successful nests).

We modeled the contribution of BSR to population growth rate and trajectory using 2 separate sets of input parameters. We modeled the population under the assumption of 50:50 BSR, and at the BSR we found during our study (see Results). Additionally, we modeled the population's response by drawing randomly from a uniform distribution bounded at the lower and upper values we estimated from our study. We based annual survival for adults and juveniles on estimates from Collier et al. (2007). Because RGWT population productivity is dependent on precipitation rate (Schwertner et al. 2005) and poult survival to 17 days (2 weeks; Spears et al. 2005), we based lower bounds for estimates of clutch sizes, nesting and renesting rates, and breeding probabilities (Table 1) on data collected in 2005–2006 (poor production yr) as part of an ongoing RGWT research project in the EP of Texas (M. J. Peterson, Texas A&M University, unpublished data); we based upper bounds for those parameter estimates on the highest values previously published for RGWT research during more productive years (Beasom and Pattee 1980; Ransom et al. 1987; Hennen and Lutz 1996; Spears et al. 2005; T. W. Schwertner, Texas Parks and Wildlife Department, unpublished data).

Using capture records and observational data from 2005–2006, we estimated population age structure at several winter roost sites as 40% juvenile and 60% adult and we

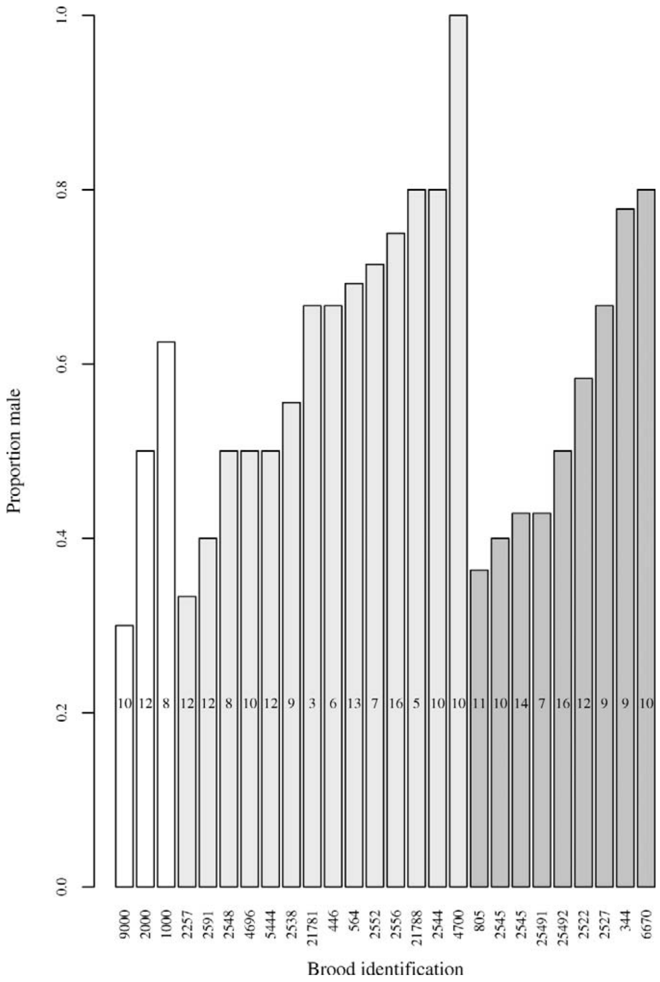

Figure 2. Rio Grande wild turkey brood sex ratio (expressed at proportion M) for 26 broods collected on the Edwards Plateau and South Texas Plains of Texas, USA, during 2005–2006. Numbers contained within the bars are brood size (no. of eggs from which we attempted to extract genomic material). Light gray bars representing broods from which we did not collect genomic material from ≥1 egg, dark gray bars indicate complete broods, and white bars indicate broods with unknown brood sizes.

