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Original article

Tests of an additive harvest mortality model for northern bobwhite *Colinus virginianus* harvest management in Texas, USA

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We evaluated the application of using an additive harvest mortality model (AHMM) as a harvest management strategy for northern bobwhites *Colinus virginianus* during the 2007/08 and 2008/09 hunting seasons in two ecoregions of Texas: the Rolling Plains (RP) and the South Texas Plains (STP). We collected field data on three study sites/ecoregion (of 400-1,900 ha each; two treatment and one control) to estimate four demographic parameters (i.e. fall and spring density, overwinter survival in the absence of hunting and harvest rate). We used these data to parameterize an AHMM (a theoretical component of sustained-yield harvest; SYH) for bobwhites and compare model-based predictions of spring bobwhite populations with field estimates. Our goal was to compare predictions from the AHMM to field estimates of spring density based on known rates of harvest. Compared to field estimates, the AHMM consistently underestimated spring population density (mean % ± SE) by 55.7 ± 17.8% (2007/08) and 34.1 ± 4.9% (2008/09) in the RP and by 26.4 ± 25.3% (2007/08) and 49.1 ± 2.1% (2008/09) in the STP. Prescribing a fall bobwhite harvest to achieve a specific, target spring density may be difficult given the wide variation in the model parameters (i.e. fall and spring density, and natural mortality) that we observed.

Key words: additive harvest mortality model, Colinus virginianus, harvest, hunting, northern bobwhite, sustained-yield harvest, Texas

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Fixed, liberal state-wide bag limits set by wildlife agencies of the United States of America are not designed to regulate northern bobwhite *Colinus virginianus* harvest at small spatial scales (Peterson 1999, 2001, Williams et al. 2004a). For example, in the State of Texas, the bobwhite hunting season runs for 120 consecutive days and allows a daily bag of 15 birds/hunter. Where intensively exploited, discrete populations of northern bobwhites exist, harvest mortality is at least partially additive to natural mortality (Guthery 2002:101-102, Williams et al. 2004b). Additive mortality creates the potential for negative impacts of harvest on populations at a local scale (i.e. 500-1,500 ha) such as individual farms, ranches or pastures (Roseberry 1979). As available habitat patches continue to decline in size and increase in isolation, biologically justifiable and sustainable rates of harvest should be considered a necessary component of bobwhite management (Williams et al. 2004a).

Fixed, liberal harvest regulations set by state wildlife agencies have been criticized because they often have little or no biological justification (Peterson 1999, 2001, Williams et al. 2004a, Cooke 2007:305-308). Sustained-yield harvest (SYH) has been recommended as an approach to regulate quail harvest in discrete areas (Roseberry 1982, DeMaso 1999, Guthery 2002, Peterson 1999, 2001, Brennan et al. 2008). Previous authors have provided theoretical strategies for prescribing SYH for bobwhite population management in discrete areas (e.g. pasture or ranch; Guthery 2002:107-114, Brennan & Guthery 2007, Brennan et al. 2008), but no study has, to date, conducted a field application of SYH to evaluate its feasibility for northern bobwhite harvest management. This is because the veracity of the fundamental components of SYH, such as the additive harvest mortality model (AHMM), remains to be tested.

Guthery (2002:107-114) provided a theoretical prescription for regulating bobwhite harvests. Field application of this concept requires estimation of four variables: pre-hunt (fall) density, post-hunt (spring) density, natural overwinter survival (i.e. survival in the absence of hunting) and total harvest. Sustainable harvest rates are based on the fall population to achieve a target spring population, generally designed to maximize spring-fall population gains as a function of density-dependence (Guthery 2002:107).

Given the continued decline of bobwhite populations across their range and the fact that state-wide harvest regulations are not designed to manage bobwhite populations at small scales (Peterson 1999, 2001, Williams 2004b), managing harvest based on local population density is potentially an important management approach to conserve bobwhite populations. SYH is an appealing harvest strategy because it provides managers with a straight-forward tool for regulating harvest, and it scales down harvest from a state-wide scale set by fixed, liberal harvest regulations, to a local scale.

