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Quail abundance, hunter effort, and harvest of two Texas quail species: implications for hunting management

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Managing exploited species characterized by declining abundance, such as northern bobwhite *Colinus virginianus* and scaled quail *Callipepla squamata*, presents challenges for regulatory agencies and wildlife managers. Our objective was to determine the influence of quail abundance and quail hunter effort on annual bobwhite and scaled quail harvest in Texas, USA. We formulated competing models accounting for quail harvest at both statewide and regional scales using hunter survey and quail abundance data collected by the Texas Parks and Wildlife Department (1978–2012) and evaluated them using multiple linear regression and model selection (AICc). Statewide bobwhite and scaled quail harvest was best predicted by models that included quail abundance, quail hunter-days or total quail hunters, respectively ($R^2 = 0.969$ and 0.915 , respectively). Our most plausible models also predicted regional quail harvest reasonably well ($R^2 \geq 0.67$), but in some regions diverged from statewide models, with hunter effort alone best explaining quail harvest. Despite our models' high predictive ability, current hunting regulations do not reflect variability in factors driving harvest at the spatial scales we evaluated. Species characterized by limited dispersal ability, such as quails, are at risk of localized overharvest when hunting management cannot limit harvest at the same spatial scale where hunting occurs. For Texas quails, harvest management implemented by individual property managers, rather than statewide hunting regulations, is the most appropriate way to avoid localized overharvest because property managers can control harvest at the scale relevant to both quails and quail hunters.

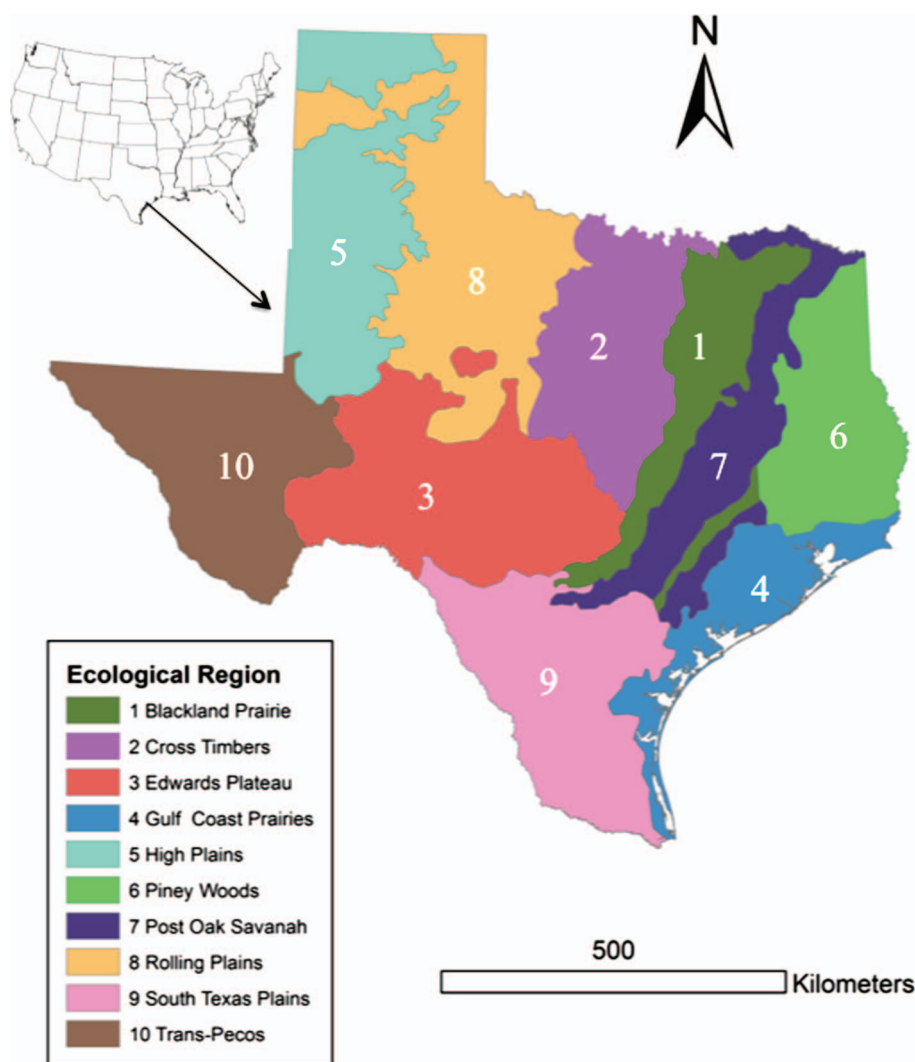
Management of exploited wildlife species presents difficulties for those tasked by statute with their conservation, particularly when abundance of these species has declined for decades and numbers fluctuate markedly among years. Stakeholders often perceive short-term (3–5 year) swings in abundance as proof that the long-term decline in abundance is markedly worsening or improving when neither conclusion is justified. Despite the fact that limiting hunting season length, bag limits, and/or means and methods contributed to the restoration of some exploited species (Leopold 1933, Allen 1954, Rosene 1969, Ayal and Baharav 1983, deCalesta 1983, Miller 1990), others still experienced long-term declines in abundance and range extent despite these measures (Marboutin and Peroux 1995, Johnson and Braun 1999, Silvy and Hagen 2004). Logically, this is true when harvest is not the sole factor in declines in abundance and range, or if harvest is totally compensatory to non-harvest mortality. Harvest management for two New World quail species, northern bobwhite *Colinus virginianus* (hereafter bobwhite) and scaled quail *Callipepla squamata*, in the United States epitomizes this situation. Bobwhite, once one of the most common and widely hunted North American gamebird species, has declined in abundance over large