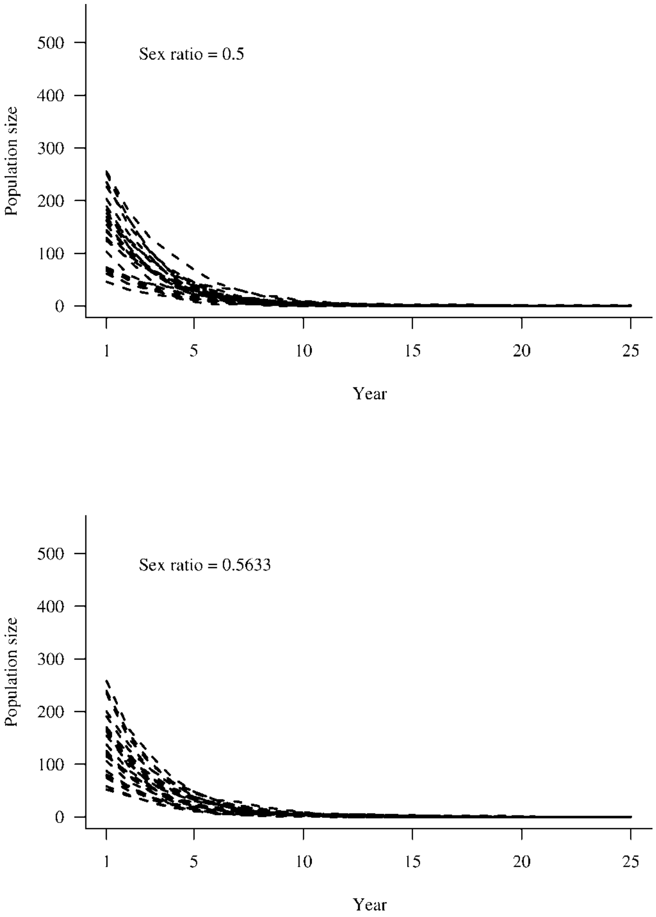

Figure 3. Population trajectory curves ($n = 25$) for Rio Grande wild turkeys during simulated poor production years, on the Edwards Plateau and South Texas Plains of Texas, USA, with brood sex-ratio estimates at parity (0.5) and based on estimates from our study (0.563).

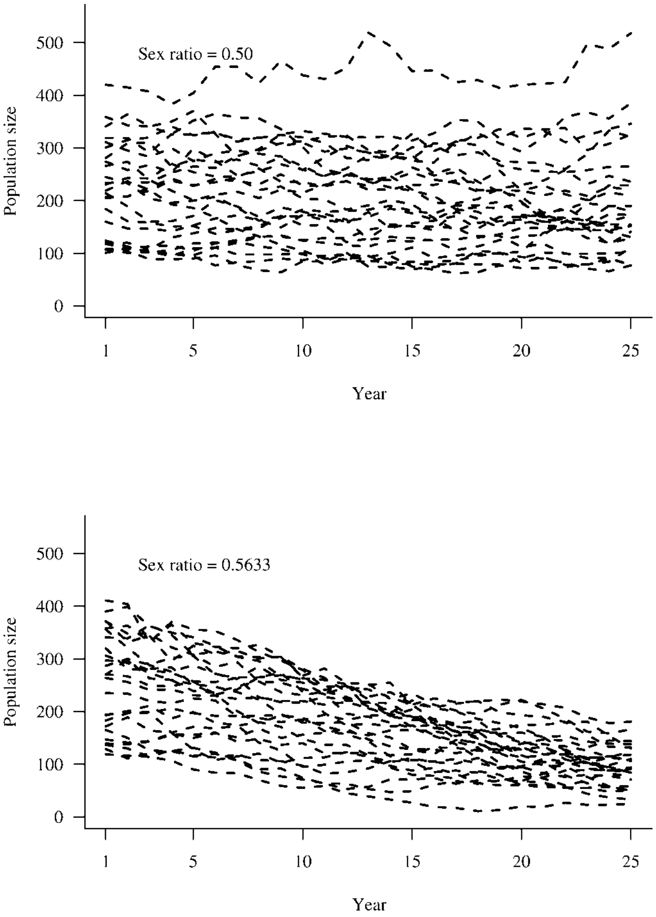

Figure 4. Population trajectory curves ($n = 25$) for Rio Grande wild turkeys during simulated good production years, on the Edwards Plateau and South Texas Plains of Texas, USA, with brood sex-ratio estimates at parity (0.5) and based on estimates from our study (0.563).

used these values for model initiation. Based on intensive monitoring of nesting females (Metz et al. 2006), we estimated average clutch size of successfully nesting females ($\bar{x} = 11$; Table 1) and modeled this parameter as a Poisson random variate bounded between 1 and 18 (min. and max. clutch sizes obs). Population size and BSR at model initiation was drawn from a uniform distribution (Table 1). We did not incorporate a parameter for annual harvest or sex-specific dispersal because <5% of total mortality in both study populations was due to harvest (Collier et al. 2007; W. L. Kuvleskey, Texas A&M University-Kingsville, unpublished data) and we found no evidence of differential dispersal by sex (M. J. Peterson, unpublished data). We conducted 5,000 simulations using random combinations of parameters described above to evaluate population growth rate over 20 years due to variation in BSR.

RESULTS

Sex Ratio

We examined 261 RGWT eggs from 26 broods collected 2005–2006. We failed to isolate genomic material or had questionable results (i.e., weak genotypic signals) in 21 samples, so our effective sample size was 240 eggs. Sex ratio across all eggs in our study population was 56.3% male (135/240; $\chi^2_1 = 3.75$, $P = 0.053$). One nest with a clutch size of 10 had only one egg from which we collected enough genomic material to evaluate (F 4700; Fig. 2), so we removed this egg from further analyses.

