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# Factors influencing reproductive performance of northern bobwhite in South Florida

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**Abstract** Reproductive success is a critical component of individual fitness, and also an important determinant of growth rates of populations characterized by early maturity and high fecundity. We used radiotelemetry data collected during 2003–2008 to estimate reproductive parameters in a declining northern bobwhite (*Colinus virginianus*) population in South Florida, and to test hypotheses regarding factors influencing these parameters. The overall clutch size was 12.10±0.22, but females laid more eggs in their first clutch (12.43±0.24) than in subsequent clutches (10.19±0.53) within a nesting season. Daily nest survival was higher for first (0.966±0.003) than subsequent nests (0.936±0.011). Hatchability (proportion of laid eggs that hatched conditional upon nest survival to hatching) was 0.853±0.008, but was higher for nests incubated by females (0.873±0.009) than those incubated by males (0.798±0.018). The proportion of individuals attempting a second nest was 0.112±0.024 and 0.281±0.040 when the first nest was successful and failed, respectively. Hatchability was lower when the nesting habitat was burned the previous winter. We found no evidence that food strip density (a management practice to provide supplemental food) influenced any of the reproductive parameters. Mean summer temperature affected hatchability, nest survival, and proportion of nests incubated by males. Overall, the reproductive output in our study population was lower than that reported for most other bobwhite populations, indicating that low reproductive performance may have contributed to bobwhite population declines in our study site. These results suggest that current management practices, particularly those related to habitat and harvest management, need careful evaluation.

**Keywords** Burning · *Colinus virginianus* · Hatchability · Male participation · Nest survival · Weather conditions

## Introduction

Reproductive success is a critical component of individual fitness, and also an important determinant of growth rates of populations characterized by early maturity and high fecundity (Cole 1954; Saether and Bakke 2000; Oli and Dobson 2003; Stahl and Oli 2006). In most species of birds and mammals, fecundity is composed of several components (e.g., clutch or litter size, breeding probabilities, nest survival). Although nesting success seems to be the key reproductive parameter in many short-lived species of birds (see Clark and Martin 2007 for a review), the relative contribution of various components of reproduction on

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overall reproductive success and population growth rate remains poorly explored in most species (but see Wisdom and Mills 1997; Bernard-Laurent and Leonard 2000; Clark et al. 2008). Furthermore, reproductive parameters can vary substantially over space and time, and understanding causes and consequences of such variations is important for understanding population dynamics, regulation, and persistence (Frederiksen et al. 2005; Jenouvrier et al. 2005; Saether et al. 2006). Therefore, estimates of various components of reproduction and knowledge of factors influencing these parameters are essential for understanding life-history variation and population dynamics, and for developing or implementing effective management strategies.

The northern bobwhite (*Colinus virginianus*), a gallinaceous game bird species, exhibits a very complex breeding strategy, generally described as a rapid multiclutch ambisexual polygamous mating system (Emlen and Oring 1977; Curtis et al. 1993) where males may incubate a nest. Females may lay up to three clutches in a nesting season (e.g., Burger et al. 1995; Cox et al. 2005). These characteristics of uniparental incubation (but biparental brood rearing) and multiple clutches combined with a large clutch size give them a high reproductive potential (e.g., Burger et al. 1995). Nevertheless, this species is declining throughout its range in North America (Sauer et al. 2008), primarily due to changes in land use and potentially because of excessive hunting (Brennan 1991). This decline has resulted in hunter attrition, which causes important economic losses to rural communities (e.g., $13.3 million between 1991 and 1992 in the southeastern USA) and specific industries through reduced quail hunting expenditures (Burger et al. 1999). The bobwhite has recently become the focus of intensive management efforts to reverse the trend (Brennan 1999; Williams et al. 2004). Common habitat management practices include disking, roller chopping, prescribed burning, and food plots. Prescribed burning occurs during the dormant season to improve habitat of bobwhites and other pine-grassland and grassland birds, through stimulation of the vegetation growth for food and cover (Plentovich et al. 1998; Brennan et al. 2000; Butler et al. 2009).

Despite intensive research and management efforts, surprisingly, a few, if any, studies have used long-term field data and statistically robust analytical methods to estimate all components of the bobwhite reproduction and to test for effects of intrinsic and extrinsic environmental factors on the different components of reproduction.

Several parameters are necessary to describe the northern bobwhite reproductive biology: clutch size, nest survival, hatchability, probability of nesting again after a successful ("double-clutching") and a failed ("renesting") nesting attempt, proportion of nests incubated by males, brood survival (see Sandercock et al. 2008 for a review), and breeding probability. Here, we used data collected from a 6-year (2003–2008) study of radio-tagged birds to estimate and model all reproductive parameters of a northern bobwhite population in South Florida, near the southern edge of the geographic distribution. The study area is subject to extreme weather conditions such as droughts or floods. Food strips and prescribed fire are management actions that have been implemented to improve habitat of bobwhites by increasing food availability and accessibility, and cover. Our objectives were to (1) provide estimates of the eight reproductive parameters listed above; (2) test for differences in reproductive performance between the first and subsequent nesting attempts; and (3) test hypotheses regarding the effect of extrinsic factors (i.e., food strip density, status—burned or not the previous winter—of the nest location, mean summer temperature, and total summer precipitation) on bobwhite reproductive parameters.