Our objective was to evaluate the AHMM (Ricker 1958) as a potential strategy to regulate harvest of bobwhites at local scales, using empirical data from two ecological regions in Texas, USA. Specifically, we 1) collected field data on the four variables needed to parameterize and evaluate the AHMM (Ricker 1958): pre-hunt (fall) population, post-hunt (spring) population, natural overwinter survival (i.e. survival in the absence of hunting) and total harvest; and 2) compared AHMM population predictions with field estimates of spring density. Our goal was to compare predictions from the AHMM to field estimates of spring density based on estimated rates of harvest.

Material and methods

Study areas

We collected field data in the Rolling Plains (RP) and the South Texas Plains (STP) ecoregions of Texas (Gould 1975). These ecoregions experience highly-variable annual and seasonal rainfall, and bobwhite populations therein exhibit irruptive population behaviour (Jackson 1969, Lehmann 1984). We used three study sites (of 400-1,000 ha each; two treatment and one control) per ecoregion. Study sites in the RP and STP were separated by ≥ 2 km and ≥ 5 km, respectively. Tracking of radio-marked bobwhites indicated no movements of bobwhites among study sites during the hunting season (i.e. November-February; Teinert 2009). All study sites were thus considered spatially independent. Treatment study sites were subject to recreational hunting using contemporary hunting techniques commonly employed by Texas bobwhite hunters, including walk-hunting with dogs or following dogs from vehicles or horses. The control sites were not hunted.

The RP comprises approximately 9.7 million ha in northwestern Texas and is an important ecoregion for both bobwhites and bobwhite hunting (Jackson 1969). Study sites were located on the Rolling Plains Quail Research Ranch and two private ranches in Fisher County near Roby, Texas. Cattle production was the primary land use on the site serving as a non-hunted control. On the two hunted sites (Rolling Plains Quail Research Ranch and a private ranch), management priorities were bobwhite hunting and habitat conservation. Soils on each study site are deep sands and loams (Natural Resource Conservation Service Web Soil Survey 2008). The average annual precipitation in the region was 559 mm, with an average snowfall of 254 mm (National Climate Data Center 2008). The average winter temperature (November-March) is 7.8°C and summer (April-August) is 23.3°C (National Climate Data Center 2008). The vegetation community was predominantly honey mesquite *Prosopis glandulosa*, catclaw acacia *Acacia greggii*, oaks *Quercus* spp., prickly pear *Opuntia* sp., common broomweed *Amphiachyris dracunculoides*, silver bluestem *Bothriochloa saccharoides*, sideoats grama *Bouteloua curtipendula* and buffalo grass *Buchloë dactyloides* (Gould 1978, Hatch & Pluhar 1993, Everitt et al. 1999).

The STP study areas were on the Encino Division of the King Ranch in Brooks County, 32 km south of Falfurrias, Texas. Historic accounts of the region vary greatly (e.g. barren desert or lush grassland) depending on the rainfall conditions at the time (Lehmann 1984:3-7). Soils are primarily sands (Natural Resource Conservation Service Web Soil Survey 2008) and average annual rainfall was 617 mm (National Climate Data Center 2008). Mean winter (during November-March) temperature was 16.7°C and summer (April-August) temperature was 30.0°C (National Climate Data Center 2008). Land uses on the study area included cattle production, oil and gas production, and wildlife management for commercial hunting.

The predominant plant community was a mixed-brush community characteristic of the STP (McLendon 1991). Brush and cactus species included mesquite, huisache *Acacia farnesiana*, granjeno *Celtis pallida* and brasil *Condalia hookeri* (Everitt et al. 2002), and Texas prickly pear *Opuntia lindheimeri* (Hatch & Pluhar 1993). Common forbs included doveweed *Croton* spp. and sunflower *Helianthus* spp. (Everitt et al. 1999). Common grasses were seacoast bluestem *Schizachyrium scoparium*, gulf cordgrass *Spartina spartinae*, sandbur *Cenchrus incertus* and purple threeawn *Aristida purpurea* (Gould 1978).

Methods

We estimated bobwhite density (bobwhites/ha) on each hunted study site using helicopter-based distance sampling surveys (Rusk et al. 2007, Schnupp 2009, DeMaso et al. 2010). Transects were traversed during pre-hunt (October-November 2007/08) and post-hunt (February-March 2008/09). The total survey effort was approximately 92 km/study site (Schnupp 2009).