We found no differences in sex ratio from broods collected in the EP or STP. Sex ratios across all eggs in the EP and STP samples were, respectively, 55.8% (101/181; $\chi^2_1 = 2.918$, $P = 0.138$) and 58.6% male (34/58; $\chi^2_1 = 1.724$, $P = 0.189$). Known adult and juvenile females had more male offspring (57.0% [85/149] and 59.0% [36/61], respectively). Brood sex ratio for 2005 (57%; 88/154) and 2006 (55.0%; 41/74) appeared skewed towards males, but neither difference was statistically significant. Across broods, there was considerable evidence of variation in the proportion of males regardless of brood size (Fig. 2).

Population Model

Based on the population parameter estimates from 2005 to 2006 and the published literature, all simulated populations exhibited declines regardless of BSR estimates (Fig. 3). We do not consider the lower range of parameter estimates other than BSR further, as the implications of BSR on turkey populations are essentially inconsequential during poor production years. Using the higher range of population

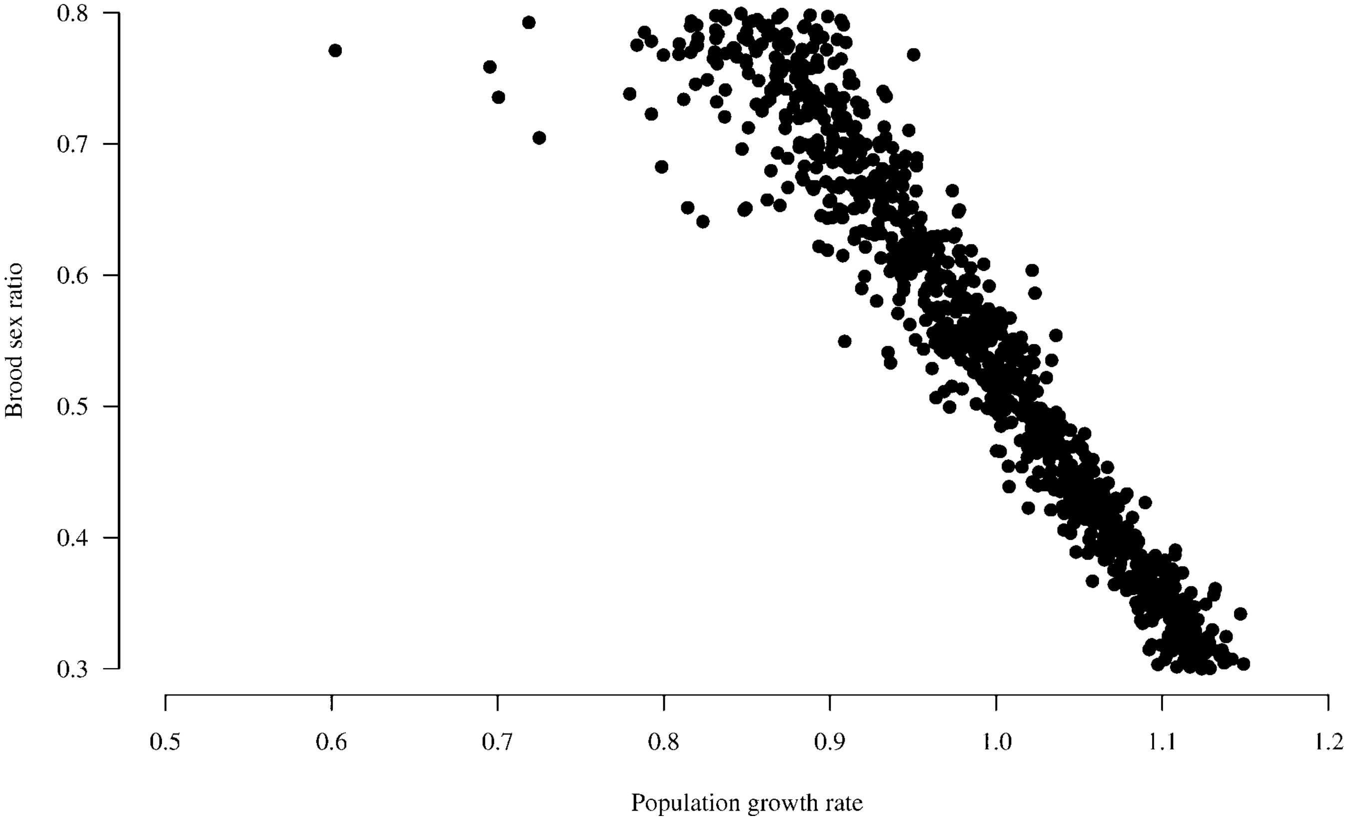

Figure 5. Simulated ($n = 5{,}000$) Rio Grande wild turkey population growth rates (after 20 simulated yr) across the range of brood sex-ratio estimates from our study on the Edwards Plateau and South Texas Plains of Texas, USA.

parameter estimates, populations with BSR at unity exhibited consistent trajectories, deviating stochastically around initial population sizes (Fig. 4), but BSR estimates from our field study caused nearly all simulated populations to exhibit declining trajectories (Fig. 4).