## Methods

### Species and study site

Northern bobwhites are small (140–170 g) and short-lived (average <1 year) land birds (Brennan 1999), listed as near threatened (BirdLife International 2008). The breeding season, in our study area, starts in late winter with courtship displays. First clutches are laid in April and are incubated for 23 days (Rosene 1969). The first peak of hatching occurs between late May and mid-June. With renesting, the breeding season ends in September.

The study was conducted on the Fred C. Babcock-Cecil M. Webb Wildlife Management Area (26,799 ha; hereafter BW area), Charlotte County, in southwestern Florida (Fig. 1). The most significant plant communities included dry prairie (9,737 ha), pine-palmetto (9,145 ha), and wet prairie (7,047 ha). A detailed description of the native vegetation on our study site can be found in Frye (1954) and Singh et al. (2010). The area is subject to periodic short-duration flooding and prolonged drought that likely affect bobwhite habitat selection and demography.

Prescribed burning and roller chopping are currently the primary habitat management activities. About 50% of the area is burned annually in the dormant season (M. Kemmerer, personal communication). Cattle grazing (stocking rate of one cow per 24 ha) is permitted in various places on the area under lease agreements with local ranchers. Efforts to reduce or eliminate noxious nonnative plants are ongoing, and have been successful. The BW area is divided into five adjacent management zones: A (6,342 ha), B (6,258 ha), C (5,396 ha), D (5,689 ha), and a field trial course, F (3,132 ha; Fig. 1). Several kilometers of 3-m-wide food strips of 100% *Sesbania* sp. were planted in spring, rejuvenated, and fertilized on annual basis, to provide

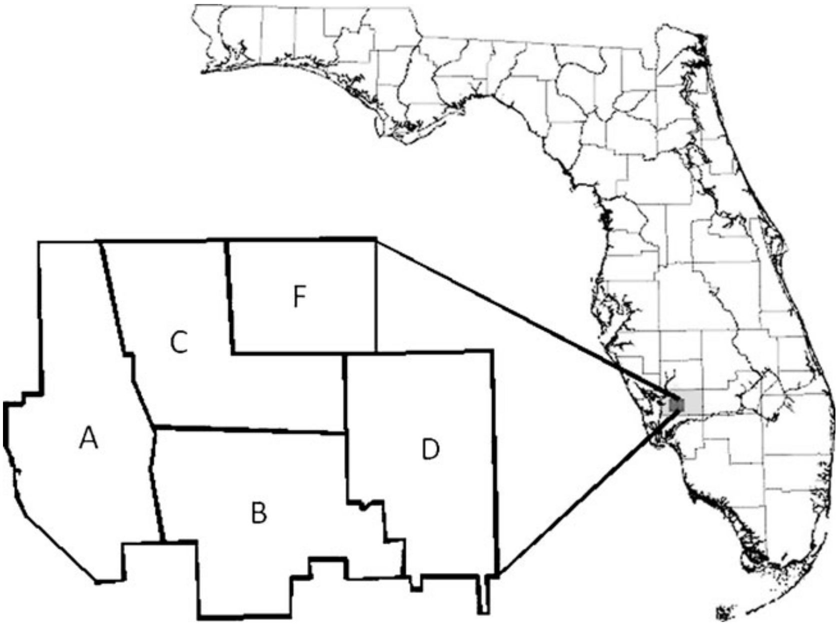

**Fig. 1** Location of the BW area, Charlotte County, South Florida, USA. The area is divided into five management zones (**a**, **b**, **c**, **d**, and **f**) with different levels of hunting pressure and food strip density (see text for details)

bobwhites with a supplemental winter food source. Those strips, covering 151 ha (0.56%) of the area, have different spatial densities among zones (30.81, 39.77, 49.22, 52.25, and 161.24 $m^2$/ha for zones A, B, C, D, and F, respectively); these did not change over the study period.

## Field methods

We collected data between October 2002 and March 2009 (i.e., for the years 2002–2008 since we considered a biological year from October of a calendar year $t$ to September of year $t+1$). We captured birds year-round opportunistically except during hunting season, using baited funnel traps. We used cast nets approximately 3 m in diameter to capture unmarked birds that were associated with radio-tagged birds both during daylight hours and at night. Birddogs helped to locate new birds not associated with radio-tagged birds. We weighed to the nearest gram, aged, sexed, and leg-banded birds. We only radio-marked birds (1,884 females and 3,076 males) weighing >130 g with a 6-g necklace-style transmitter with a mortality sensor (American Wildlife Enterprises, B. Mueller, Monticello, USA). We located radio-tagged birds every 3–5 days using hand-held receivers and Yagi antennas. All trapping and handling protocols were approved by the University of Florida Institutional Animal Care and Use Committee (protocol number A-794).

We located nests by tracking radio-tagged birds from the middle of March through the middle of October each year. If a bobwhite of either gender was located in the same area >2 consecutive visits during the nesting season, the area was thoroughly searched until we observe a nest, which could be at a stage of either laying or incubation. For each located nest, we recorded the burn history of the area (burned or unburned the previous winter) and counted the number of eggs when the parent was away from the nest. We attempted to check each nest at least every 3 days from the time it was located until its fate was determined. Nest fates were: hatched (when at least one egg had successfully hatched), destroyed, or abandoned. We considered nests as *hatched* when a distinctive "hatching cap" cut from the blunt end of an egg was observed; as *destroyed* when there was no eggs left in nest or evidence of crushed eggs in and around the nest's vicinity; or as *abandoned* when adults left the nest during egg laying or incubation and did not return. Nest depredation was the major cause of failure (74%) for the 130 nests classified as destroyed.

