

# Effects of harvest and climate on population dynamics of northern bobwhites in south Florida

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## Abstract

**Context.** Hunting-related (hereafter harvest) mortality is assumed to be compensatory in many exploited species. However, when harvest mortality is additive, hunting can lead to population declines, especially on public land where hunting pressure can be intense. Recent studies indicate that excessive hunting may have contributed to the decline of a northern bobwhite (*Colinus virginianus*) population in south Florida.

**Aims.** This study aimed to estimate population growth rates to determine potential and actual contribution of vital rates to annual changes in population growth rates, and to evaluate the role of harvest and climatic variables on bobwhite population decline.

**Methods.** We used demographic parameters estimated from a six-year study to parameterise population matrix models and conduct prospective and retrospective perturbation analyses.

**Key results.** The stochastic population growth rate ( $\lambda_S = 0.144$ ) was proportionally more sensitive to adult winter survival and survival of fledglings, nests and broods from first nesting attempts; the same variables were primarily responsible for annual changes in population growth rate. Demographic parameters associated with second nesting attempts made virtually no contribution to population growth rate. All harvest scenarios consistently revealed a substantial impact of harvest on bobwhite population dynamics. If the lowest harvest level recorded in the study period (i.e. 0.08 birds harvested per day per km<sup>2</sup> in 2008) was applied,  $\lambda_S$  would increase by 32.1%. Winter temperatures and precipitation negatively affected winter survival, and precipitation acted synergistically with harvest in affecting winter survival.

**Conclusions.** Our results suggest that reduction in winter survival due to overharvest has been an important cause of the decline in our study population, but that climatic factors might have also played a role. Thus, for management actions to be effective, assessing the contribution of primary (e.g. harvesting) but also secondary factors (e.g. climate) to population decline may be necessary.

**Implications.** Reducing hunting pressure would be necessary for the recovery of the bobwhite population at our study site. In addition, an adaptive harvest management strategy that considers weather conditions in setting harvest quota would help reverse the population decline further.

**Additional keywords:** elasticity analysis, harvest management, LTRE analysis, management scenarios, stochastic demography, weather conditions.

## Introduction

Investigating population dynamics through demographic perturbation analyses is a key step for the management or conservation of a wildlife species. Retrospective analyses help understand what causes year-to-year changes in population growth rates by exploring the contributions of past changes in vital rates; prospective analyses can be used to identify potential

management targets based on sensitivity or elasticity of population growth rate ( $\lambda$ ) to demographic parameters (Caswell 2000). Changes in vital rates with high sensitivity will produce large changes in population growth rate.

Furthermore, vital rates are driven by environmental factors. Thus, in addition to identifying key demographic parameters, it is crucial to understand how environmental factors affect the

population dynamics via their influence on the vital rates. This knowledge would help wildlife managers target influential vital rates as well as devise and implement management actions that would produce desired effects on the influential vital rates.

For the effective management of exploited species, it is crucial to know how harvest and other potential drivers, such as climatic variables, influence population dynamics. Harvest must be sustainable to ensure the persistence of the population. Three hypotheses relate harvest and mortality. The additive mortality hypothesis states that harvest mortality is additive to natural mortality, and harvesting reduces the overall survival rate. The compensatory mortality hypothesis postulates that reduction in survival due to harvest is compensated for by density-dependent increases in survival up to a harvest threshold, above which harvest mortality would be additive to natural mortality. Finally, harvest mortality may be partially compensatory if survival decreases with increasing harvest more rapidly above than below the harvest threshold (Williams *et al.* 2002). In general, harvest mortality is assumed to be compensatory in exploited species. However, evidence for compensatory mortality is not always compelling, as reviewed for tetraonid birds by Ellison (1991). Partially compensatory mortality is difficult to detect (Pedersen *et al.* 2004), and erroneously concluding that harvest mortality is compensatory may lead to overharvest or even population extinction (Lande and Engen 1995; Myers and Cadigan 1995; Bender *et al.* 2004). Furthermore, demographic parameters (e.g. survival and reproductive rates) may vary substantially over time and space (Sæther *et al.* 1996, 2006; Jenouvrier *et al.* 2005; Frederiksen *et al.* 2007; Ozgul *et al.* 2009a), and effects of exploitation on population should be evaluated regularly. Indeed, harvest-related mortality of a population may be determined as compensatory one year, but the same population may be overexploited the next year even at the same harvest levels (Hilborn *et al.* 1995).

The role of global climate change as a driver of population dynamics is increasingly being recognised; its role in population decline in some species may be comparable to that of habitat loss, overexploitation or invasive species (Sala *et al.* 2000). Climate change has been reported to already profoundly affect animals and plants through changes in species physiology, distribution, phenology or abundance (Hughes 2000; Walther *et al.* 2002; Ozgul *et al.* 2009b). Moreover, climate change and other anthropogenic influences, such as overexploitation or habitat destruction, may have synergistic effects that can compensate for each other, or alternatively, amplify each other's effects on population dynamics (Root *et al.* 2003). A recent study revealed that failure to account for such synergistic effects may lead to an underestimation of extinction risk (Brook *et al.* 2008). However, only a few studies have simultaneously investigated the effects of multiple factors (including harvest) on population dynamics of exploited species inhabiting terrestrial habitats (but see Carroll 2007).

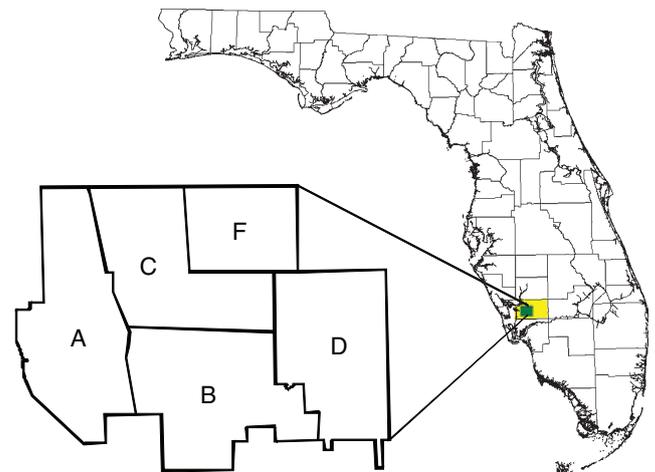
The northern bobwhite *Colinus virginianus* (hereafter bobwhite) is an economically important game species in the south-eastern United States (Burger *et al.* 1999). The species has declined dramatically throughout most of its range (Sauer *et al.* 2008), primarily because of habitat loss and fragmentation (Brennan 1991). On some public lands, such as the Babcock–

Webb Wildlife Management Area (BW area), south-west Florida, USA, where effort in habitat management and hunting pressure are intense, the bobwhite population has continued to decline (unpubl. data). A previous study showed that harvest mortality may be additive to natural mortality in winter in the BW area (Rolland *et al.* 2010), but the consequences of harvest on population dynamics have remained unclear. Additionally, this site is subject to extreme weather conditions (drought and flooding). Bobwhite demography has been shown to be influenced by temperature and precipitation (Rolland *et al.* 2011). Moreover, climatic variables will undoubtedly be affected by global climate change (Fiedler *et al.* 2001). Therefore, the impact of harvest on bobwhite populations needs to be assessed along with effects of climatic variables for effective harvest management. Here, we parameterised population matrix models using estimates of demographic parameters based on six years of field data (Rolland *et al.* 2010, 2011), and explicitly examined the consequences of harvest and climatic variables on demographic and population dynamics. Our objectives were to: (1) estimate the deterministic and stochastic growth rates of the bobwhite population in the BW area; (2) determine the potential and actual contribution of vital rates to deterministic and stochastic population growth rates using prospective and retrospective perturbation analyses; and (3) evaluate the impact of harvest and climatic variables on population growth rates.