spatial areas since at least the 1960s and perhaps for more than 100 years; scaled quail abundance has declined for several decades, especially in the State of Texas, USA (Leopold 1931, Peterson et al. 2002, Merola-Zwartjes 2005, Sauer et al. 2012). Although most quail biologists agree that habitat loss, fragmentation, and degradation, rather than harvest, are the primary causes of declining bobwhite and scaled quail abundance and range (Roseberry and Klimstra 1984, Peterson 2001, Williams et al. 2004), there is considerable stakeholder pressure to alter hunting regulations in an attempt to halt or reverse these long-term trends (Godfrey 2012, Simms 2012, Texas Parks and Wildlife Commission 2012).

Quail hunting opportunities are readily available in Texas for those who can afford hunting leases on private property. Most hunters hunt with shotguns over dogs, bounded by a season between late October and late February, with a statewide daily bag limit of 15 birds. Because few hunters hunt the entire season, and fewer still fill a daily bag limit, quail hunting in Texas is functionally unregulated, except by land managers or hunters themselves (Peterson and Perez 2000, Peterson 2001). Peterson and Perez (2000) demonstrated that both bobwhite and scaled quail hunting in Texas was

consistent with the hypothesis that quail hunting was largely self-regulatory (hunter effort responds to fluctuations in quail abundance). This relationship seems clear when one compares the long-term trends for quail abundance and hunter effort for both statewide and ecoregion spatial scales (Fig. 1–5). Peterson and Perez (2000) maintained that hunters expended less time hunting quail (i.e. spent few days afield or did not hunt at all) during low as opposed to high quail abundance years. Guthery et al. (2004a) examined roadside surveys and harvest data for bobwhites in the States of Oklahoma and Missouri, USA, concluding that bobwhite hunting was not self-regulatory at low quail densities. The ratio of hunters to bobwhites tended to increase as bobwhite and hunter numbers decreased, and the remaining hunters harvested a greater proportion of remaining bobwhites than in times of greater abundance due to increased hunter efficiency (birds killed per hunter per day), a phenomenon known as hyperstability (Hilborn and Walters 1992,

Erismann et al. 2011, Ward et al. 2013). Thus, under such hyperstable harvest the number of birds harvested would be disproportionate to the number of hunters afield and quail abundance. Guthery et al. (2004b) reported similar results for bobwhites, scaled quail, and Gambel's quail *Callipepla gambelii* using data from the States of Arizona, Kansas, Missouri, Oklahoma and Texas, USA. Regardless, both the self-regulatory (Peterson and Perez 2000) and differential hunter efficiency (Guthery et al. 2004a, b) explanations predict that modestly restrictive daily bag limits (e.g. 5–7 birds) may be too conservative when quail are abundant, yet too liberal when quail are scarce (Peterson 2001). Whereas both explanations suggest that restrictive fixed daily bag limits (e.g. 2–3 birds) and/or major reductions in season length (e.g. 1–2 week season) may indeed prevent overharvest during periods of low quail abundance, Peterson (2001) and Guthery et al. (2004a, b) asserted that many quail hunters are unlikely to view such restrictive changes favorably.



Source: Gould, F. W. 1969. Texas plants: a checklist and ecological summary.
– Texas Agricultural Experimental Station, Texas A&M University System.

Figure 1. Texas ecological regions (Gould 1969). Trends in northern bobwhite abundance (mean quail per 32 km survey route), total number of bobwhite hunters, and total bobwhite hunter-days in Texas, 1978–2012.

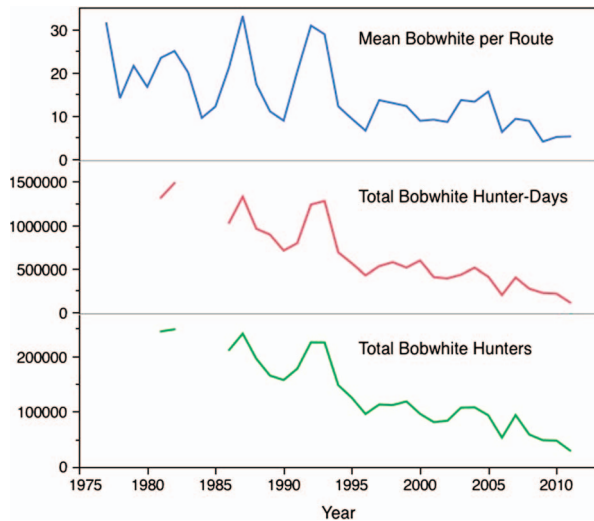


Figure 2. Trends in northern bobwhite abundance (mean quail per 32 km survey route), total number of bobwhite hunters, and total bobwhite hunter-days in Texas, 1978–2012.