## Data analyses

In our study site, the nesting season spanned the 6-month period, from 1 April to 30 September; only three birds initiated nesting prior to 1 April. Based on 365 nests incubated by 300 individuals during 2003–2008 nesting seasons, we estimated and modeled the following eight parameters that characterize bobwhite reproduction. All estimates are mean ± SE.

(1) *Clutch size* is the number of eggs laid per clutch. We analyzed this parameter with a Poisson regression, i.e.,

generalized linear model (GLM) with Poisson distribution and log link function.

(2) *Nest survival* is the probability that a nest survives the laying and incubation period to successfully hatch. We considered a nest as successful when at least one egg hatched. We estimated and modeled this parameter using the nest survival model, implemented in program MARK (Rotella 2009) using the RMark interface in the R software (Laake and Rexstad 2009). The overall nest survival was estimated as the daily nest survival raised to the power of length of the incubation period.

(3) *Hatchability* is the proportion of eggs that hatched successfully, conditional upon survival of the nest until hatching. We used logistic regression models (GLM with binomial distribution and logit link function) for the analysis of hatchability.

(4) *Double-nesting* is the probability of an individual incubating a subsequent nest, conditional upon successful hatching of its first clutch. Although double-nesting primarily involves females, a few males were observed to incubate two nests (the first being successful) within a nesting season.

(5) *Renesting* is the probability of an individual incubating a replacement clutch (i.e., when the first nest failed). We recorded only five females attempting a third clutch, all after a failed second nesting attempt. We thus included those individuals as renesters. We used logistic regressions to estimate and model both renesting and double-nesting probabilities.

(6) *Proportion of nests incubated by males*. Some bobwhite nests are incubated by males while the paired female generally attempts to lay and incubate a second clutch. We used logistic regression models to analyze variations in the proportion of nests incubated by males.

(7) *Brood survival* is the proportion of chicks surviving the brood-rearing period, from hatching to 21 days (Burger et al. 1995). Twenty-one days after hatching, the radio-tagged parents were flushed with their brood, and the number of chicks was recorded. However, parents could have died before broods were flushed, and this could have led to death of some or all of chicks. Since we could not know whether the brood survived or died with their parents, we calculated two estimates of brood survival: a lower estimate by assuming that the brood died with their parents, and an upper estimate by assuming that the brood survived. Indeed, adoption of a part or whole brood by other parents is also possible (Faircloth et al. 2005). We also estimated brood survival for each year of the study, and we used CONTRAST software to test for the differences in brood survival among years (Hines and Sauer 1989). Estimates of brood survival were the survival of a brood from hatching to 3 weeks of age; thus, if the whole brood survived, brood survival was 1, but if parents of this brood adopted and reared chicks from another brood, brood survival would be $\geq 1$. Because of that, we could not use modeling approaches such as logistic regression for the analysis of this parameter.

(8) *Age-specific breeding probability* is the probability that a female bobwhite nests at least once during a nesting season, conditional on survival. Males were not considered because we could not distinguish between breeding and nonbreeding males except for those incubating a nest. We based estimates of breeding probabilities only on females radio-tagged before the beginning of the nesting season and alive on April 1st. To test for an age effect, we considered birds hatched the previous nesting season as juveniles and those hatched before that as adults. This distinction was made easily based on plumage characteristics (Rosene 1969) at the first capture for radio tagging. We used logistic regressions to estimate and model female breeding probabilities.

We used GLM (either Poisson or logistic regression) implemented in R (*glm* procedure; Crawley 2007) for the analysis of all parameters except brood survival. We used an information theoretic approach for comparison of competing models and for statistical inferences using Akaike's Information Criterion corrected for small sample size (AICc; Akaike 1973; Burnham and Anderson 2002). We started the model selection with the null model and then modeled additive and interactive effects of sex and year, two independent variables that are not of interest here but effects of which need to be taken into account. We used the resulting most parsimonious model (i.e., the model with the least parameters among models with lowest AICc and $\Delta$AICc $\leq 2$) as a base model for testing additive effects of other independent variables: whether the clutch was the first or the second (or third) laid (hereafter, nesting attempt), as well as variables related to habitat management (i.e., food strip density and burn status—"burned" or "unburned" the previous winter—of the nest location), and weather conditions (mean summer temperature and total summer precipitation at Punta Gorda, Florida: http://cdo.ncdc.noaa.gov/ancsum/ACS?coban=087397). Finally, because burn status was recorded on the nest location, we could not test for a burn effect on female breeding probability because the choice of nest location follows a female's decision to breed.

The model with the lowest AICc was considered the "best model". We assumed models with $\Delta$AICc $\leq 2$ to be not different (Burnham and Anderson 2002).

## Results

### Clutch size

The overall average clutch size was 12.10±0.22 eggs, but it varied annually from 11.25±0.46 to 13.60±0.74 (Table 1). There was some evidence for annual variation in clutch size, but the difference in AIC between this model and the constant clutch size model being <2 (Table 2a), we used the latter model as the base model for subsequent analyses. The best model included the nesting attempt variable (Table 3a), suggesting that clutch size differed between first clutch and those laid subsequently. Females laid more eggs in their first clutch (12.43±0.24) than in subsequent clutches (10.19±0.53). Addition of other variables did not improve the fit of the model (Table 3a); there was thus no evidence for an effect of food strip density, weather conditions, or burn status on clutch size.