## Material and methods

### Study site and species

The study was conducted in the Fred C. Babcock/Cecil M. Webb Wildlife Management Area (BW area; 26 799 ha), Charlotte County, in south-west Florida (Fig. 1). The most significant plant communities include dry prairie, pine-palmetto and wet prairie (Singh *et al.* 2011). The area is subject to periodic short-duration flooding and prolonged drought. Patches of  $\geq 400$  ha are burned every other year during the dormant season. Roller



**Fig. 1.** Location of the Babcock–Webb (BW) Wildlife Management Area, Charlotte County, south-west Florida, USA. The area is divided into five management zones (A, B, C, D and F) with different levels of hunting pressure (see text for details).

chopping and *Sesbania* sp. food strips (composing 0.56% of the total area) are also current primary habitat management activities. The BW area is divided into five management zones (A–D and a field trial course F; Fig. 1). Zones A–D are heavily hunted during 40 days in November and December, whereas the hunting season is limited to two days in January in zone F (for a maximum of 25 hunters each day). The daily bag limit is set at six bobwhites per hunter for every zone. However, zones A and B are designated as limited access (10 hunters per day), whereas access to zones C and D is unlimited. Hunting regulations have changed since 2007, lowering the number of hunter days from a mean of 1135 to 876 and 848 in 2007 and 2008, respectively. The period from 1 October to 31 March is considered winter, whereas between 1 April and 30 September is designated as summer. Hunting occurs only during winter, whereas reproduction occurs only during summer.

Bobwhites at our study site begin nesting as early as April when females lay one egg per day, and the 23-day incubation period starts after the last egg is laid. Females may lay second (or subsequent) nests regardless of whether the first nest succeeded (double nesting) or failed (re nesting). About 30% of the nests are incubated by males (Rolland *et al.* 2011). The first peak of hatching occurs between late May and mid-June. A 30-day brood rearing period follows hatching; birds are considered fledglings from hatching until 30 September, and then juveniles until the following April (i.e. next breeding season) when they begin to reproduce as adults.

Both adults and juveniles are subject to hunting in winter. Other causes of bobwhite mortality throughout the year include

predation by mammalian and avian predators (Rolland *et al.* 2010).

#### Field methods

We captured birds between October 2002 and March 2009 with baited funnel traps. Captured birds were aged, sexed, leg-banded and, when  $\geq 130$  g, were radio-marked with a 6-g necklace-style transmitter with a mortality sensor (American Wildlife Enterprises, B. Mueller, Monticello, FL, USA). Birds were tracked year-round every 3–5 days until death or censoring, using hand-held receivers and Yagi antennas (Telonics, Inc., Mesa, AZ). During the nesting season, if a bobwhite of either gender was located in the same area on more than two consecutive visits, the area was thoroughly searched for nests. Located nests were monitored at least every three days. For each of them, the number of eggs was recorded when the attending adult was away from the nest, and their fate (i.e. hatched, destroyed or abandoned) was determined. All trapping and handling protocols were approved by the University of Florida Institutional Animal Care and Use Committee (protocol number A-794). More details on the field methods can be found in Rolland *et al.* (2010, 2011).

#### Demographic parameters

Our study relied on estimates of survival and reproductive parameters reported by Rolland *et al.* (2010, 2011). These estimates were based on six years (2002–08) of field data.

Estimates of demographic parameters used in this study are summarised in Table 1. Rolland *et al.* (2010) found no evidence

**Table 1. Mean estimates ( $\pm$ s.e.) of demographic parameters for northern bobwhites in the BW area, Florida, 2002–08**  
Lower-level elasticities of deterministic population growth rate to vital rates ( $E^{\text{det}}$ ) and those of stochastic population growth rate to overall ( $E^{\text{stoch}}$ ), mean ( $E^{\mu}$ ) and variance ( $E^{\sigma}$ ) of the vital rates. See Rolland *et al.* (2010, 2011) for details

Parameters	Symbol	Mean $\pm$ s.e.	$E^{\text{det}}$	$E^{\text{stoch}}$	$E^{\mu}$	$E^{\sigma}$
<i>Adult survival</i>						
Summer survival	$S_s$	0.340 $\pm$ 0.014	0.783	1.028	1.102	-0.074
1 April to 28 April (first nesting)	$S_{aF}$	0.920 $\pm$ 0.003	0.202	0.152	0.151	0.001
20 June to 27 July (double nesting)	$S_{aD}$	0.936 $\pm$ 0.002	0.003	0.002	0.002	0.000
3 June to 25 July (re nesting)	$S_{aR}$	0.931 $\pm$ 0.003	0.012	0.007	0.007	0.000
Winter survival	$S_w$	0.319 $\pm$ 0.014	1.000	1.188	1.214	-0.026
<i>Fledging survival</i>						
From first nests	$S_{jF}$	0.186 $\pm$ 0.029	0.202	0.152	0.238	-0.086
From double nests	$S_{jD}$	0.614 $\pm$ 0.028	0.003	0.002	0.001	0.000
From re nests	$S_{jR}$	0.477 $\pm$ 0.033	0.012	0.007	0.007	0.000
<i>Clutch size</i>						
First clutch size	$CS_1$	12.429 $\pm$ 0.239	0.202	0.152	0.151	0.001
Subsequent clutch size	$CS_2$	10.189 $\pm$ 0.525	0.015	0.009	0.009	-0.001
<i>Nest survival</i>						
First nest success	$NS_1$	0.294 $\pm$ 0.032	0.200	0.150	0.140	0.010
Subsequent nest success	$NS_2$	0.111 $\pm$ 0.043	0.015	0.009	0.009	0.000
<i>Hatchability</i>						
Nest hatchability	$Hatch$	0.853 $\pm$ 0.008	0.217	0.160	0.157	0.003
<i>Brood survival</i>						
First brood survival (high)	$BS_1$	0.229 $\pm$ 0.003	0.202	0.152	0.168	-0.016
Subsequent brood survival (high)	$BS_2$	0.086 $\pm$ 0.009	0.015	0.009	0.009	0.000
Proportion of male-incubated nests	$P_{IM}$	0.305 $\pm$ 0.024	0.095	0.067	0.068	-0.001
<i>Probability of a second nesting attempt</i>						
Double-nesting probability	$DN$	0.112 $\pm$ 0.024	0.003	0.002	0.001	0.000
Renesting probability	$RN$	0.281 $\pm$ 0.040	0.012	0.007	0.006	0.001

that winter survival ( $S_w$ ) differed between adults and juveniles, whereas summer survival for adults ( $S_s$ ) was higher than for fledglings. These authors estimated summer survival for fledglings over a six-month summer period (1 April to 30 September), but birds fledged, at earliest, in July. In addition, fledglings hatched from a first nesting attempt needed to survive longer than those from subsequent nesting attempts. Likewise, only survival of adult females from the beginning of the nesting season (1 April) to the beginning of incubation needs to be considered in the fecundity term of the population model because nest and brood survival probabilities implicitly account for survival of the incubating adult. Therefore, we estimated an adjusted fledging survival based on whether fledglings were produced in a first, double or renesting attempt ( $S_fF$ ,  $S_fD$  and  $S_fR$ ; Fig. 2). Similarly, summer adult female survival was adjusted based on nesting attempts ( $S_aF$ ,  $S_aD$  and  $S_aR$ ; Fig. 2). For more details on the calculations, see Appendices A and B (available as Accessory Publications on the *Wildlife Research* website).

Reproductive parameters were assumed to be independent of the age. However, clutch size ( $CS$ ), nest survival (i.e. during laying and incubation;  $NS$ ) and brood survival (i.e. 30-day survival period after hatching;  $BS$ ) were higher for the first nesting attempt than for subsequent attempts. Although hatchability (i.e. proportions of hatched eggs in successful nests;  $Hatch$ ) and probabilities of incubating a second nest (renew;  $RN$ , or double-nest;  $DN$ ) were higher for females than for males (Rolland *et al.* 2011), we used the same estimate for both sexes to limit sources of variation in the overall fecundity estimate and because nests from a second attempt or those

incubated by males contributed little to the population growth rate. Rolland *et al.* (2011) reported low and high estimates of brood survival; we used only high estimates here to consider the best case scenario.

Female probability of breeding (i.e. probability that a female initiates at least one nest during a breeding season) was assumed to be 1 (Sandercock *et al.* 2008); this assumption was supported by data in our study population (Rolland *et al.* 2011).