Mean population growth rate (λ) for simulations with BSR at unity (Fig. 4) averaged 1.02 (range = 0.924–1.058), declining to 0.978 (range = 0.816–1.037) using BSR estimates from our study (0.563). Following this trend, as BSR shifted further—towards or away from males—population growth rates continued to change (Fig. 5). Our results indicated that across the range of BSR evaluated, λ averaged 0.99 (range = 0.60–1.14) and that BSR influenced predictions of population trajectory (Fig. 5).

DISCUSSION

We identified 5 cases of wild turkey sex ratios at unity (1:1; Beasom and Wilson 1992). However, 4 of these 5 cases were from incomplete broods or broods of unknown size (Fig. 2), so it is possible that sex ratios of 1:1 are the exception rather than the rule. Our results suggest that sex ratios in RGWT broods during our study were skewed toward males, and there do not seem to be differences in BSR between years or nesting female ages. We acknowledge that in some cases we were evaluating incomplete broods and the addition of one sampled egg may have pushed some of the broods toward unity (e.g., Fig. 2: broods 2591 or 2538). Additionally, it is important to consider the distribution of clutch sizes, as odd clutch sizes cannot be at unity. However, our results indicated that only one case of unity occurred for even-numbered known brood sizes (Fig. 2: No. 25492). Thus, although we found variation in sex ratios among broods exists, our results suggest the assumption of 1:1 sex ratio frequently used in population modeling (Alpizar-Jara et al. 2001, Brooks et al. 2002) might not be justified biologically.

Although our statistical analyses did not detect BSRs different from unity, our simulation modeling demonstrated that under the same input parameters, BSR variation caused biologically significant differences in mean population growth rates. Our model predicted a stable population trajectory ($\lambda = 1.02$) for BSR at unity, but across the range of BSRs in our study, most populations exhibited declining abundance (Fig. 5). Additionally, we suggest that even though a parameter such as BSR may not differ statistically from unity, this should not negate application of data-based values from use in population models; on the contrary, empirical information should result in better prediction during modeling than relying on assumptions of parity.

Variation in reproductive performance has been documented in wild turkeys (Ransom et al. 1987), and research results suggest that poult survival could be one factor limiting RGWT populations (Vangilder et al. 1997, Spears et al. 2005). However, RGWT poult survival studies have been sex-invariant; thus, no information is available to accurately estimate sex-specific recruitment. If differential mortality exists, then evolutionarily it may be beneficial for parents to adaptively manipulate sex ratio in order to increase recruitment of the favored sex. Offspring survival is difficult to estimate in precocial avian species as capture and marking protocols typically used for adults are inappropriate given the rapid growth of offspring. However, given new approaches for estimating survival in dependent young (Lukacs et al. 2004), combining capture–mark–recapture survival estimates for RGWT offspring with estimates of BSR, one should be able to reliably estimate sex-specific recruitment into autumn RGWT populations, if one assumes sex-specific differential mortality does not exist.

Our study did not address mechanisms accounting for variations in BSRs in RGWT. Several factors could influence BSR in galliforms, including parental physiological condition (Trivers and Willard 1973, Nager et al. 1999), social conditions (Hasselquist and Kempernaers 2002), ecological conditions (Daan et al. 1996), dispersal mechanisms (Caley and Nudds 1987), and offspring sexual size dimorphism (Trivers and Willard 1973). These hypotheses should be evaluated to further our understanding of how sex-ratio variation influences population trajectories of galliforms, including RGWT.

MANAGEMENT IMPLICATIONS

Our research indicates that optimal management of wild turkey populations in Texas and across the United States requires accurate estimates of demographic parameters necessary to predict population performance and trajectory. Even though the biological mechanism controlling primary sex ratio is unknown for many avian species, our estimates of BSR should result in more reliable predications of population dynamics for developing management prescriptions and insuring viable RGWT populations across Texas. We suggest that wildlife managers should focus on 1) combining BSR with poult survival to estimate recruitment rates and 2) developing methods to evaluate sex ratio at recruitment into the reproductive population.

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