Although many factors (e.g. access, weather) influence quail harvest, a clear understanding of both quail abundance and hunter effort is required to achieve harvest objectives. Logically, quail harvest is both additive and compensatory to non-harvest mortality: some quail that would have otherwise survived were shot, where some shot would have died anyway. Although quail biology, additive and compensatory models of harvest mortality, and overwinter survival have been studied in detail, the contribution of hunter effort to quail harvest has received less attention. Texas presents an excellent opportunity for clarifying the influence of the quail abundance and hunter effort on quail harvest for four primary reasons. First, bobwhite and scaled quail occur both allopatrically and sympatrically in Texas, with one or both species occupying portions of all 10 ecological regions of the state (Fig. 5; Gould 1969, Hernández and Peterson 2007, Silvy

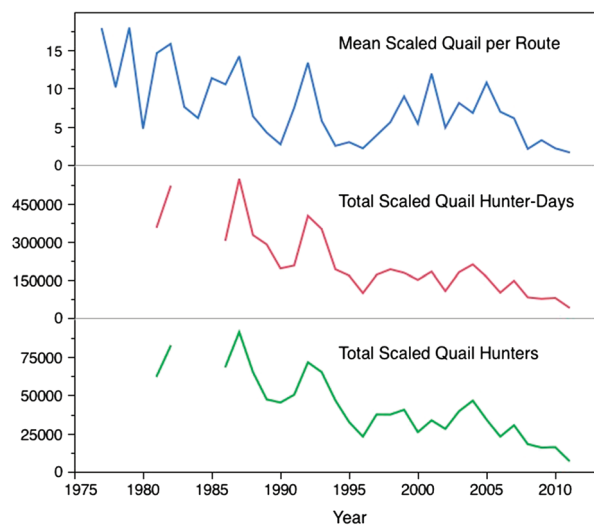


Figure 3. Trends in scaled quail abundance (mean quail per 32 km survey route), total number of scaled quail hunters, and total scaled quail hunter-days in Texas, 1978–2012.

et al. 2007). Second, Texas Parks and Wildlife Department (TPWD) used identical methods for monitoring abundance and harvest for these species since 1978 (Peterson and Perez 2000, Purvis 2012). Third, the abundance of bobwhite and scaled quail has declined for many years, primarily due to habitat conversion and loss (Brennan 1991, Bridges et al. 2002, Lusk et al. 2002, Merola-Zwartjes 2005), with marked fluctuations in abundance among years due to environmental stochasticity (Bridges et al. 2001, Lusk et al. 2007). Finally, stakeholders recently demonstrated a continued belief that minor changes to hunting regulations could halt or reverse the decline in quail abundance in Texas (Texas Parks and Wildlife Commission 2012).

Our objective was to determine the influence of quail abundance and quail hunter effort on annual total harvest of bobwhites and scaled quail in Texas. We explore how localized overharvest can contribute to declining abundance and range extent of quails and similar exploited species characterized by limited dispersal ability. We end with suggestions for managing harvest for such species more effectively.

Methods

We modeled total annual bobwhite and scaled quail harvest using quail abundance and harvest data from TPWD roadside counts (1978–2012) and the TPWD Small Game Harvest Survey Results (1981–1983 and 1986–2012), respectively. TPWD staff biologists survey these 32.2 km (20 mile) transects at sunrise (east-to-west) or one hour before sunset (west-to-east) each August at a rate of 32.2 km h⁻¹ (20 mph), and record the number of quail seen on every 1.6 km of road (1 mile). Peterson and Perez (2000) detail the design and history of these surveys and incongruity of survey years. We used counts of abundance from 162 TPWD roadside survey routes in the High Plains, Rolling Plains, Edwards Plateau, South Texas Plains, Gulf Prairies, Cross Timbers and Trans-Pecos ecological regions of Texas (Fig. 5; Gould 1969). We did not include data from the remaining three ecological regions (i.e. Piney Woods, Post Oak Savannah and Blackland Prairies) because TPWD discontinued quail surveys for these regions in 1988. We used hunter harvest survey data for the same seven ecological regions (182 counties). We first pooled these data at the statewide level for analysis to reflect the scale at which hunting is currently regulated. We then analyzed these data at the ecological region level for each species to determine whether there were differences between the hunting of bobwhites and scaled quail at statewide and regional scales.

We developed a series of competing models, using multiple linear regression, with the total number of bobwhite or scaled quail harvested per year (hereafter total quail harvest) as the dependent variable in all models. Because quail harvest cannot occur without both quarry and hunters, our independent variables represented these factors. Specifically, we used the mean number of bobwhites or scaled quail observed on each August survey route (hereafter quail abundance) to represent quail abundance and the total number of quail hunters (hereafter total quail hunters), and the total number of days hunters spent afield hunting quail (hereafter quail hunter-days) to represent hunter behavior.