*Matrix population model*

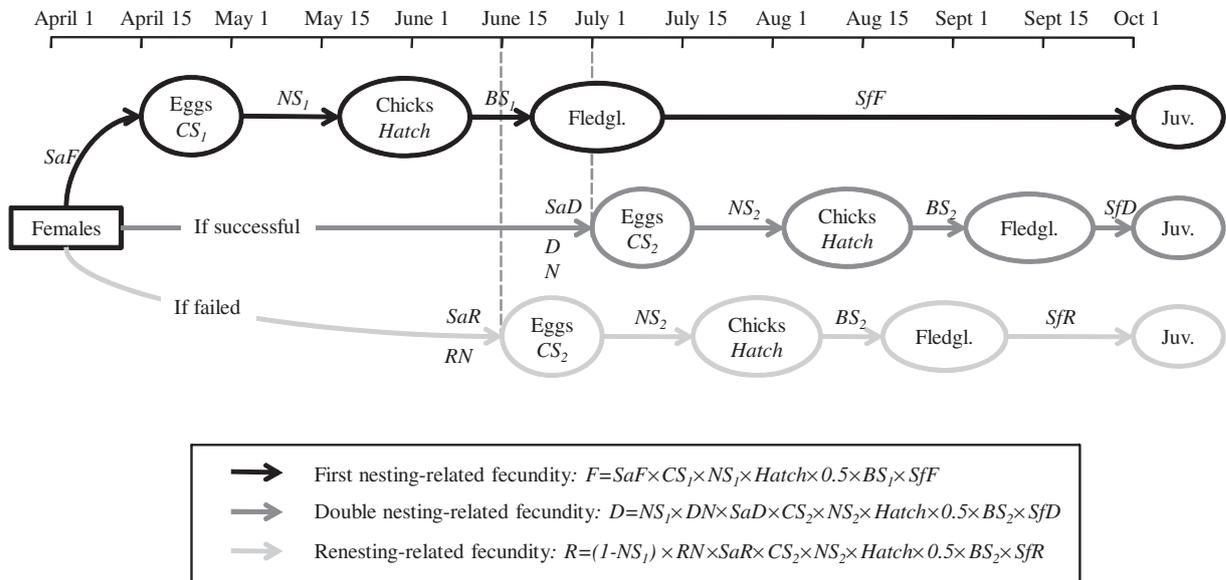
We considered a matrix population model with an anniversary date on 1 April and two age classes: juveniles and adults. We estimated the fertility rate ( $F$ ) using the pre-breeding census method (Caswell 2001) as  $F = f \times S_w$ , where  $f$  and  $S_w$  are the fecundity rate and winter survival probability, respectively. The fecundity rate ( $f$ ) is the sum of the number of female offspring produced per female (hereafter, productivity) from first ( $FN$ ), double ( $DN$ ) and renesting ( $RN$ ) attempts as described in Fig. 2. The productivities from the three nesting attempts were calculated using modified versions of Sandercock *et al.*'s formulae (2008). We included a parameter ( $\alpha$ ) to account for male participation:

$$\alpha = 1 + P_{IM} / (1 - P_{IM}) \tag{1}$$

where  $P_{IM}$  is the proportion of nests incubated by males. This results in:

$$f = \alpha \times (FN + DN + RN) \tag{2}$$

Then, using estimates of survival and fecundity rates, we constructed the following time-dependent population projection



**Fig. 2.** Flow diagram of events occurring within a bobwhite nesting season. Equations for fecundities for first (F, black), double (D, dark grey) and renesting (R, light grey) attempts are expressed as functions of probabilities that females survive to the onset of laying of first ( $S_aF$ ), double ( $S_aD$ ) and renesting ( $S_aR$ ) attempts; clutch size ( $CS_1$  and  $CS_2$ ), nest survival ( $NS_1$  and  $NS_2$ ) and brood survival ( $BS_1$  and  $BS_2$ ) in a first and subsequent attempts; hatchability ( $Hatch$ ); probabilities of double ( $DN$ ) and renesting ( $RN$ ); and probabilities of fledgling (Fledgl.) survival from 30 days after hatching in first ( $S_fF$ ), double ( $S_fD$ ) and renesting ( $S_fR$ ) attempts to 30 September (Juv.: juvenile). Sex ratio of hatchlings was assumed to be balanced (0.5). Subscripts in symbols indicate first (<sub>1</sub>) or subsequent (<sub>2</sub>) nesting attempts.

matrix (see Appendix C, an Accessory Publication on the *Wildlife Research* website, for details):

$$\mathbf{A}(t) = \begin{pmatrix} f(t) \times Sw(t) & f(t) \times Sw(t) \\ Ss(t) \times Sw(t) & Ss(t) \times Sw(t) \end{pmatrix} \quad (3)$$

where  $t$  stands for year, with  $t = \{1, 2, \dots, 6\}$ . However, to describe the overall population dynamics, we pooled data from all years and estimated relevant parameters; those estimates were then used to parameterise the overall population projection matrix.

We performed the demographic analysis using four approaches: (1) deterministic demographic analyses to calculate overall and annual population growth rates, and elasticity of the population growth rate to entries of the population projection matrix and to lower-level vital rates; (2) life table response experiment (LTRE) analysis to decompose observed annual changes in population growth rates into contribution from demographic parameters; (3) stochastic demographic analysis to calculate stochastic population growth rate and stochastic elasticities; and (4) deterministic and stochastic methods to evaluate the potential impact of harvest and climatic variables.

#### *Deterministic demographic analysis*

We used a time-invariant population projection matrix (i.e. with parameters estimated from pooled data from all years) to estimate overall deterministic population growth rate, and elasticity of population growth rate to matrix entries as well as to lower-level vital rates (Caswell 2001; Morris and Doak 2004). Likewise, we calculated annual population growth rate and elasticities using annual population projection matrices  $\mathbf{A}(t)$ . In both cases, we calculated the standard error of population growth rates using the delta method (Caswell 2001). Associated confidence intervals were then derived using normal approximation.

#### *LTRE analysis*

Population growth rate changed substantially from year to year during our study period. Thus, we used the LTRE analysis to decompose year-to-year differences in population growth rate into contributions from vital rates. In that analysis, sensitivities to both matrix entries and lower-level parameters were evaluated midway between a reference matrix  $\mathbf{A}(t)$  and a treatment matrix  $\mathbf{A}(t+1)$  for each pair of consecutive years using the following equation (Caswell 2001):

$$\lambda_{t+1} - \lambda_t \approx \sum (\pi_i^{(t+1)} - \pi_i^{(t)}) \frac{\partial \lambda}{\partial \pi_i} \bigg|_{\frac{\pi_{t+1} + \pi_t}{2}} \quad (4)$$

where  $\lambda_{t+1}$  and  $\lambda_t$  are the growth rates under conditions in year  $t+1$  and the reference year  $t$ , respectively, and  $\pi_i$  is a matrix entry or a lower-level vital rate.

#### *Stochastic analyses*

Deterministic analyses provide information on projected population growth rate (and associated population statistics) if environmental conditions were to be constant over time. However, vital rates vary intrinsically and also in response to stochastic environmental fluctuations, hence the need to consider stochastic population models. Thus, we conducted

stochastic demographic analyses using the six year-specific matrices. We considered an independent and identically distributed (*iid*) environment, and assumed that each year occurred with equal probability. We used a stochastic simulation approach to calculate stochastic population growth rate, and its elasticity to mean ( $E^{\mu}$ ) and variance ( $E^{\sigma}$ ) of the matrix elements because they describe more accurately the effect of mean and variability in vital rates on stochastic population growth rate (Haridas and Tuljapurkar 2005). We also calculated stochastic elasticity with respect to the lower-level parameters (Caswell 2005; Hunter *et al.* 2010).

#### *Population projections and scenarios*

We evaluated the population-level impact of hunting on bobwhites in four different ways. First, hunting pressure in zone F was much lower than in all other management zones; thus, we compared population growth rates with winter survival estimated in zone F versus A–D (all years combined).

Second, a 33% reduction in hunting effort occurred in 2007–08 compared with the average hunting effort exerted during 2002–06; consequently, winter survival was substantially higher in 2008 compared with all previous years (0.475 in 2008 vs 0.340 in all previous years; Rolland *et al.* 2010). Thus, population growth rates calculated using winter survival estimated in 2008 (year of the lowest hunting effort) and 2004 (year of the highest hunting effort) were compared.