### Nest survival

Daily nest survival was estimated at 0.962±0.003, but it varied from 0.950±0.016 to 0.982±0.007 among years (Table 1). The number of days in the laying period equals clutch size (12.10 on average) because females lay one egg per day, and the incubation period (23 days) starts with the laying of the last egg (Rosene 1969). So, an average of about $0.962^{23}=41.0\%$ of nests survived the incubation period, and about $0.962^{23+12.10}=25.7\%$ from the day when the first egg was laid to hatching. In comparison, apparent nest success (proportion of successful nests) was 56.9%. We found no evidence of a sex or year effect (Table 2b) and thus used the constant nest survival model as a base model for further analyses.

Daily nest survival differed between first (0.966±0.003) and subsequent clutches (0.936±0.011; Table 1b; model 2, Table 3b). Nest survival was inversely related to mean summer temperature (model 1; Table 3b), but this effect was not significant (model 1 slope=−0.777±0.431, $P=0.071$). Addition of other variables did not lower the AICc, indicating that there was no evidence for an effect of food strip density, total summer precipitation, or burn status of habitat where the nest was located.

### Hatchability

Hatchability was 0.853±0.008 on average, ranging from 0.770±0.054 to 0.892±0.019 (Table 1). The most parsimonious model included the interactive effects of sex and year (Table 2c); this model was thus used for subsequent analyses. Hatchability varied among years (Fig. 2) and was higher for nests incubated by females (0.873±0.009) than those incubated by males (0.798±0.018; Fig. 2). Model 1 also indicated an additive effect of burn status (Table 3c); hatchability for nests located in an area burned the previous winter was lower (0.844±0.014) compared to those in unburned areas (0.858±0.010). When we attempted to explain annual variation in hatchability by weather conditions, models with an interaction between sex and weather variables were better supported than models with the sex effect only (ΔAICc >2; Table 3c). Effects of both mean summer temperature (slope=−1.017±0.380, $P=0.007$) and total summer precipitation (slope=0.0012±0.0004, $P=0.007$) were significant (Table 3c). There was no evidence that nesting attempt or food strip density influenced hatchability.

### Double-nesting probability

Overall, the proportion of individuals attempting a second nest when the first nesting attempt was successful was 0.112±0.024, varying from 0 to 0.212±0.071 (Table 1). The most parsimonious model that we used as

**Table 1** Annual estimates of reproductive parameters (±SE) for northern bobwhite on the BW area, Florida

| | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 |
|---|---|---|---|---|---|---|
| CS | 13.23±1.01 | 13.60±0.74 | 12.37±0.40 | 11.50±0.51 | 11.25±0.46 | 12.07±0.54 |
| DNS | 0.950±0.016 | 0.982±0.007 | 0.962±0.006 | 0.966±0.007 | 0.962±0.006 | 0.952±0.008 |
| Hatch | 0.770±0.054 | 0.892±0.019 | 0.878±0.014 | 0.860±0.019 | 0.807±0.022 | 0.835±0.020 |
| DN | 0 | 0 | 0.149±0.052 | 0.065±0.044 | 0.212±0.071 | 0.100±0.047 |
| RN | 0.111±0.105 | 0 | 0.227±0.063 | 0.412±0.120 | 0.400±0.098 | 0.308±0.091 |
| $P_{IM}$ | 0.389±0.115 | 0.222±0.080 | 0.410±0.048 | 0.281±0.060 | 0.205±0.047 | 0.286±0.051 |
| $BS_l$ | 0.174±0.042 | 0.607±0.051 | 0.257±0.008 | 0.346±0.013 | 0.265±0.012 | 0.203±0.009 |
| $BS_h$ | 0.464±0.054 | 0.759±0.045 | 0.305±0.008 | 0.413±0.013 | 0.339±0.012 | 0.203±0.009 |
| $BP_{ap}$ | 0.875±0.117 | 0.594±0.087 | 0.517±0.054 | 0.549±0.070 | 0.416±0.056 | 0.456±0.066 |

Reproductive parameters are: clutch size (CS), daily nest survival (DNS), hatchability (Hatch), double-nesting (DN) and renesting (RN) probabilities, proportion of nests incubated by a male ($P_{IM}$), low and high estimates of brood survival ($BS_l$ and $BS_h$), and breeding probability of females alive on April 1st ($BP_{ap}$)