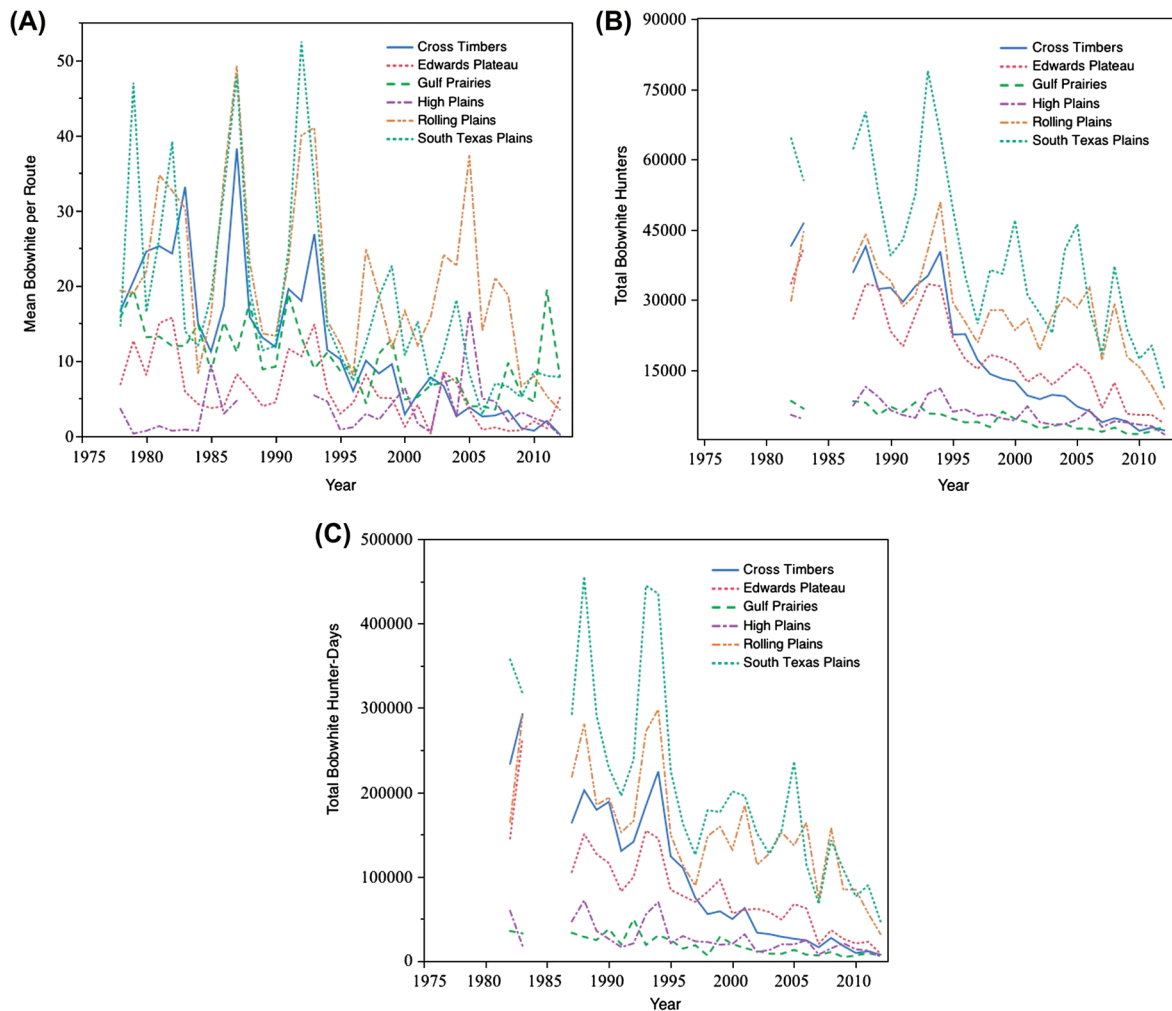


Figure 4. Trends in (a) northern bobwhite abundance (mean quail per 32 km survey route), (b) total number of bobwhite hunters, and (c) total bobwhite hunter-days in Texas by ecological region, 1978–2012.

These variables representing hunter effort included all hunters, regardless of hunting success. Although the summary of annual Small Game Harvest Survey Results (Purvis 2012) includes the mean number of birds harvested per hunter per day calculated from other variables, only total quail harvest, total quail hunters, and quail hunter-days are provided by respondents, so we used only these three variables in our models.

Because these count data are Poisson distributed, we log-transformed each variable (Zar 2010), and checked that transformed data were normally distributed using normal probability plots. Because it is reasonable to assume that harvest survey variables could be related, we tested for multicollinearity among these variables using the variance inflation factor (VIF; Neter et al. 1996). Total quail hunters and quail hunter-days were highly collinear ($VIF = 21.09\text{--}53.55$), so we restricted these variables to separate regression models, and thus did not provide a global model in our candidate model set. Our candidate models included all other combinations of quail abundance, total quail hunters, and quail hunter-days. Because quail hunters alter participation and effort due to changes in quail abundance harvest (Peterson and Perez 2000, Guthery et al. 2004a), we also modeled the interaction between quail abundance and total quail hunters or quail hunter-days. Residual plots for all analy-

ses were randomly distributed. We ran all models separately for bobwhites and scaled quail using JMP Pro 11.0.0 (SAS Institute 2013), and selected among candidate models using Akaike's information criterion corrected for small sample size (AICc). Models were considered plausible if they were within the 95% confidence set of models ($\sum W_i \geq 0.95$). We did not present models that included interaction terms if the model added one parameter (interaction term) and had a $-2 \log$ likelihood (-2LnL) similar to the other model, and the Δ_i was within 2 units of the model without the interaction (Burnham and Anderson 2002; p. 131). We included coefficients of determination (R^2) in tables so that we could determine how much of the total variance in the data was explained by plausible models (Guthery et al. 2005).