Third, because harvest was the most important cause of winter mortality in our study area (Rolland *et al.* 2010), we aimed to project population growth rates with proportions of winter mortality due to harvest ranging from zero to 60% (47.1% during the 2002–08 study period). To achieve this, winter survival  $Sw$  must be expressed as a function of the proportion of winter mortality due to harvest ( $\%_h$ ). Thus, we transformed the equation relating harvest-related mortality  $m_h$  and winter survival  $Sw$  as follows:

$$Sw = 1 - (m_h + m_{other}) \quad (5)$$

where  $m_{other}$  is mortality resulting from other causes of death (including raptor and mammal predation). We know that:

$$\%_h = \frac{m_h}{1 - Sw} \quad (6)$$

Equations 5 and 6 lead to:

$$m_h = \frac{m_{other} \times \%_h}{1 - \%_h} \quad (7)$$

Finally,  $m_h$  in equation 5 was replaced by the right-hand side of equation 7 and  $m_{other}$  was held constant (0.361), assuming that hunting-related mortality was additive to natural mortality in winter; this assumption was supported by data (Rolland *et al.* 2010).

Fourth and last, we modelled winter survival as a function of hunting effort (Rolland *et al.* 2010). We then used this model to calculate population growth rates for various levels of hunting effort (0–0.40 hunters  $\text{day}^{-1} \text{km}^{-2}$ ; the mean hunting effort for 2002–08 was 0.103).

Because hunting effort and winter mortality were the lowest in 2008 (i.e. after the change in hunting regulations), we estimated

the population growth rate using the stochastic population model where winter survival was constrained to be equal to that in 2008 (i.e. 0.475). This scenario simulates the likely stochastic population growth rate with a higher winter survival due to reduced hunting effort, but assuming that values of other vital rates and temporal variations therein were similar to those observed during 2002–07.

Bobwhite hatchability (i.e. proportion of laid eggs that hatched conditional upon nest survival to hatching) and adult survival probabilities varied among years in the BW area (Rolland *et al.* 2010, 2011). This annual variation can be partially explained by the effect of mean summer (or winter) temperature and total summer (or winter) precipitation on both hatchability (Rolland *et al.* 2011) and winter survival (Appendix D, available as an Accessory Publication on the *Wildlife Research* website). Therefore, population growth rates were projected using mean values for all parameters, but replacing the values of hatchability and winter survival with functional relationships between hatchability and mean summer temperatures (25–28°C) and total summer precipitation (600–1300 mm), and that between winter survival and hunting effort (0–0.45 hunters day<sup>-1</sup> km<sup>-2</sup>), mean winter temperature (18–22°C) and total winter precipitation (50–600 mm).

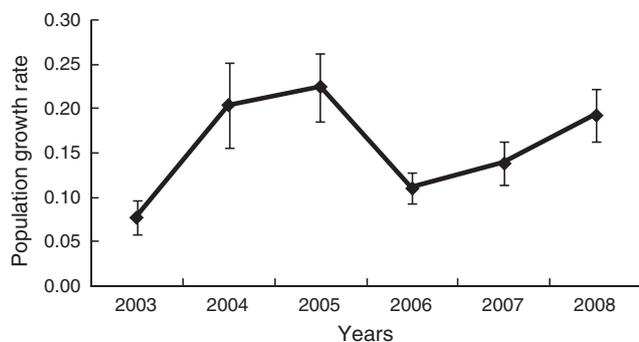
All analyses were performed with Matlab (Mathworks, Natwick, MA, USA).

## Results

### Deterministic demography

The population growth rate ( $\lambda$ ) estimated with the time-invariant model was low and indicated a declining population ( $\lambda = 0.138$ ; 95% CI: 0.120–0.156). Annual population growth rates ranged from 0.078 (0.039–0.116) in 2003 to 0.224 (0.149–0.300) in 2005 (Fig. 3).

Elasticity analysis indicated that  $\lambda$  was proportionately most sensitive to changes in adult survival ( $E = 0.619$ ), followed by juvenile survival and adult fertility ( $E = 0.168$ ), and juvenile fertility ( $E = 0.046$ ). Elasticity to lower-level parameters revealed that the population growth rate was proportionately most sensitive to winter survival and summer survival (Table 1). Lower-level elasticities further revealed that changes in hatchability and all parameters associated with the first nesting



**Fig. 3.** Annual population growth rates (derived from the deterministic model) of the bobwhite population in the Babcock–Webb Wildlife Management Area, south-west Florida, during the study period 2003–08. Error bars represent SE.

attempt impacted on  $\lambda$  similarly, whereas elasticity to parameters associated with subsequent nesting attempt was the lowest (Table 1).

The stable age distribution computed using the time-invariant population projection matrix indicated an autumn population comprising more adults (78.67%) than juveniles (21.33%).

### LTRE analysis

We used LTRE analysis to decompose the annual differences in  $\lambda$  into contributions from each of the vital rates (Fig. 4). The close correspondence between differences in  $\lambda$  among years and the associated sum of contributions was  $r = 0.986$ , which indicated a good fit of the LTRE model. For most years, the same four parameters were most responsible for the observed variability in population growth rate: winter survival ( $S_w$ ) and summer survival of fledglings from first nesting attempt ( $S_fF$ ), followed by nest success ( $NS_j$ ) and survival of broods ( $BS_j$ ) from first nesting attempt. Conversely, parameters associated with the second nesting attempt and clutch size made little or no contribution to year-to-year changes in the population growth rate. The increase in population growth rate from 2003 and 2004 was due to an increase in three of the four important parameters (i.e.  $S_fF$ ,  $NS_j$  and  $BS_j$ ). The 2005 population growth rate was the highest during our study period, owing to a substantial increase in  $S_fF$ . In 2008, the higher winter survival contributed to an increased population growth rate; however, the growth rate was limited by negative contributions of  $S_fF$ ,  $NS_j$  and  $BS_j$ .

### Stochastic demography

The stochastic growth rate ( $\lambda_s$ ) was 0.148. This value was lower than the deterministic growth rate calculated from the mean of the annual population projection matrices (0.158). Stochastic elasticity analyses indicated that  $\lambda_s$  was proportionately most sensitive to adult annual survival (0.514) and least sensitive to juvenile fertility (0.080), with elasticity to adult fertility and juvenile survival being intermediate (0.203). All three measures of stochastic elasticities of  $\lambda_s$  (i.e. overall stochastic elasticity, and elasticity to vital rate means and variances) displayed the same elasticity pattern as that observed with the deterministic model (Table 1). Elasticities to mean and variance further revealed that changes in mean of vital rates had a higher impact on  $\lambda_s$  than changes in variances of these vital rates.