**Table 2** Results of base model selection for each reproductive parameter

| Number | Model | np | AICc | ΔAICc |
|---|---|---|---|---|
| (a) Clutch size ($n$=254) | | | | |
| 1 | Year | 6 | 1,286.77 | 0.00 |
| **2** | **Null** | **1** | **1,287.66** | **0.89** |
| 3 | Year+Sex | 7 | 1,288.56 | 1.79 |
| 4 | Sex | 2 | 1,289.28 | 2.51 |
| 5 | Year×Sex | 12 | 1,296.00 | 9.23 |
| (b) Nest survival ($n$=310) | | | | |
| **1** | **Null** | **1** | **1,031.73** | **0.00** |
| 2 | Sex | 2 | 1,033.21 | 1.48 |
| 3 | Year | 6 | 1,033.58 | 1.85 |
| 4 | Year+Sex | 7 | 1,035.38 | 3.65 |
| 5 | Year×Sex | 12 | 1,043.64 | 11.91 |
| (c) Hatchability ($n$=147) | | | | |
| **1** | **Year×Sex** | **12** | **685.81** | **0.00** |
| 2 | Year+Sex | 7 | 705.07 | 19.26 |
| 3 | Sex | 2 | 713.97 | 28.16 |
| 4 | Year | 6 | 721.94 | 36.13 |
| 5 | Null | 1 | 727.45 | 41.64 |
| (d) Double-nesting probability ($n$=179) | | | | |
| 1 | Year+Sex | 7 | 116.64 | 0.00 |
| **2** | **Sex** | **2** | **118.36** | **1.72** |
| 3 | Year×Sex | 12 | 125.39 | 8.75 |
| 4 | Year | 6 | 126.50 | 9.86 |
| 5 | Null | 1 | 127.34 | 10.70 |
| (e) Renesting probability ($n$=128) | | | | |
| **1** | **Sex** | **2** | **132.70** | **0.00** |
| 2 | Year+Sex | 7 | 133.40 | 0.70 |
| 3 | Year×Sex | 12 | 136.97 | 4.27 |
| 4 | Year | 6 | 154.10 | 21.53 |
| 5 | Null | 1 | 154.23 | 21.40 |
| (f) Proportion of nests incubated by males ($n$=356) | | | | |
| 1 | Year | 6 | 440.72 | 0.00 |
| **2** | **Null** | **1** | **441.33** | **0.61** |
| (g) Female breeding probability ($n$=312) | | | | |
| **1** | **Null** | **1** | **434.51** | **0.00** |
| 2 | Year | 6 | 435.38 | 0.86 |
| 3 | Age | 2 | 437.14 | 2.63 |

AICc is the Akaike's Information Criterion corrected for small sample size. ΔAICc is the difference in AICc between the best model and each of the other models, and np is the number of parameters. ΔAICc ≤2 indicates top models. The most parsimonious models are in bold types. Symbols "+" and "×" indicate, respectively, additive and interactive effects and include main effects; $n$ is the sample size. Variables tested were sex and year. The null model includes no covariate

**Table 3** Results of tests of various factors for each reproductive parameter

| No. | Model | np | AICc | ΔAICc |
|---|---|---|---|---|
| (a) Clutch size ($n$=254) | | | | |
| **1** | **NA** | **2** | **1,275.93** | **0.00** |
| 2 | NA+TSP | 3 | 1,276.88 | 0.95 |
| 3 | NA+FSD | 3 | 1,277.43 | 1.50 |
| 4 | NA+BSt | 3 | 1,277.73 | 1.80 |
| 5 | NA+MST | 3 | 1,277.93 | 2.00 |
| 6* | Null | 1 | 1,287.66 | 11.73 |
| (b) Nest survival ($n$=310) | | | | |
| 1 | NA+MST | 3 | 1,023.17 | 0.00 |
| **2** | **NA** | **2** | **1,024.64** | **1.47** |
| 3 | NA+FSD | 3 | 1,025.41 | 2.24 |
| 4 | NA+BSt | 3 | 1,025.81 | 2.64 |
| 4 | NA+TSP | 3 | 1,026.11 | 2.94 |
| 5* | Null | 1 | 1,031.73 | 8.56 |
| (c) Hatchability ($n$=147) | | | | |
| **1** | **Year×Sex+BSt** | **13** | **682.42** | **0.00** |
| 2* | Year×Sex | 12 | 685.81 | 3.39 |
| 3 | Year×Sex+FSD | 13 | 687.06 | 4.64 |
| 4 | Year×Sex+NA | 13 | 687.47 | 5.05 |
| *Test for weather effects (note: because weather covariates are temporally variable, the base model only includes "sex")* | | | | |
| **5** | **Sex×MST** | **4** | **709.63** | **0.00** |
| **6** | **Sex×TSP** | **4** | **710.09** | **0.46** |
| 7 | Sex+TSP | 3 | 712.79 | 3.16 |
| 8 | Sex+MST | 3 | 713.21 | 3.58 |
| 9* | Sex | 2 | 713.97 | 4.34 |
| (d) Double-nesting probability ($n$=179) | | | | |
| 1 | Sex+MST | 3 | 117.31 | 0.00 |
| 2 | Sex+TSP | 3 | 117.65 | 0.34 |
| **3*** | **Sex** | **2** | **118.36** | **1.05** |
| 4 | Sex+BSt | 3 | 118.73 | 1.42 |
| 5 | Sex×MST | 4 | 119.16 | 1.85 |
| 6 | Sex×TSP | 4 | 119.47 | 2.16 |
| 7 | Sex+FSD | 3 | 120.33 | 3.02 |
| (e) Renesting probability ($n$=128) | | | | |
| 1 | Sex+FSD | 3 | 131.87 | 0.00 |
| **2*** | **Sex** | **2** | **132.70** | **0.83** |
| 3 | Sex+TSP | 3 | 134.14 | 2.27 |
| 4 | Sex×MST | 4 | 134.34 | 2.47 |
| 5 | Sex+MST | 3 | 134.63 | 2.76 |
| 6 | Sex+BSt | 3 | 134.67 | 2.80 |
| 7 | Sex×TSP | 4 | 135.50 | 3.63 |
| (f) Proportion of nests incubated by males ($n$=356) | | | | |
| **1** | **NA+MST** | **3** | **415.74** | **0.00** |
| 2 | NA×MST | 4 | 417.24 | 1.50 |
| 3 | NA+FSD | 3 | 417.69 | 1.95 |
| 4 | NA+TSP | 3 | 418.14 | 2.40 |
| 5 | NA | 2 | 418.71 | 2.97 |