Results

Statewide

Statewide bobwhite harvest in Texas was best accounted for by the model that included quail abundance and quail hunter-days (Table 1). The model including quail abundance and total quail hunters also was plausible, but

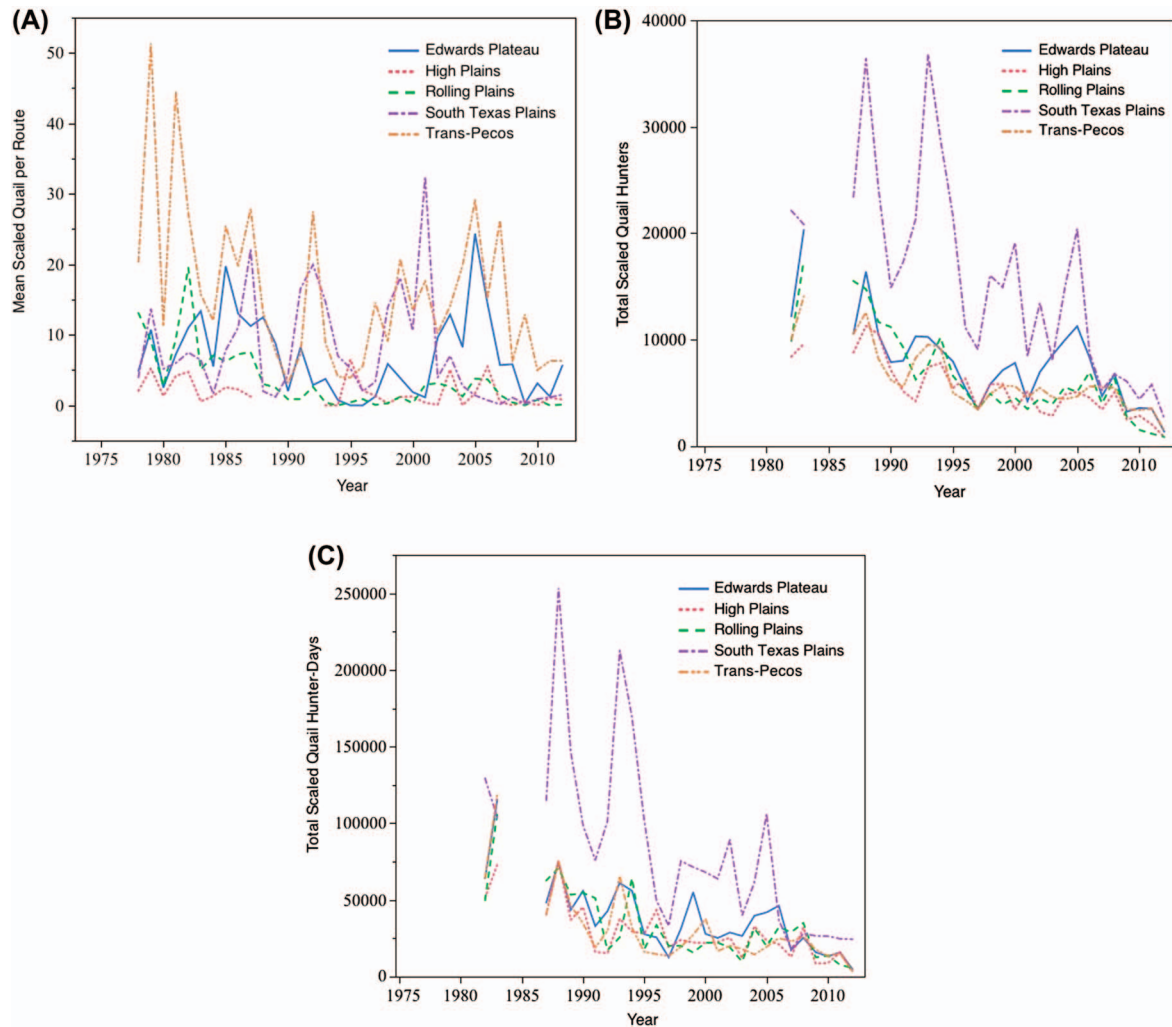


Figure 5. Trends in (a) scaled quail abundance (mean quail per 32 km survey route), (b) total number of scaled quail hunters, and (c) total scaled quail hunter-days in Texas by ecological region, 1978–2012.

was 5.65 times less likely to be the best-supported model among those evaluated than the best-supported model based on evidence ratios (ω_1/ω_i ; Table 1). None of the models including interactions were plausible. The only plausible model for scaled quail harvest at the statewide

level included quail abundance and total quail hunters (Table 1). Interestingly, all models evaluated did a reasonably good job of accounting for the variability in bobwhite and scaled quail harvest among years ($R^2 \geq 0.830$, and $R^2 \geq 0.672$, respectively; Table 1).

Table 1. Candidate regression models using quail abundance (QA), total quail hunters (QH), and total quail hunter-days (QHD) to account for statewide annual total harvest of northern bobwhites and scaled quail in Texas from log-transformed harvest and abundance survey data 1978 through 2012 using AICc model selection.

| Species | Model | K^a | $-2\ln L$ | $AICc^b$ | Δ_i^c | ω_i^d | ω_1/ω_i | R^2 |
|-------------------|------------------------------|-------|-----------|----------|--------------|--------------|---------------------|-------|
| Northern bobwhite | QA + QHD | 3 | -29.56 | -22.56 | 0.0 | 0.839 | 1 | 0.969 |
| | QA + QH | 3 | -26.10 | -19.10 | 3.5 | 0.149 | 5.651 | 0.965 |
| | QHD | 2 | -17.54 | -13.06 | 9.5 | 0.007 | 115.833 | 0.952 |
| | QH | 2 | -16.65 | -12.17 | 10.4 | 0.005 | 180.594 | 0.950 |
| | QA | 2 | 16.09 | 20.57 | 43.1 | 0.000 | 2328872309 | 0.830 |
| Scaled quail | QA + QH | 3 | 2.10 | 9.10 | 0.0 | 0.983 | 1 | 0.915 |
| | QA + QHD + (QA \times QHD) | 4 | 8.36 | 18.09 | 9.0 | 0.011 | 89.873 | 0.894 |
| | QH | 2 | 15.97 | 20.45 | 11.3 | 0.003 | 291.081 | 0.859 |
| | QA + QHD | 3 | 13.69 | 20.69 | 11.6 | 0.003 | 328.504 | 0.871 |
| | QHD | 2 | 24.95 | 29.43 | 20.3 | 0.000 | 25936.331 | 0.865 |
| | QA | 2 | 39.61 | 44.09 | 35.0 | 0.000 | 39673737.390 | 0.672 |