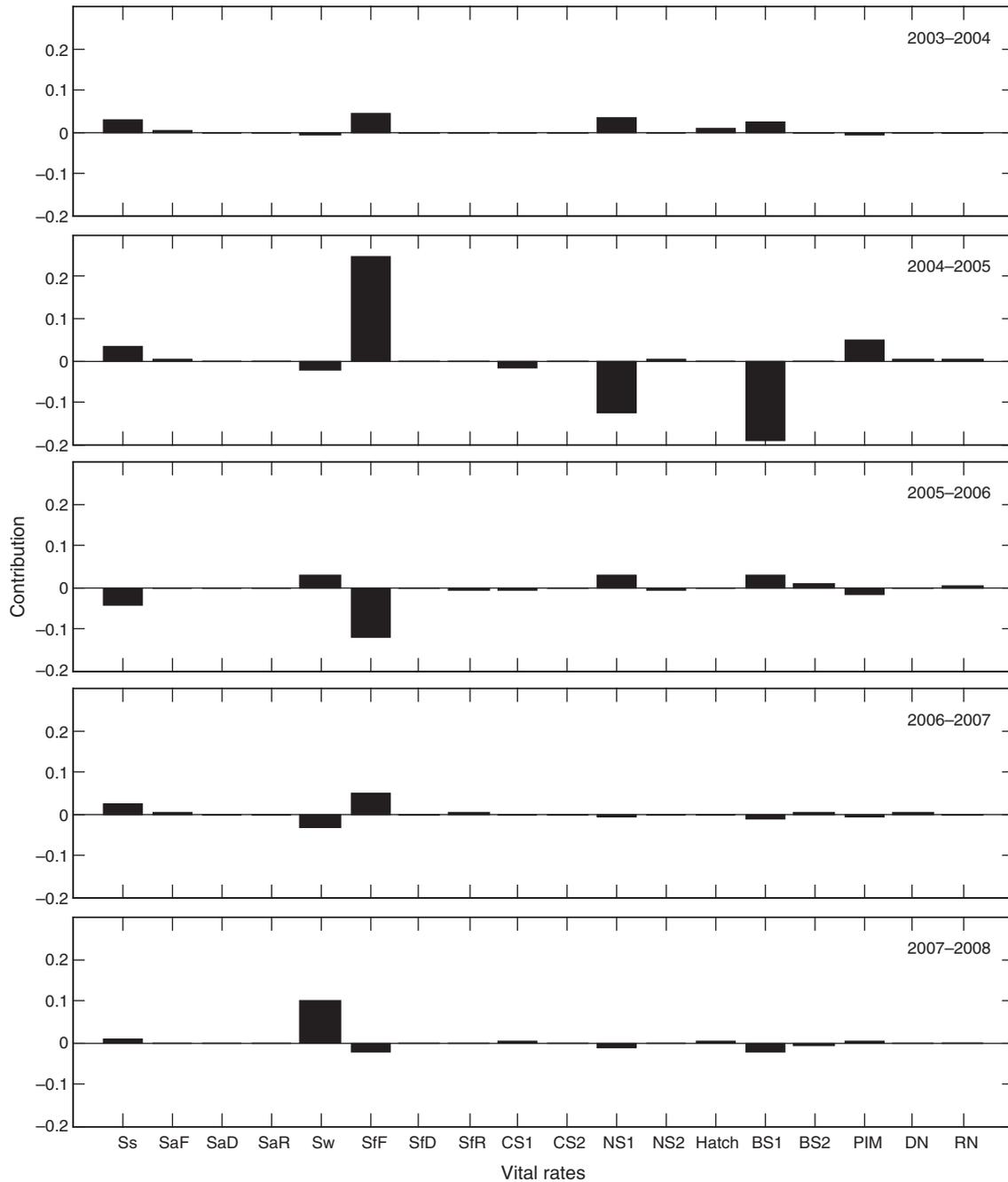
### Population projections and scenarios

#### Impact of harvest

We used four approaches to evaluate the effect of harvest on the deterministic population growth rate. Because harvest only occurs during winter, we assumed that only winter survival was affected by harvest; all the other parameters were held constant at the mean values (Table 1).

First, we used winter survival as estimated in management zone F ( $S_w = 0.414$ ; Rolland *et al.* 2010) where harvesting was lower than in all other management zones. Here, the population growth rate was 0.179, which was higher than that estimated with average winter survival in the more heavily harvested zones A–D ( $\lambda = 0.138$ ;  $S_w = 0.319$ ).

Second, the lowest (in 2008) and highest (in 2004) hunting effort resulted in winter survival of 0.475 and 0.306, respectively



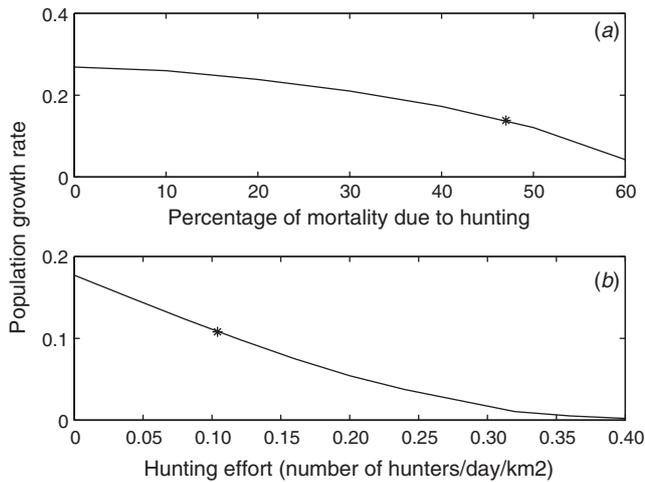
**Fig. 4.** Contribution of vital rates to year-to-year change in bobwhite population growth rate during the study period 2003–08, in the Babcock–Webb Wildlife Management Area, south-west Florida. Vital rates include: survival during winter (*Sw*), during summer (*Ss*), for females attempting a first (*SaF*), double (*SaD*) or renesting attempts (*SaR*) and for fledglings from first (*SfF*), double (*SfD*) or renesting attempts (*SfR*); clutch size for the first (*CS1*) and subsequent (*CS2*) nesting attempts; nest success for both nesting attempts (*NS1* and *NS2*); hatchability (*Hatch*); survival of brood from first (*BS1*) and second (*BS2*) nesting attempts; and proportion of nests incubated by males (*PIM*), and double and renesting probabilities (*DN* and *RN*).

(Rolland *et al.* 2010), and corresponding estimates of population growth rates were 0.205 and 0.132, respectively.

Third, we assumed that harvest mortality was additive during winter. We calculated population growth rate with winter survival modelled as a function of harvest mortality.

The population growth rate decreased from 0.268 with 0% harvest-related mortality to 0.042 with 60% of the mortality due to harvest (Fig. 5a).

Finally, using winter survival modelled as a function of hunting effort, population growth rate steeply declined as we



**Fig. 5.** Deterministic population growth rate for the bobwhite population in the Babcock–Webb Wildlife Management Area, south-west Florida, as a function of two harvest measures: (a) percentage of winter mortality due to hunting, and (b) hunting effort (hunters day<sup>-1</sup> km<sup>-2</sup>). Average conditions of hunting during 2002–08 are represented by an asterisk.

increased the hunting effort from 0.176 with no harvest to 0.075 with 0.16 hunters day<sup>-1</sup> km<sup>-2</sup> (Fig. 5b). This suggests that eliminating the hunting effort alone would not be sufficient to ensure persistence of our study population.

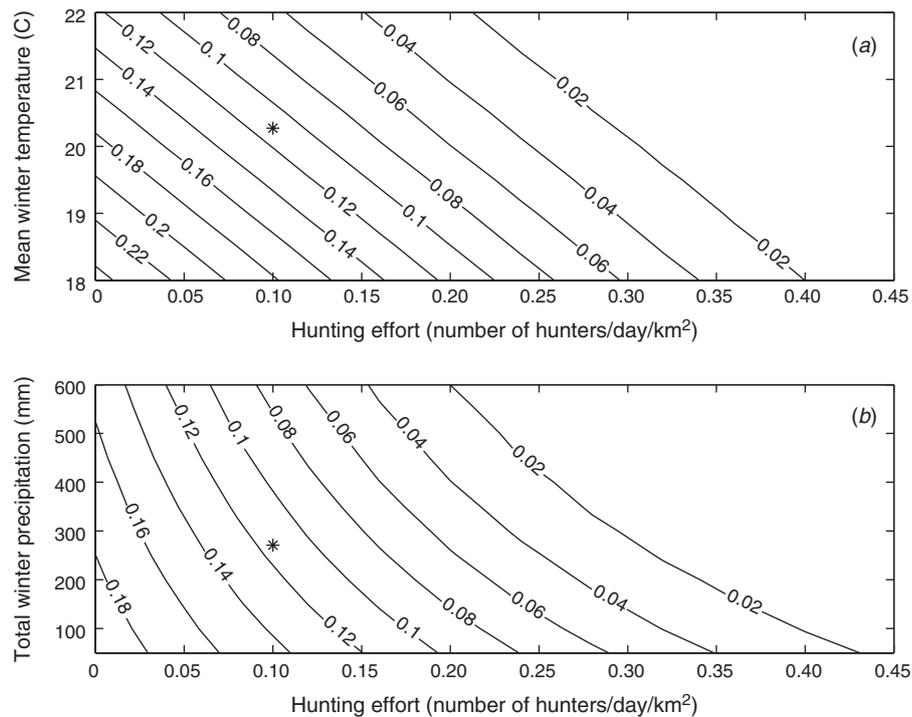
The stochastic model indicated that with the 2008 hunting conditions (i.e. hunting effort of 0.080 and 0.095 hunters day<sup>-1</sup> km<sup>-2</sup> in zones F and A–D, respectively), the population growth rate would be 0.217, indicating a substantial increase.