**Table 3** (continued)

| No. | Model | np | AICc | ΔAICc |
|---|---|---|---|---|
| 6 | NA×TSP | 4 | 419.97 | 4.23 |
| 7 | NA+BSt | 3 | 420.67 | 4.93 |
| 8* | Null | 1 | 441.33 | 25.59 |
| (g) Female breeding probability (*n*=312) | | | | |
| **1*** | **Null** | **1** | **434.51** | **0.00** |
| 2 | FSD | 2 | 436.44 | 1.93 |

Variables tested were nesting attempt (NA), food strip density (FSD), mean summer temperature (MST), total summer precipitation (TSP), and burn status (BSt). Base model (selected in Table 2) is indicated by an asterisk. See Table 2 for the definition of other symbols

a base model for subsequent analyses indicated only a sex effect (Table 2d). The double-nesting probability was 0.161±0.039 for females and 0.016±0.016 for males. The addition of other variables did not improve the fit of the base model (Table 3d), suggesting that food strip density, burn status, or weather factors did not affect the probability of double-nesting.

### Renesting probability

Overall, the probability of an individual attempting a second nest when the first nest failed was 0.281±0.040, ranging from 0 to 0.412±0.120 (Table 1). The most parsimonious model indicated a sex effect (Table 2e) and was used for subsequent analyses. Probabilities of incubating a replacement clutch by females and males were 0.410±0.054 and 0.044±0.031, respectively. The best model indicated an effect of food strip density, but this was not significant (slope=−0.007±0.004, *P*=0.104). There was no evidence that burn status or weather factors influenced renesting probability (Table 3e).

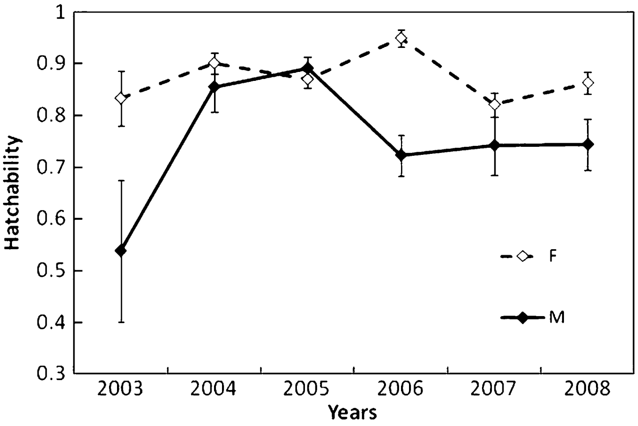

**Fig. 2** Bobwhite hatchability (i.e., proportion of eggs that successfully hatched, conditional upon survival of the nest until hatching) modeled with an interaction between sex and year (Table 2c), on the BW area, Florida

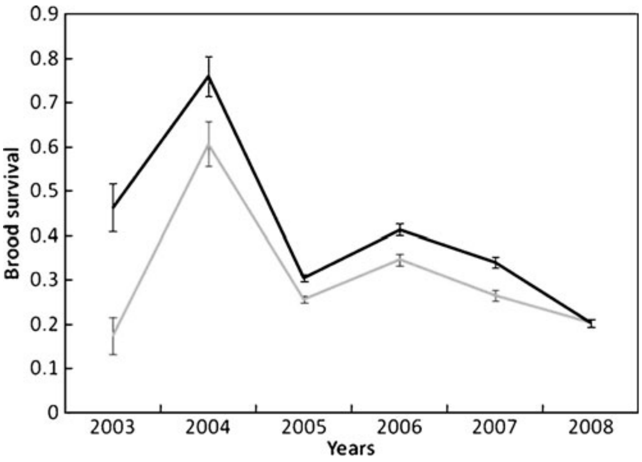

**Fig. 3** Interannual variation in bobwhite brood survival, on the BW area, Florida. Low (*gray line*) and high (*dark line*) estimates are provided depending on whether we assumed that brood died or survived, respectively, after the parent had died

### Proportion of nests incubated by males

Overall, 30.5 (±2.4)% of the nests were incubated by males. This proportion varied among years from 20.5 (±4.7)% to 41.0 (±4.8)% (Table 1). The most parsimonious model was the null model (Table 2f). Including the nesting attempt variable improved the model (Table 3f); the probability for a nest to be incubated by a male that had already incubated a nest earlier in the nesting season was lower (5.5±3.1%) than that by a male that had not incubated a nest earlier in the season (35.1±2.7%). There was no evidence of an effect of food strip density. However, mean summer temperature positively influenced this proportion (slope= 1.298±0.593, *P*=0.028, model 1; Table 3f).

### Brood survival

Overall, brood survival probability over 21 days after hatching was estimated between 0.281±0.002 and 0.336± 0.002 (low and high estimates, respectively; Table 1). Brood survival varied significantly among years with both low ($\chi_5^2 = 134.32$, $P<0.001$) and high ($\chi_2^5 = 315.68$, $P<0.001$) estimates (Fig. 3). Broods from the first clutch survived twice (between 0.299±0.003 and 0.356±0.003) as well as those broods from subsequent clutches (between 0.144±0.005 and 0.180±0.006).

Effects of burn status and food strip density on brood survival were not tested because, unlike nests, adults and their brood are likely to move, and the environmental conditions may thus vary within 21 days.