^ano. of estimable parameters, including the intercept.

^bAkaike's information criterion corrected for small sample size.

^c ΔAIC .

^dAkaike weight.

Table 2. Set of plausible ($\Sigma W_i \geq 0.95$) candidate regression models using quail abundance (QA), total quail hunters (QH), and total quail hunter-days (QHD) to account for annual total harvest of bobwhite in six ecological regions of Texas from log-transformed harvest and abundance survey data from the years 1978 through 2012 using AICc model selection.

| Ecological region | Model | K^a | $-2\ln L$ | AICc ^b | Δ_i^c | ω_i^d | ω_i/ω_1 | R^2 |
|---------------------|------------------------------|-------|-----------|-------------------|--------------|--------------|---------------------|-------|
| High Plains | QA + QH | 3 | 9.34 | 16.60 | 0.0 | 0.468 | 1 | 0.891 |
| | QH | 2 | 12.29 | 16.89 | 0.3 | 0.406 | 1.155 | 0.877 |
| | QA + QH + (QA \times QH) | 4 | 9.37 | 19.60 | 3.0 | 0.105 | 4.462 | 0.892 |
| Rolling Plains | QA + QHD | 3 | -22.01 | -15.01 | 0.0 | 0.609 | 1 | 0.962 |
| | QA + QHD + (QA \times QHD) | 4 | -22.21 | -12.47 | 2.5 | 0.171 | 3.565 | 0.963 |
| | QA + QH | 3 | -18.70 | -11.71 | 3.3 | 0.117 | 5.228 | 0.957 |
| Edwards Plateau | QHD | 2 | -6.39 | -1.91 | 0.0 | 0.399 | 1 | 0.949 |
| | QA + QH + (QA \times QH) | 4 | -10.38 | -0.65 | 1.3 | 0.213 | 1.879 | 0.957 |
| | QH | 2 | -4.27 | 0.21 | 2.1 | 0.139 | 2.885 | 0.945 |
| | QA + QHD | 3 | -6.47 | 0.53 | 2.4 | 0.118 | 3.380 | 0.950 |
| | QA + QH | 3 | -4.94 | 2.06 | 4.0 | 0.055 | 7.252 | 0.947 |
| South Texas Plains | QHD | 2 | -12.03 | -7.55 | 0.0 | 0.659 | 1 | 0.928 |
| | QA + QHD | 3 | -11.84 | -4.84 | 2.7 | 0.170 | 3.878 | 0.928 |
| | QH | 2 | -6.43 | -1.95 | 5.6 | 0.040 | 16.458 | 0.911 |
| Gulf Coast Prairies | QA + QH | 3 | 33.76 | 40.76 | 0.0 | 0.702 | 1 | 0.679 |
| | QH | 2 | 39.21 | 43.69 | 2.9 | 0.162 | 4.326 | 0.607 |
| | QA + QHD + (QA \times QHD) | 4 | 35.62 | 45.36 | 4.6 | 0.070 | 10.000 | 0.660 |
| | QHD | 2 | 41.94 | 46.42 | 5.7 | 0.041 | 16.935 | 0.566 |
| Cross Timbers | QA + QH + (QA \times QH) | 4 | 8.47 | 18.21 | 0.0 | 0.470 | 1 | 0.954 |
| | QH | 2 | 14.03 | 18.51 | 0.3 | 0.406 | 1.158 | 0.943 |
| | QA + QH | 3 | 14.04 | 21.04 | 2.8 | 0.114 | 4.115 | 0.943 |

^ano. of estimable parameters, including the intercept.

^bAkaike's information criterion corrected for small sample size.

^c ΔAIC .

^dAkaike weight.

Ecoregions

The most plausible model for bobwhite harvest in the Rolling Plains included quail abundance and hunter-days, with and without the interaction term, although the model that incorporated quail abundance and total quail hunters also was plausible (Table 2). The best-supported models for bobwhite harvest in the High Plains, Gulf Coast Prairies and Cross Timbers incorporated quail abundance and total quail hunters, but the model including quail abundance and quail hunter-days also was plausible for the Gulf Coast Prairies, as in the Rolling Plains. Although bobwhite harvest in the Edwards Plateau and South Texas Plains was best accounted for by the model that considered only hunter-days, as in other regions, the next most plausible models for both regions included quail abundance.

Scaled quail harvest in the High Plains and Edwards Plateau was best accounted for by models that included quail abundance and total quail hunters (Table 3). In the Trans-Pecos, the most plausible model included quail abundance and quail hunter-days, but the model including only quail hunter-days also was plausible. The model that included only total quail hunters best explained scaled quail harvest in the Rolling and South Texas Plains, although models that considered quail abundance and total quail hunters also were plausible.