*Impact of climate and management activities*

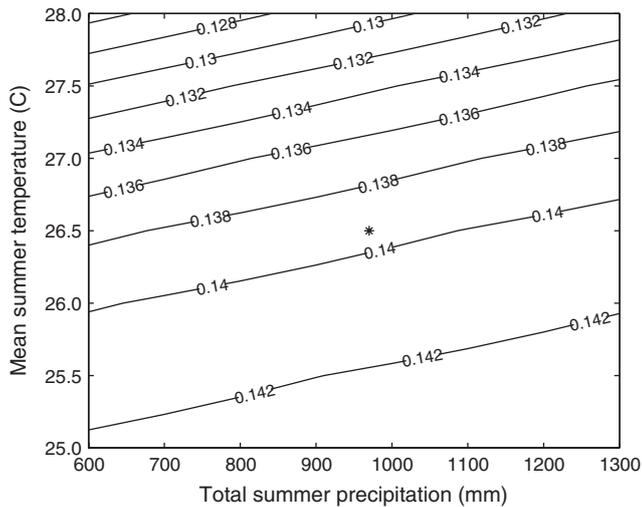
We used hatchability and winter survival modelled as functions of temperature and precipitation. Population growth rate decreased with an increase in mean winter temperature and winter precipitation (Fig. 6). In addition, the higher the total winter precipitation, the higher the negative impact of hunting effort on population growth rate (Fig. 6b). However, when hatchability was modelled as a function of mean summer temperature and total summer precipitation, population growth rate was predicted to increase with a decrease in mean summer temperature and/or an increase in total summer precipitation (Fig. 7).

**Discussion**

Development or implementation of management plans for conservation of declining populations requires knowledge of the causes of population decline. Although habitat change is often the main cause, overharvest may also contribute to population decline in game species, and unfavourable weather conditions may exacerbate the adverse impact of other factors.



**Fig. 6.** Deterministic growth rate for the bobwhite population in the Babcock–Webb Wildlife Management Area, south-west Florida as a function of hunting effort and two climatic variables: (a) mean winter temperature (°C), and (b) total winter precipitation (mm). Population growth rates are represented by isoclines. Average conditions of hunting effort, winter temperature and precipitation during 2002–08 are represented by asterisks.



**Fig. 7.** Deterministic growth rate for the bobwhite population in the Babcock–Webb Wildlife Management Area, south-west Florida, as a function of mean summer temperature and total summer precipitation influencing hatchability. Population growth rates are represented by isoclines. Average conditions of summer temperature and precipitation during 2002–08 are represented by an asterisk.

Thus, our goal was to explicitly evaluate the respective roles of harvest and climatic factors as potential causes of the reported declines of a heavily harvested bobwhite population in south-west Florida.

#### *Population status*

Not surprisingly, matrix population models indicated that the BW area bobwhite population had been rapidly declining. Sandercock *et al.* (2008) also reported a very low growth rate for bobwhites using published data. However, we do not precisely know why our estimates of population growth rate indicate such a high rate of decline. It may be at least in part due to some parameters being depressed below sustainable levels by environmental conditions or overharvest (Sandercock *et al.* 2008), but it is also possible that some population parameters may have been underestimated. We believe that the statistical methods we used to estimate bobwhite demographic parameters (Rolland *et al.* 2010, 2011) were rigorous, but the possibility of sampling bias cannot be ruled out. Birds in poorer condition may have been more easily captured, whereas fledglings may have been more difficult to detect. This would cause survival rates to be underestimated. Because brood survival estimates were based on flush rates, they may not be unbiased (Rolland *et al.* 2011). We estimated all other bobwhite demographic parameters based on telemetry data. Some studies report that radio-transmitters handicap radio-marked bobwhites (e.g. Cox *et al.* 2004), while others fail to detect a negative effect on their survival (e.g. Terhune *et al.* 2007). Thus, radio-transmitters may have reduced bobwhite survival or reproductive performances at our study site. Despite their low values, precision of annual population growth rates was reasonably good. In addition, the estimation of variance components revealed that annual variability in 12 of the 18 demographic parameters, in the population model, was mostly due to temporal rather than

sampling variance (Appendix E, available as an Accessory Publication on the *Wildlife Research* website), which suggests that the level of uncertainty was low. We are thus confident in the qualitative results of the present study.

Growth rates of declining populations are expected to be driven by survival (hypothesis 1; Meats 1971), whereas growth rates of populations with high reproductive rates and low adult survival are expected to be proportionally most sensitive to reproductive parameters (hypothesis 2; Stahl and Oli 2006). Our prospective and retrospective analyses revealed that winter survival ( $S_w$ ), and survival of nests ( $NS_I$ ), broods ( $BS_I$ ) and fledglings ( $S_fF$ ) produced in a first nesting attempt all substantially contributed to bobwhite population growth rate, and year-to-year changes in the growth rate. Thus, our results corroborated the first hypothesis because winter survival made a large contribution to the population growth rate. Similar results were reported for several declining galliform populations (e.g. Bro *et al.* 2000; Sandercock *et al.* 2005; Tirpak *et al.* 2006). The second hypothesis was also supported as reproductive parameters characterising the first nesting attempt substantially contributed to bobwhite population growth rate, as has been reported for other galliforms (Wisdom and Mills 1997; Clark *et al.* 2008). These results suggest a synergistic effect of low survival and low reproductive performance on the population growth rate of our study population. On the other hand, elasticity and LTRE analyses both indicated a very low contribution of parameters related to second (or subsequent) nesting attempts, which was in agreement with results from previous studies (Guthery and Kuvlesky 1998; Bro *et al.* 2000; Sandercock *et al.* 2008).

The LTRE results also revealed that  $S_fF$ ,  $S_w$ ,  $BS_I$  and  $NS_I$  contributed consistently to both increases and declines in population growth rates among years, highlighting the need for a careful consideration of these parameters when making management decisions. In particular, our results revealed that winter survival was an important factor for the bobwhite population in the BW area, suggesting that this parameter should be one of the primary targets for management. In healthy bobwhite populations, winter survival may be up to 0.54 (Sisson *et al.* 2009). In comparison, in the BW area, winter survival was very low (0.32). Given that harvest was the most important cause of mortality during winter (Rolland *et al.* 2010), overharvest most likely was an important factor contributing to bobwhite population decline at our study site. Nesting or escape cover during summer may also have contributed to the low growth rate, as these factors can influence survival of nests, chicks and fledgling bobwhites.

#### *Impact of harvest*

Harvest mortality is often assumed to be compensatory in exploited populations; additive harvest mortality can eventually lead to extinction of the population. Compensation may occur either through a reduction in natural mortality (e.g. predation; Ellison 1991) or through an increase in reproductive success (e.g. Williams 1999) as a feedback response to low density. However, compensatory harvest mortality may become additive with time if the dynamics of the population considered changes over time (Pöysä *et al.* 2004).

At our study site, where hunting pressure is intense and habitat is suboptimal, there was strong evidence that harvest mortality was most likely additive to natural mortality in winter (Rolland *et al.* 2010). Furthermore, the average productivity was low (Rolland *et al.* 2011), precluding the possibility of natality compensation. In addition, variation in winter mortality substantially affected the population growth rate. Finally, results from the four different methods to evaluate hunting impact all suggested that hunting substantially negatively affected bobwhite population dynamics during the study period. The LTRE analysis revealed that the higher  $\lambda$  in 2008, compared with that in 2007, was primarily due to the much higher winter survival in 2008 resulting from lower hunting effort. If the 2008 harvest level was applied to all years, the population growth rate might be increased by  $\geq 32\%$ . Thus, evidence for the negative impact of hunting in our study population is overwhelming. This is not surprising given that harvest rates in our study population are  $>40\%$  (unpubl. data), while it should not exceed 30% for southern bobwhite populations to be sustainable (Guthery *et al.* 2000). For instance, harvest pressure in a bobwhite population in Georgia was  $<10\%$ , which resulting in high winter survival (0.54; Sisson *et al.* 2009).

Nonetheless, we note that our assessment of the impact of harvest on the bobwhite population assumed that harvest mortality was additive to natural mortality in winter, as suggested by a previous study (Rolland *et al.* 2010) and that there was no compensation via density-dependent mechanisms in this declining population. We constrained natural winter mortality (i.e. due to causes other than harvest) to be constant, but it may have varied somewhat.