### Breeding probabilities

On average, 50.3 (± 2.8)% of the females nested at least once during a breeding season, but the female breeding probability ranged from 41.6±5.6% to 87.5±11.7% (Table 1). These results suggested that a substantial proportion of females died by the time we located all the nests. An a posteriori analysis indicates that on average, 73% of females survived during the first 2 months of the nesting season. The most parsimonious model was the null model, and there was no evidence for an effect of age or year, suggesting that adult and juvenile females had a similar breeding probability, and that breeding probability was fairly constant over the study period. Subsequent analyses did not reveal an influence of food strip density on breeding probability (Tables 2 and 3g).

## Discussion

Understanding the causes of population decline such as that of bobwhites (Sauer et al. 2008) necessitates knowing factors and processes that influence demographic parameters which can vary substantially over space and time (Frederiksen et al. 2007; Ozgul et al. 2009; Sandercock et al. 2008). Understanding these relationships would also be essential for devising management strategies for reversing such trends (Krebs 2002). Our study is one of the few studies of bobwhites to simultaneously provide estimates of all reproductive parameters (see Sandercock et al. 2008 for a review) for the same population (BW area, South Florida) during the same study period (2003–2008), and to test for the effects of habitat management practices and environmental factors on these parameters.

Sandercock et al. (2008) reviewed published estimates of bobwhite demographic parameters, and calculated a median values for various parameters. We will refer to these reported median reproductive parameters as “population median” throughout the discussion.

### Nesting performances

Although temporal variation in reproduction has been reported in many bird species (Frederiksen et al. 2005; Jenouvrier et al. 2005; Dykstra et al. 2009), including short-lived galliforms (Vangilder and Kurzejeski 1995; Wilson et al. 2007; Casas et al. 2009), most bobwhite reproductive components (i.e., all but hatchability and brood survival) in the BW area did not differ among years. Similar results were reported for other bobwhite populations (Burger et al. 1995; Taylor and Burger 1997; Rader et al. 2007; Mueller et al. 1999; Taylor et al. 1999).

Size of the first clutch was higher than that of the subsequent ones, which was also found in other studies (Burger et al. 1995; Taylor and Burger. 1997), and broods from a first nesting attempt survived better than broods from subsequent nesting attempts. Nest survival was also higher for first than for subsequent nests in our study site, whereas other studies found no difference in survival between first and subsequent nests (Burger et al. 1995; Taylor and Burger 1997; Cox et al. 2005). Our results would thus support the life history theory which predicts a higher investment of resources in the current reproduction than in subsequent ones, in short-lived birds (Stearns 1992).

Previous studies reported that second and third clutches contribute less than first clutches to the reproductive output and to the population growth rate of other bobwhite populations and gamebird species (Guthery and Kuvlesky 1998; Bro et al. 2000). This contribution might be even lower in our study population because the probability of double-nesting was one of the lowest recorded in bobwhite populations (Sandercock et al. 2008).

Clutch size in our study site was similar to those reported for other populations (12.1 in the BW area vs. 12.8 for the population median; Sandercock et al. 2008). Larger clutch size of first nests compared to subsequent nests is common in birds (e.g., Vangilder and Kurzejeski 1995); consistently, we found that bobwhites laid larger clutches during the first—compared to subsequent—nesting attempt. This pattern may be due to deterioration of parental physiological condition (Price et al. 1988), or declines in environmental quality, including increase in predator density (Cody 1966; Young 1994). Nest depredation was the main cause of failure of bobwhite nests, but more data on predation and female physiological condition would help conclude between the condition and the environmental hypotheses.

Nest survival in the BW area was lower than the population median (BW area: 0.26; population median: 0.42). However, in most studies, nest survival was estimated as an apparent nest success, which tends to be biased high because it fails to account for exposure prior to nest discovery (Mayfield 1961). A more recent study that used the nest survival model implemented in MARK reported a daily nest survival of 0.959 in a bobwhite population in Texas (Rader et al. 2007), which was comparable to what we found (0.962). Consistent with results in other bobwhite populations, nest survival was not influenced by the sex of the parent incubating the nest (Burger et al. 1995; Puckett et al. 1995; Taylor and Burger 1997; Cox et al. 2005; Rader et al. 2007). Renesting probability was higher than double-nesting probability, which indicates that second nests mainly corresponded to renests. Because low-quality females perform less well in general (e.g., Hamel et al. 2009), female renesters (i.e., females that failed their first attempt) may also fail in their second nesting attempt. The lower nest survival of double and renests—nests that are attempted later—compared to first nests might also be explained by an increasing predation rate as the nesting season progresses (Rollins and Carroll 2001; Wilson et al. 2007). Another explanation might be that a seasonal change in vegetation cover favored nest depredation later in the season. The lack of data on predator abundance and vegetation changes did not allow us to rigorously test these ideas. Also, Dinsmore et al. (2002) recommended accounting for a temporal trend of daily nest survival within a nesting season, but nest initiation dates were not available.

Hatchability was lower in the BW area than the population median (0.85 and 0.92, respectively). We tested for a sex effect on hatchability, which to our knowledge has not been done before for this species. We found that hatchability was higher for nests incubated by females compared to those incubated by males. Similar results have been reported for red-legged partridge *Alectoris rufa* (Casas et al. 2009). Higher hatchability of female-incubated nests suggests that females generally might be better incubators than males or that eggs they lay for males to incubate are of poorer quality.

One reproductive parameter that was lower in our study site than the lowest observed in other bobwhite populations was the proportion of double-nesting females (0.161 in the BW area vs. 0.180 in Iowa; Suchy and Munkel 1993). This is likely a result of two factors. First, nest survival being low, most breeders renest rather than attempting a double-nest. Second, summer survival on the BW area is low (30%; Rolland et al. 2010), which precludes breeders from either renesting or double-nesting. The probability of renesting was also low compared to the population median (0.28 and 0.50, respectively; Sandercock et al. 2008).