Discussion

We found that quail abundance and hunter effort (total hunter-days and total hunters) accounted for 96.9 and 91.5% of the variability in statewide bobwhite and scaled quail harvest

in Texas, respectively. In fact, all models that included both quail abundance and a measure of hunter effort accounted well for quail harvest ($R^2 \geq 0.871$; Table 1). These results are consistent with the self-regulatory explanation of quail harvest at the statewide scale (Peterson and Perez 2000), as all plausible models included quail abundance and reflected the influence of hunter effort – quail hunter-days, and to a lesser extent total quail hunters – on total bobwhite harvest, or the number of people hunting one or more days on total scaled quail harvest. The difference between the measure of hunter effort for the species may be the result of scaled quail hunters hunting the same number of days during a given hunting season, whereas some bobwhite hunters may hunt many more days than others due to factors such as expensive hunting rights leases (Conner 2007).

At the ecoregion scale, similar models were most plausible for bobwhites in the High Plains, Rolling Plains, Gulf Coast Prairies and Cross Timbers, and for scaled quail in the High Plains, Edwards Plateau and Trans-Pecos. In all these cases, quail abundance and a measure of hunter effort accounted for most ($\geq 67.9\%$) of the variation in quail harvest. Divergence occurred from statewide models in regions, such as the Trans-Pecos, where quail abundance and hunter-days best explained quail harvest, rather than total quail hunters. This is likely because scaled quail are not typically hunted coincidental to bobwhites in this region, as they are in others. Interestingly, hunter effort alone accounted for most ($\geq 82.6\%$) of the variation in quail harvest in some regions (i.e. South Texas Plains, Edwards Plateau for bobwhites; Rolling Plains and South Texas Plains for scaled quail). The lack of quail abundance in most plausible models for the Rolling and South Texas Plains may be due to lucrative quail fee-hunting operations that dominate quail harvest in these

Table 3. Set of plausible ($\Sigma W_i \geq 0.95$) candidate regression models using quail abundance (QA), total quail hunters (QH), and total quail hunter-days (QHD) to account for annual total harvest of scaled quail in five ecological regions of Texas from log-transformed harvest and abundance survey data from the years 1978 through 2012 using AICc model selection.

| Ecological region | Model | K^a | $-2\ln L$ | AICc ^b | Δ_i^c | ω_i^d | ω_i/ω_1 | R^2 |
|---------------------------------|----------------------------|-------|-----------|-------------------|--------------|--------------|---------------------|-------|
| High Plains | QA + QH | 3 | 31.32 | 39.04 | 0.0 | 0.800 | 1 | 0.796 |
| | QA + QH + (QA \times QH) | 4 | 31.84 | 42.91 | 3.9 | 0.115 | 6.953 | 0.797 |
| | QA + QHD | 3 | 36.20 | 43.92 | 4.9 | 0.070 | 11.499 | 0.733 |
| Rolling Plains | QH | 2 | 36.66 | 41.20 | 0.0 | 0.562 | 1 | 0.826 |
| | QA + QH | 3 | 35.11 | 42.25 | 1.1 | 0.332 | 1.694 | 0.790 |
| | QA + QH + (QA \times QH) | 4 | 35.39 | 45.39 | 4.2 | 0.069 | 8.117 | 0.790 |
| Edwards Plateau ^e | QA + QH | 3 | 24.89 | 31.89 | 0.0 | 0.496 | 1 | 0.853 |
| | QH | 2 | 28.84 | 33.31 | 1.4 | 0.243 | 2.040 | 0.835 |
| South Texas Plains ^e | QH | 2 | -11.33 | -6.85 | 0.0 | 0.671 | 1 | 0.960 |
| | QA + QH | 3 | -11.52 | -4.52 | 2.3 | 0.209 | 3.207 | 0.960 |
| Trans-Pecos ^e | QA + QHD | 3 | 34.84 | 41.84 | 0.0 | 0.563 | 1 | 0.763 |
| | QHD | 2 | 39.47 | 43.95 | 2.1 | 0.195 | 2.880 | 0.718 |

^ano. of estimable parameters, including the intercept.

^bAkaike's information criterion corrected for small sample size.

^c ΔAIC .

^dAkaike weight.

^ewe did not report 95% confidence sets for these regions because the model that included the interaction term increased the $\Delta AIC < 2$ with a similar $-2 \log$ likelihood, which means this additional parameter provided no new information relative to the model without the interaction term (Burnham and Anderson 2002, p. 131).

regions. Although some hunters and lease managers voluntarily restrict hunting during times of low quail abundance (Howard 2007), lessees pay so much for hunting access that some may hunt regardless of abundance (Conner 2007). Further, if quail harvest is best explained by hunter effort alone, harvest may have achieved hyperstability. Thus, lower quail abundance would not necessarily regulate harvest, contrary to the self-regulatory explanation of quail harvest (Peterson and Perez 2000). Thus, those formulating hunting regulations should consider variability in quail abundance as well as specific measures of hunter effort.