#### Impact of climatic variables

Mean temperature and total precipitation had significant effects on the bobwhite population in the BW area during summer, through influences on hatchability, and in winter, through influences on winter survival. Weather impacts on bobwhites have been previously reported in other populations (Robel and Kemp 1997; Hernández *et al.* 2005; Rader *et al.* 2007). However, we observed a synergistic effect of precipitation and harvesting on winter survival and thus on  $\lambda$ . An increase in total winter precipitation negatively affected  $\lambda$ : the higher the total precipitation, the more severe the impact of harvesting on  $\lambda$ . A possible explanation for this may be that as a result of increased precipitation, water levels rise, forcing birds into higher, restricted areas, making them more vulnerable to hunting and possibly to predation. Alternatively, hunting could be breaking up coveys, stressing birds, ultimately making them vulnerable to the wet conditions.

Increases in temperature predicted by models of climate change (IPCC 2007a) might increase the vulnerability of many species (IPCC 2007b), including bobwhites. In addition, more frequent extreme climatic events, such as storms or heavy rainfall are expected in Florida (Fiedler *et al.* 2001). Our study population may be particularly vulnerable. For example, excessive rainfall in 1995 resulted in the inundation of the BW area and the subsequent closure of the bobwhite hunting season (Mike Kemmerer pers. comm.). Assessing harvest impact along with climatic conditions may be important for annual adjustments of hunting regulations.

#### Synthesis and applications

Our results, along with those of Rolland *et al.* (2010) suggest that mortality due to harvesting, abetted secondarily by inclement weather, are likely important causes of decline in our bobwhite study population; similar results have been reported in other terrestrial and marine taxa (e.g. Carroll 2007; Rolland *et al.* 2009). Our results further highlight the importance of assessing the role of harvesting and other potential drivers (e.g. climate) on population dynamics of exploited species to propose more effective management actions.

Spatiotemporal variation in population dynamics is a rule rather than an exception in the natural world (e.g. Hagen *et al.* 2009) due to variation in habitat attributes and other variables. Because populations inhabiting different habitats can potentially respond differently to the same management activities, the effect of these activities should be evaluated. Our results revealed evidence that nest, brood and fledging survival from first nesting attempt contributed substantially to the dynamics of the bobwhite population; contributions of parameters associated with reneesting and double-nesting attempts were negligible. Vegetative cover may play a role in protecting nests, chicks and fledglings from high temperatures and predators. Predation is an important cause of mortality (Rollins and Carroll 2001; Rolland *et al.* 2010) but predator control on public land, such as the BW area, is not feasible. Thus any habitat management practices aimed at improving the quality of nesting and escape cover would benefit bobwhite population at our study site. Given the additive effect of hunting mortality on winter survival (the most influential vital rate), reduction in hunting pressure would be necessary for the recovery of our study population. An adaptive harvest management approach (e.g. Nichols *et al.* 2007) that allows harvest quotas to be set annually depending on habitat and weather conditions would help further elucidate factors influencing bobwhite population dynamics and recovery at our study site.

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#### References

- Bender, L. C., Schirato, G. A., Spencer, R. D., McAllister, K. R., and Murphy, B. L. (2004). Survival, cause-specific mortality, and harvesting of male black-tailed deer in Washington. *The Journal of Wildlife Management* **68**, 870–878. doi:10.2193/0022-541X(2004)068[0870:SCMAHO]2.0.CO;2
- Brennan, L. (1991). How can we reverse the northern bobwhite population decline? *Wildlife Society Bulletin* **19**, 544–555.
- Bro, E., Sarrazin, F., Clobert, J., and Reitz, F. (2000). Demography and the decline of the grey partridge *Perdix perdix* in France. *Journal of Applied Ecology* **37**, 432–448. doi:10.1046/j.1365-2664.2000.00511.x
- Brook, B. W., Sodhi, N. S., and Bradshaw, V. J. A. (2008). Synergies among extinction drivers under global change. *Proceedings. Biological Sciences* **23**, 453–460.