We estimated natural, overwinter survival on the control (non-hunted) sites using radio-marked bobwhites (Teinert 2009). Bobwhites were trapped 20 October 2007 - 29 February 2008 and 20 October 2008 - 1 March 2009. We relocated radio-marked bobwhites $\geq$ 2 times /week during this period. We used the known-fates platform in Program MARK (White & Burnham 1999) to estimate survival from Teinert (2009). Teinert's (2009) survival estimates were based on sample sizes of 92 and 41 radio-marked bobwhites in the STP (2007/08 and 2008/09, respectively) and 53 and 55 radio-marked bobwhites in the RP (2007/08 and 2008/09, respectively). Detailed information regarding methodology and the results of survival estimation is provided in Teinert (2009).

We obtained estimates of total bobwhite harvest from landowners and lease managers. Landowners and lease managers recorded the sex and age of bobwhites harvested during the hunting season (i.e. October-February). Harvest data from the RP sites incorporated estimates of crippling loss based on observations of birds shot but not recovered during hunting. Long-term harvest data collection on the STP sites did not include estimates of crippling loss, and these data were not collected during our study.

We estimated total mortality during the winter period using the AHMM (Ricker 1958):

$$Q_a = H_o + V_o - H_oV_o \quad (1),$$

where Q_a = total mortality rate from start to end of hunting season, H_o = harvest rate in a population with no natural mortality and V_o = natural mortality in the absence of hunting. H_o is impossible to measure in the field (Anderson & Burnham 1981); therefore we assumed that H_o was equal to the harvest rate in a population with natural mortality (Guthery 2002). There is support in the literature for the AHMM providing suitable approximations of Q_a. Guthery (2002:100-101) provides a discussion on this with respect to the results of Glading & Saarni (1944), Roseberry & Klimstra (1984) and Robinette & Doerr (1993). Thus we felt justified in using this relationship as a basis for testing the use of AHMM as a harvest management tool in the field. The AHMM incorporates additional losses from harvest while accounting for a portion of individuals harvested that would have been lost due to natural mortality (Guthery 2002). It is considered to be conceptually superior to Errington's (Errington & Hamerstrom 1935, Errington 1945) 'doomed-surplus' model (Roseberry 1982, Guthery 2002:101-102). Additive harvest mortality in bobwhites is also supported in the literature (Roseberry 1979, Robinette & Doerr 1993, Williams et al. 2004b).

The key point for conducting this project was to evaluate the comparison between field estimates and AHMM predictions of spring abundance. Thus, our specific goal was to compare predictions from the AHMM to field estimates of spring density based on known rates of harvest, and not to prescribe a harvest for achieving a particular spring bobwhite population density. To illustrate this concept, assume a fall population of 1,000 bobwhites on a 1,000 ha property (i.e. 1 bobwhite/ha), a natural mortality of 500 bobwhites (i.e. $V_o = 0.50$) and a harvest of 200 bobwhites (i.e. $H_o = 0.20$). Using equation 1, total mortality (Q_a) would be 0.60 or 600 bobwhites:

$$0.60 = 0.20 + 0.50 - (0.20) \times (0.50).$$

Thus, the predicted spring population would be 400 bobwhites (i.e. 1,000-600) or 0.4 bobwhites/ha.

We compared the spring population size predicted by the AHMM with field estimates of bobwhite population density based on distance sampling. Our study was descriptive and our objective was to provide a first approximation that assessed whether the use of the AHMM has the potential to operate in an applied setting or not. We compared 95% confidence intervals of predicted spring populations with estimated spring densities reported by Schnupp (2009). We presumed that if the predicted estimates of spring population density were similar to field estimates of spring population density (e.g. within 10-15%), then use of AHMM would be a viable method for regulating bobwhite harvest because harvest rates could be prescribed for the fall population to reach a desired spring density.

Results

Harvest rates varied between and within ecoregions and study areas during each hunting season (Table 1). Estimated harvest rates across ecoregions were 7.7-60.1% in 2007/08 and 5.7-50.7% in 2008/09 (see Table 1). Harvest rates were most consistent on RP #1 in the RP (2007/08: 13.3%; 2008/09: 6.6%) and on STP #2 in the STP (2007/08: 12.2%; 2008/09: 5.7%; see Table 1).