Current statewide quail hunting regulations cannot address variability in either quail demographic parameters or most quail hunter behaviors that drive harvest in Texas. Thus, we concur with earlier studies that concluded minor changes in statewide hunting regulations are unlikely to reduce harvest (Peterson and Perez 2000, Peterson 2001, Guthery et al. 2004a, b). Regardless, some stakeholders continue to believe that minor reductions in daily bag limits (i.e. 1–2 birds lower) or season lengths (i.e. 1–2 weeks shorter) could halt or reverse declining quail abundance in Texas (Sasser 2012). Other researchers maintained that, although more draconian reductions in daily bag limits and/or season lengths probably would reduce statewide quail harvest when birds are abundant, they are much less likely to be effective when quail numbers are low (Peterson 2001, Guthery et al. 2004a). Possibly for these reasons, some stakeholders in Texas recently argued for more extreme changes to hunting regulations, such as a statewide closed season (Texas Parks and Wildlife Commission 2012).

Quail biologists long have been aware of bobwhite vulnerability to localized overharvest (Roseberry et al. 1979, Williams et al. 2004), yet no one has analyzed the influence of spatially heterogeneous quail harvest, despite Roseberry's (1991) call for such research. Ignoring the spatial aspects of quail ecology results in hunting regulations that may limit some aspects hunter effort across a state, but do not limit hunter take within quail subpopulations in any measurable

way. For this reason, current bobwhite and scaled quail hunting regulations in Texas cannot limit hunter effort or annual harvest at the regional scale, much less the spatial scale relevant to quail and quail hunters (i.e. the pasture; Williams et al. 2004), even if minor adjustments are made to reflect fluctuations in abundance statewide and certain aspects of hunter effort that influence each species. Thus, overharvest on individual properties can produce localized extirpations that may accelerate broad scale declines in abundance or range extent for any metapopulation where emigration and immigration cannot easily occur, while still operating within statewide hunting regulations.

For Texas quails, a number of solutions may be effective to prevent localized overharvest, including spatially explicit hunting regulations already employed for similar galliform species characterized by declining abundance and range extent (Williams et al. 2004, California Dept of Fish and Wildlife 2013, South Dakota Dept of Game Fish and Parks 2014). These solutions could include marked reductions in statewide season lengths and bag limits (Peterson 2001), replacing daily bag limits with annual quotas (Andersen et al. 2014), regulating season lengths and bag limits at the ecoregion or finer scale (Williams et al. 2004), or even closing the quail hunting season statewide, except on individual properties (including cooperatives) that maintain habitat demonstrated to be suitable to support hunted subpopulations (Guthery et al. 2000), thereby effectively managing harvest at the pasture scale. Although regulation at ecoregion or county scales may be viable alternatives, under any regulatory option, aside from closing the season or issuing individual property hunting permits, localized overharvest can still occur on individual properties. This is large due to the large size of properties where quail are hunted (often ≥ 1000 ha; Wilkins et al. 2003) relative to the limited dispersal ability of the species (often ≤ 1 km from hatch location; Duck 1943, Baumgartner 1944, Madison 1998, Taylor et al. 1999, Liu et al. 2002, Townsend et al. 2003, Terhune et al. 2010). Therefore, the most effective way to prevent localized over-

harvest in a private-land state such as Texas ($\geq 97\%$ privately owned; Wilkins et al. 2009), lies with those who functionally manage harvest at the scale relevant to both quail and quail hunters: the individual hunting property manager. Thus, it is critical that regulations do not de-incentivize habitat management for Texas quails by restricting hunting opportunities that are economically valuable to landowners. Therefore, we recommend that regulatory agencies and other wildlife professionals promote awareness of the potential for and effects of localized overharvest, and help land managers develop strategies to avoid this potential consequence of hunting.

The implications of localized overharvest extend beyond Texas quails: vulnerability of species characterized by limited dispersal ability to extirpation from localized overharvest is of concern for conservationists worldwide. In North America, greater sage-grouse *Centrocercus urophasianus* and ruffed grouse *Bonasa umbellus*, thereby contributing to population decline (Small et al. 1991, Gibson 1998, Connelly et al. 2003). In Europe, Scotland banned all capercaillie *Tetrao urogallus* hunting in 2001 in the face of rapidly changing landscapes (The Scottish Government 2001). Concern has been expressed for the brown hare *Lepus europaeus* in Denmark, as changing agricultural landscapes effectively isolated subpopulations (Jensen 2009). In South America, concern has been directed toward subsistence hunting of many Amazonian vertebrates exhibiting various levels of limited dispersal ability in increasingly fragmented landscapes (Peres 2001). Clearly, those seeking to conserve exploited species characterized by limited dispersal ability in fragmented habitats are beginning to address vulnerability to localized harvest.

Conclusions

Given the potential biological and political ramifications of changes in hunting regulations, wildlife policy makers must ensure their perceptions of hunting regulations match regulations' ability to influence quail harvest. Our models that included both quail abundance and some measure of hunter effort explained nearly all variability in statewide bobwhite and scaled quail harvest among years in Texas, but the specific measure of hunter effort was different in some regions. Further, quail harvest in some regions was best predicted by hunter effort alone. Thus, most regulatory changes are unlikely influence quail abundance. Although adding large expanses of contiguous habitat would certainly be the best action to reverse declining abundance of such species, harvest management strategies must function at a scale relevant to the species and its hunters to avoid accelerating declines of these limited dispersal species through localized overharvest. For Texas quails, harvest management by individual property managers, not statewide hunting regulations, are the best way to avoid localized overharvest. Due to the long-term decline in bobwhite and scaled quail, there is a critical need for wildlife professionals and hunting property managers to engage in dialogue regarding the array of management strategies that could prevent localized overharvest.

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