- Burger, L. W., Miller, D. A., and Southwick, R. I. (1999). Economic impact of northern bobwhite hunting in the southeastern United States. *Wildlife Society Bulletin* **27**, 1010–1018.
- Carroll, C. (2007). Interacting effects of climate change, landscape conversion, and harvest on carnivore populations at the range margin: marten and lynx in the northern Appalachians. *Conservation Biology* **21**, 1092–1104. doi:10.1111/j.1523-1739.2007.00719.x
- Caswell, H. (2000). Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology* **81**, 619–627. doi:10.1890/0012-9658(2000)081[0619:PARPAT]2.0.CO;2
- Caswell, H. (2001). 'Matrix Population Models: Construction, Analysis and Interpretation.' 2nd edn. (Sinauer: Sunderland, MA.)
- Caswell, H. (2005). Sensitivity analysis of the stochastic growth rate: three extensions. *Australian and New Zealand Journal of Statistics* **47**, 75–85. doi:10.1111/j.1467-842X.2005.00373.x
- Clark, W. R., Bogenschutz, T. R., and Tessin, D. H. (2008). Sensitivity analyses of a population projection model of ring-necked pheasants. *The Journal of Wildlife Management* **72**, 1605–1613. doi:10.2193/2007-419
- Cox, S. A., Peoples, A. D., DeMaso, S. J., Lusk, J. J., and Guthery, F. S. (2004). Survival and cause-specific mortality of northern bobwhites in western Oklahoma. *The Journal of Wildlife Management* **68**, 663–671. doi:10.2193/0022-541X(2004)068[0663:SACMON]2.0.CO;2
- Ellison, L. N. (1991). Shooting and compensatory mortality in tetraonids. *Ornis Scandinavica* **22**, 229–240. doi:10.2307/3676595
- Fiedler, J., Mays, F., and Siry, J. (2001). 'Feeling the Heat in Florida: Global Warming on the Local Level.' (Nature Resources Defense Council: New York and Orlando, NY and FL, USA.)
- Frederiksen, M., Edwards, M., Mavor, R. A., and Wanless, S. (2007). Regional and annual variation in black-legged kittiwake breeding productivity is related to sea surface temperature. *Marine Ecology Progress Series* **350**, 137–143. doi:10.3354/meps07126
- Guthery, F. S., and Kuvlesky, W. P. (1998). The effects of multiple-brooding on age ratios of quail. *The Journal of Wildlife Management* **62**, 540–549. doi:10.2307/3802327
- Guthery, F. S., Peterson, M. J., and George, R. R. (2000). Viability of northern bobwhite populations. *The Journal of Wildlife Management* **64**, 646–662. doi:10.2307/3802735
- Hagen, C. A., Sandercock, B. K., Pitman, J. C., Robel, R. J., and Applegate, R. D. (2009). Spatial variation in lesser prairie-chicken demography: a sensitivity analysis of population dynamics and management alternatives. *The Journal of Wildlife Management* **73**, 1325–1332. doi:10.2193/2008-225
- Haridas, C. V., and Tuljapurkar, S. (2005). Elasticities in variable environments: properties and implications. *American Naturalist* **166**, 481–495. doi:10.1086/444444
- Hernández, F., Hernández, F., Arredondo, J. A., Bryant, F. C., Brennan, L. A., and Bingham, R. L. (2005). Influence of precipitation on demographics of northern bobwhites in southern Texas. *Wildlife Society Bulletin* **33**, 1071–1079. doi:10.2193/0091-7648(2005)33[1071:IOPODO]2.0.CO;2
- Hilborn, R., Walters, C. J., and Ludwig, D. (1995). Sustainable exploitation of renewable resources. *Annual Review of Ecology and Systematics* **26**, 45–67. doi:10.1146/annurev.es.26.110195.000401
- Hughes, L. (2000). Biological consequences of global warming: is the signal already. *Trends in Ecology & Evolution* **15**, 56–61. doi:10.1016/S0169-5347(99)01764-4
- Hunter, C. M., Caswell, H., Runge, C. M., Regehr, E. V., Amstrup, S. C., and Stirling, I. (2010). Climate change threatens polar bear populations: a stochastic analysis. *Ecology* **91**, 2883–2897. doi:10.1890/09-1641.1
- IPCC (2007a). 'Climate Change 2007 – The Physical Science Basis.' Contribution of working group I to the Fourth Assessment Report of the (IPCC) Intergovernmental Panel on Climate Change. (Cambridge University Press: Cambridge, UK.)
- IPCC (2007b). 'Climate Change 2007 – Impacts, Adaptation and Vulnerability.' Contribution of Working group II to the Fourth Assessment Report of the (IPCC) Intergovernmental Panel on Climate Change. (Cambridge University Press: Cambridge, UK.)
- Jenouvrier, S., Barbraud, C., Cazelles, B., and Weimerskirch, H. (2005). Modelling population dynamics of seabirds: importance of climate fluctuations on breeding proportions. *Oikos* **108**, 511–522. doi:10.1111/j.0030-1299.2005.13351.x
- Lande, R., and Engen, S. (1995). Optimal harvesting of fluctuating populations with a risk of extinction. *American Naturalist* **145**, 728–745. doi:10.1086/285765
- Meats, A. (1971). The relative importance to population increase of fluctuations in mortality, fecundity and the time variables of the reproductive schedule. *Oecologia* **6**, 223–237. doi:10.1007/BF00344916
- Morris, W. F., and Doak, D. F. (2004). Buffering of life histories against environmental stochasticity: accounting for a spurious correlation between the variabilities of vital rates and their contributions to fitness. *American Naturalist* **163**, 579–590. doi:10.1086/382550
- Myers, R. A., and Cadigan, N. G. (1995). Was an increase in natural mortality responsible for the collapse of northern cod? *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 1274–1285. doi:10.1139/f95-124
- Nichols, J. D., Runge, M. C., Johnson, F. A., and Williams, B. K. (2007). Adaptive harvest management of North American waterfowl populations: a brief history and future prospects. *Journal fur Ornithologie* **148**, 343–349. doi:10.1007/s10336-007-0256-8
- Ozgul, A., Oli, M. K., Armitage, K. B., Blumstein, D. T., and Van Vuren, D. H. (2009a). Influence of local demography on asymptotic and transient dynamics of a yellow-bellied marmot metapopulation. *American Naturalist* **173**, 517–530. doi:10.1086/597225
- Ozgul, A., Tuljapurkar, S., Benton, T. G., Pemberton, J. M., Clutton-Brock, T. H., and Coulson, T. (2009b). The dynamics of phenotypic change and the shrinking sheep of St Kilda. *Science* **325**, 464–467. doi:10.1126/science.1173668
- Pedersen, H. C., Steen, H., Kastdalen, L., Broseth, H., Ims, R. A., Svendsen, W., and Yoccoz, N. G. (2004). Weak compensation of harvest despite strong density-dependence growth in willow ptarmigan. *Proceedings. Biological Sciences* **271**, 381–385. doi:10.1098/rspb.2003.2599
- Pöysä, H., Elmberg, J., Nummi, P., and Sjöberg, K. (2004). Ecological basis of sustainable harvesting: is the prevailing paradigm of compensatory mortality still valid? *Oikos* **104**, 612–615. doi:10.1111/j.0030-1299.2004.12788.x
- Rader, M. J., Brennan, L., Hernandez, F., Silvy, N. J., and Wu, B. (2007). Nest-site selection and nest survival of northern bobwhite in southern Texas. *Wilson Journal of Ornithology* **119**, 392–399. doi:10.1676/06-069.1
- Robel, R. J., and Kemp, K. E. (1997). Winter mortality of northern bobwhites: effects of food plots and weather. *The Southwestern Naturalist* **42**, 59–67.
- Rolland, V., Nevoux, M., Barbraud, C., and Weimerskirch, H. (2009). Respective impact of climate and fisheries on the growth of an albatross population. *Ecological Applications* **19**, 1336–1346. doi:10.1890/08-1060.1
- Rolland, V., Hostetler, J. A., Hines, T. C., Percival, H. F., and Oli, M. K. (2010). Impact of harvest on survival of a heavily hunted game bird population. *Wildlife Research* **37**, 392–400. doi:10.1071/WR09177
- Rolland, V., Hostetler, J. A., Hines, T. C., Percival, H. F., and Oli, M. K. (2011). Factors influencing reproductive performance of northern bobwhite in South Florida. *European Journal of Wildlife Research* **57**, 717–727. doi:10.1007/s10344-010-0479-5
- Rollins, D., and Carroll, J. P. (2001). Impacts of predation on northern bobwhite and scaled quail. *Wildlife Society Bulletin* **29**, 39–51.
- Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C., and Pounds, J. A. (2003). Fingerprints of global warming on wild animals and plants. *Nature* **421**, 57–60. doi:10.1038/nature01333

- Sæther, B.-E., Ringsby, T. H., and Roskaft, E. (1996). Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms. *Oikos* **77**, 217–226. doi:10.2307/3546060
- Sæther, B.-E., Grotan, V., Tryjanowski, P., Barbraud, C., Engen, S., and Fulin, M. (2006). Climate and spatio-temporal variation in the population dynamics of a long distance migrant, the white stork. *Journal of Animal Ecology* **75**, 80–90. doi:10.1111/j.1365-2656.2005.01023.x
- Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., LeRoy Poff, N., Sykes, M. T., Walker, B. H., and Wall, D. H. (2000). Global biodiversity scenarios for the year 2100. *Science* **287**, 1770–1774. doi:10.1126/science.287.5459.1770
- Sandercock, B. K., Martin, K., and Hannon, S. J. (2005). Demographic consequences of age-structure in extreme environments: population models for arctic and alpine ptarmigan. *Oecologia* **146**, 13–24. doi:10.1007/s00442-005-0174-5
- Sandercock, B. K., Jensen, W. E., Williams, C. K., and Applegate, R. D. (2008). Demographic sensitivity of population change in northern bobwhite. *The Journal of Wildlife Management* **72**, 970–982. doi:10.2193/2007-124
- Sauer, J. R., Hines, J. E., and Fallon, J. (2008). 'The North American Breeding Bird Survey, Results and Analysis 1966–2007.' USGS Patuxent Wildlife Research Center. (USGS: Laurel, MD.)
- Singh, A., Hines, T. C., Hostetler, J. A., Percival, H. F., and Oli, M. K. (2011). Patterns of space and habitat use by northern bobwhites in south Florida. *European Journal of Wildlife Research* **57**, 15–26. doi:10.1007/s10344-010-0393-x
- Sisson, D. C., Terhune, T. M., Stribling, H. L., Sholar, J. F., and Mitchell, S. D. (2009). Survival and causes of mortality for northern bobwhites in the southeastern USA. In 'Gamebird 2006: Quail VI and Perdix XII'. (Eds S. B. Cederbaum, B. C. Faircloth, T. M. Terhune, J. J. Thompson and J. P. Carroll.) pp. 467–478 (Warnell School of Forestry and Natural Resources: Athens, GA.)
- Stahl, J. T., and Oli, M. K. (2006). Relative importance of avian life-history variables to population growth rate. *Ecological Modelling* **198**, 23–39. doi:10.1016/j.ecolmodel.2006.04.001
- Terhune, T. M., Sisson, D. C., Grand, J. B., and Sibling, H. L. (2007). Factors influencing survival of radiotagged and banded northern bobwhites in Georgia. *The Journal of Wildlife Management* **71**, 1288–1297. doi:10.2193/2005-640
- Tirpak, J. M., Giuliano, W. M., Miller, C. A., Allen, T. J., Bittner, S. L., Buehler, D. A., Edwards, J. W., Harper, C. A., Igo, W. K., Norman, G. W., Seamster, M. H., and Stauffer, D. F. (2006). Ruffed grouse population dynamics in the central and southern Appalachians. *Biological Conservation* **133**, 364–378. doi:10.1016/j.biocon.2006.06.014
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O., and Bairlein, F. (2002). Ecological responses to recent climate change. *Nature* **416**, 389–395. doi:10.1038/416389a
- Williams, J. S. (1999). Compensatory reproduction and dispersal in an introduced mountain goat population in central Montana. *Wildlife Society Bulletin* **27**, 1019–1024.
- Williams, B., Nichols, J., and Conroy, M. (2002). 'Analysis and management of animal populations.' (Academic Press: San Diego, CA.)
- Wisdom, M. J., and Mills, L. S. (1997). Sensitivity analysis to guide population recovery: prairie-chicken as an example. *The Journal of Wildlife Management* **61**, 302–312. doi:10.2307/3802585

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