Compared to field estimated populations, the AHMM underestimated spring populations (mean % ± SE) in 2008 by 55.7 ± 17.8% in the RP and 26.4 ± 25.3% in the STP (Table 2). The AHMM also underestimated spring populations during 2009 by 34.1 ± 4.9% and 49.1 ± 2.1% in the RP and STP, respectively (see Table 2). Both AHMM predicted and field estimated populations had wide confidence intervals. Only one estimate (STP #2, 2008) was within the 10-15% range that we considered acceptable for AHMM-based harvest prescriptions to be a viable harvest management method (see Table 2).

Discussion

To test the veracity of the AHMM, estimates of four parameters are necessary: pre-hunt (fall) population, post-hunt (spring) population, natural overwinter survival (i.e. survival in the absence of hunting) and total harvest. Two of these parameters (pre-hunt population and post-hunt population) proved quite difficult to estimate with the precision necessary to prescribe a sustainable harvest in an applied context (Schnupp 2009), and another, overwinter survival,

Table 1. Bobwhite harvest on two ranches in the Rolling Plains (RP; in Fisher County) and South Texas Plains (STP; in Brooks County) ecoregions of Texas, during October-February 2007/08 and 2008/09.

		Harvest						
Year	Ecoregion	Pasture	Total bag	# Lost	Total harvest	Fall population	(95% CI) [a]	% Harvest rate [b] (95% CI) [a]
2007/08	Rolling Plains	RP #1	159	20	179	1342	(894-2003)	13.3 (8.9-20.0)
		RP #2	719	52	771	1282	(930-1770)	60.1 (43.6-82.9)
	South Texas Plains	STP #1	223	-[c]	223	2882	(2277-3641)	7.7 (6.1-9.8)
		STP #2	170	-[c]	170	1389	(1017-1898)	12.2 (9.0-16.7)
2008/09	Rolling Plains	RP #1	114	7	121	1847	(1264-2703)	6.6 (4.5-9.6)
		RP #2	819	88	907	1788	(1319-2420)	50.7 (37.5-68.8)
	South Texas Plains	STP #1	332	-[c]	332	900	(610-1335)	36.9 (24.9-54.4)
		STP #2	22	-[c]	22	384	(222-682)	5.7 (3.2-9.9)

[a] Note: 95% CIs are not symmetric. See Buckland et al. (2001:115-119).
[b] Harvest rate = Total harvest/fall population
[c] Crippling loss data were not collected in the field.

Table 2. Difference between predicted and field estimates of bobwhite spring population size on two ranches in the Rolling Plains (RP; in Fisher County) and South Texas Plains (STP; in Brooks County) ecoregions of Texas, during 2008-2009. Predicted population size was based on the additive harvest model (Ricker 1958). Parenthetic values are ranges (predicted population and percent difference) and 95% CI[a] (field estimated population).

			Spring population estimates		
Year	Ecoregion	Pasture	Predicted population[b]	Field estimated population	% Difference
2008	Rolling Plains	RP #1	386 (154-862)	622 (331-1147)	-37.9 (-24.8 - -53.3)
		RP #2	170 (34-469)	641 (434-939)	-73.5 (-50.1 - -92.1)
	South Texas Plains	STP #1	481 (238-931)	998 (563-1757)	-51.8 (-47.0 - -57.6)
		STP #2	221 (98-470)	223 (99-533)	-1.1 (-0.7 - -11.9)
2009	Rolling Plains	RP #1	647 (294-1326)	914 (544-1536)	-29.2 (-13.7 - -46.0)
		RP #2	330 (106-779)	542 (343-849)	-39.0 (-8.2 - - 69.2)
	South Texas Plains	STP #1	433 (165-877)	886 (590-1350)	-51.2 (-35.0 - -72.1)
		STP #2	276 (118-580)	521 (335-819)	-47.0 (-29.2 - -64.7)