The proportion of nests incubated by males was higher in the BW area than the population median (0.305 and 0.280, respectively; Sandercock et al. 2008). Our results show that males incubated not only renests but also double-nests. Only one such observation has been previously documented (Suchy and Munkel 1993). The male participation, in terms of proportion of nests incubated by males, might have been overestimated due to the male-biased sex ratio in our sample of radio-tagged birds. However, the proportion of nests incubated by males reported in red-legged partridge was similar (0.329; Casas et al. 2009).

Brood survival in the BW area was at best 0.34 at 21 days (high estimate) or, extrapolated, 0.21 at 30 days, which was lower than the population median (0.41 at 30 days; Sandercock et al. 2008) or in the wild turkey (Vangilder and Kurzejeski 1995). However, this estimate was based on flush rates, and may not be unbiased because: (1) flush rates and detection of chicks likely vary with vegetation type; and (2) brood amalgamation and abandonment are common in bobwhites (Faircloth et al. 2005), and this may incorrectly lead to 100% mortality in some broods and >100% survival in others. These results should therefore be interpreted with caution.

More than half of the females, alive on April 1, initiated and incubated at least one nest, which was as expected. Indeed, 73% of females survived the first months of the nesting season and that identity of only 70% of females was known (males incubated ca. 30% of the nests), leading to an identifiable 51% of females breeding. Therefore, our results confirm the reasonable assumption of a 100% of breeding probability used by Sandercock et al. (2008) in their population model.

## Effect of management activities and weather conditions

We found no evidence that food strip density positively influenced any of the reproductive parameters, which suggests that food supplementation had no direct effect on bobwhite reproductive parameters during summer when food is usually not a limiting factor. Indeed, the primary goal of planting food strips was to provide bobwhites with a supplemental food source during winter, season during which they do not reproduce. In addition, food strips affect positively home-range size and habitat (including nest site) selection by bobwhites in the BW area (Singh et al. 2010), which justifies the continued use of those food strips.

Hatchability fluctuated among years, and variation in hatchability was partly explained by variability in summer temperature and precipitations. This significant weather influence on hatchability has never been documented before for bobwhites. However, in other bird species, hatchability has been reported to be affected by temperature, humidity, and other environmental factors (Carey 1980). Those factors would mostly affect hatchability of first eggs laid before incubation starts.

Surprisingly, hatchability was lower in burned than in unburned areas. The benefits of burning to bobwhites depend on three characteristics: timing, scale, and frequency of burn. On the BW area, large patches (≥400 ha) of habitat were burned every other year during the dormant season (M. Kemmerer, personal communication). Whereas frequent burning is known to be beneficial to bobwhites (Lewis and Harshbarger 1986), large-scale burning has been reported to be detrimental (Wellendorf and Palmer 2009), and this might have also been the cause of the lower hatchability in burned than in unburned areas in our study site, although the underlying mechanisms remain unclear. Nests in burned areas are more exposed, and eggs would reach higher temperature, which could reduce hatchability. This idea is supported by our result that higher summer temperatures were associated with lower hatchabilities. Also, the risk of predation may increase as protective cover is reduced, especially when large areas are burned because it prevents bobwhites from establishing a nest in a neighboring unburned patch within their home range, but this may only explain a lower nest survival in burned areas compared to unburned areas. Nest success and adult survival were not affected by prescribed burns in West Central Texas (Carter et al. 2002). In contrast, we found that several components of reproduction (nest survival, renesting and double-nesting probabilities, and proportion of nests incubated by males) were lower (although not significantly) in habitats that were burned the previous winter (Online Resource 1). These results point to the possibility that at least some components of bobwhite reproduction may have been negatively affected by current burn regime at BW area. Therefore, the current fire regime (e.g., frequency and scale) on the BW area needs careful evaluation. Impact of other habitat management strategies such as grazing should also be assessed.

### Synthesis and implications

Harvest mortality is generally assumed to be compensatory in many hunted species, because of density-dependent compensatory mechanisms (Ellison 1991; Smith et al. 1993). In our study population, evidence suggests that harvest mortality is largely additive to natural winter mortality (Rolland et al. 2010). However, density-dependent reproduction is also presumed as a possible compensation mechanism. Our study shows that despite the low density at the BW area, most reproductive parameters (nest and brood survival, hatchability, double-nesting, and renesting probabilities) are low—lower than the median of those parameters reported from other bobwhite populations (Sandercock et al. 2008). This suggests that density-dependent reproduction is unlikely to be a compensatory mechanism for additive harvest mortality. Density-dependent reproduction is rare, and so is compensatory natality in gamebirds (Ellison 1991). This highlights the need to evaluate both survival and reproductive parameters in hunted declining bird populations in order to propose the most adequate management strategies. Brennan (1991) hypothesized that the bobwhite population decline might be because recruitment of juveniles into the breeding population is insufficient to offset the low adult mortality. Based on our estimates, the population on the BW area would produce 2.235 (Online Resource 2) new individuals per capita, which indicates a low recruitment rate. Thus, as suggested for ruffed grouse populations (Dorney 1963), hunting regulations may need to be adjusted to juvenile recruitment in the fall. Indeed, reducing the hunting effort might help increase recruitment of juvenile birds to the breeding pool, improving the overall productivity, and ultimately, the population growth rate.

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