[a] Note: 95% CIs are not symmetric. See Buckland et al. (2001:115-119).
[b] Using model of additive harvest mortality: $Q_a = H_o + V_o - H_oV_o$, from Ricker (1958), Kaplan-Meier estimates of overwinter mortality (± 95% CI) from Teinert (2009), and estimates of density (± 95% CI) from Schnupp (2009).

exhibited extensive variability from year to year, ranging from 18 to 76% (Teinert 2009). Thus, prescribing a fall bobwhite harvest to achieve a specific, target spring density may not be possible given the wide variation in estimates of model parameters (i.e. fall and spring density, and natural mortality) that we observed. This outcome may severely limit the applicability of AHMM harvest prescriptions as a strategy for northern bobwhite harvest management until more precise estimates of key population parameters can be obtained. Predicted estimates of spring populations were consistently lower than field estimates. These discrepancies may have been related to: 1) underestimates of survival rate, 2) the potential that our study populations were impacted by an unknown amount of immigration, or 3) parameter estimates (fall and/or spring density based on distance sampling) that were not representative of the true population.

Teinert (2009) evaluated survival estimates between radio-marked and banded-only bobwhites in our study area. He documented no difference in survival estimates between radio-marked and banded-only bobwhites. This finding suggested no evidence of radio-telemetry bias in survival estimates, although the possibility exists (Guthery & Lusk 2004); however, survival estimates for bobwhites on the STP site were highly variable between years, a result that poses difficulties for consistent harvest prescriptions, and necessitates a conservative approach to harvest management.

Immigration has the potential to strongly impact quail demography in discrete areas (Guthery 2002). Mark-recapture data collected at our control (i.e. non-hunted) sites and subsequent modeling using the approach developed by Pradel (1996) suggested that immigration and emigration were essentially zero during our study (Teinert 2009); however, immigration and emigration have occurred within hunted populations of New World Quail (Errington 1945, Glading & Saarni 1944), which could potentially mask the effects of harvest on density. Also, bobwhite distribution across the habitat matrix may change during the course of a hunting season as birds attempt to maintain optimal covey sizes (Williams et al. 2004b). Each of these phenomena should be considered carefully when prescribing bobwhite harvest as they can potentially mask the impacts of overharvesting on a population (Williams et al. 2004b).

Schnupp (2009) provided estimates of fall and spring density using helicopter-based distance sampling. Past research suggested that distance sampling and helicopter surveys are appropriate techniques for obtaining reliable estimates of bobwhite abundance (Shupe et al. 1987, Guthery 1988, Rusk et al. 2007, DeMaso et al. 2010). However, the density estimates provided by Schnupp (2009) exhibited wide 95% CIs (e.g. $\geq$ 1.69 bobwhites/ha), which may have resulted from low encounter rates. Buckland et al. (2001:240) recommend a sample size of $\geq$ 60 encounters as 'a practical minimum' for reliable density estimation, and recommend even greater sample sizes in clustered populations (i.e. coveys of bobwhites). Given the encounter rates provided by Schnupp (2009:Tables 2.7 and 2.8), bobwhite helicopter surveys in the RP would, on average, require the distance sampling effort to be increased from 92 to 117 km of sampled transect/pasture in the fall and from 92 to 235 km of sampled transect/pasture in the spring to reach the recommended minimum. In the STP, effort would need to be increased from 92 to 134 km of sampled transect/pasture in the fall and to 157 km of sampled transect/pasture in the spring.

Conclusions

Prior research has suggested that northern bobwhite management could be improved by scaling down harvest from a state-wide scale to a local scale and scaling up habitat conservation from a local level to a state level (Williams et al. 2004a). We agree that this philosophy has strong merit and represents an appropriate rescaling of the bobwhite management paradigm. However, we believe the methods for doing so remain inadequate. Using the AHMM as an SYH approach may provide a viable alternative to fixed, liberal regulations in theory, yet this approach necessitates precise estimates of three necessary parameters (fall population, spring population and overwinter mortality rate). Obtaining precise estimates of population parameters, coupled with highly variable natural overwinter mortality of northern bobwhite, pose great challenges to using the AHMM in an applied context. These two difficulties must be addressed before the AHMM can be used effectively as a bobwhite harvest management tool. Issues with key variables needed to parameterize and test the AHMM with field data will need to be resolved before further progress can be made.

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