

MULTI-STATE ANALYSIS OF FIXED, LIBERAL REGULATIONS IN QUAIL HARVEST MANAGEMENT

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Abstract: We derived consequences (realizations of hunter efficiency, relative harvest rates) of fixed, liberal quail (northern bobwhite [*Colinus virginianus*], Gambel's quail [*Callipepla gambelii*], and scaled quail [*C. squamata*]) harvest regulations applied at large scales from time series on quail abundance, total harvest, and hunter participation. Data came from Kansas (1966–2001), Missouri (1983–2001), Oklahoma (1990–2001), north and south Texas (1986–2001), and Arizona (1982–1999), USA, where harvest regulations were liberal (season length 2.5–4 months, daily bag limit 8–15 birds) during the periods of record. For all study regions, hunter-days were expressible as a linear function of quail abundance, and total harvest was expressible as a linear function of hunter-days. These results implied that hunter efficiency (harvest/hunter-day/index bird) declined monotonically and curvilinearly as quail populations increased. Likewise, relative harvest rate declined monotonically and curvilinearly as abundance increased, which implied that harvest was not self-limiting; however, the rate of decline generally was low because harvest rate was the product of an increasing (hunter-days) and a decreasing function (hunter efficiency) of quail abundance. Under fixed, liberal regulations, variations in quail abundance seem to govern harvest rates at the state or regional level; the regulations per se probably are biologically inconsequential.

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The practice of wildlife management evolves with the ideas and spirit of the times (*Zeitgeist*), the record of empirical failures and successes, and the results of research. Presumably, practice converges to state-of-the-art application, given *Zeitgeist*.

State-scale management of quail harvest provides an example of this process. Early on, restrictions on harvest were imposed as an impulsive response to declining populations of game (Leopold 1933:4). Then research (Errington and Hamerstrom 1935, Errington 1945) resulted in the innovative conjecture that thresholds of security, which manifested as relatively constant spring breeding densities, governed quail dynamics from fall to spring. The threshold construct led to the deduction that harvest was fully compensatory (0 birds lost for 1 bird harvested) if it did not take a population below the threshold level. Apparent support for the threshold concept appeared in the literature on northern bobwhites (Baumgartner 1944), California quail (*C. californicus*; Glading and Saarni 1944), Gambel's quail (Swank and Gallizioli 1954), and scaled

quail (Campbell et al. 1973). The potentially self-limiting nature of game harvest—quarry becomes more wary with exposure to hunting, hunters wax and wane with quarry populations—also came to light through research (Allen 1954:124–125, Peterson and Perez 2000). The threshold concept and self-limitation hypotheses led to progressive liberalization of quail harvest regulations (season length, daily bag limits, possession limits) that presumably converged on state-of-the-art management. The veracity of this approach to harvest management has been questioned, however, and multistate investigation of harvest has been proposed (Burger et al. 1994).

Our purpose was to evaluate consequences of fixed, liberal harvest regulations at large scales (states, regions within states). In particular, we determined whether an earlier finding that hunter efficiency declined with quail abundance in Oklahoma (Guthery et al. 2004) held in other states. Hunter efficiency must remain constant or decline with quail abundance for the self-limitation hypothesis (hunting pressure tracks quail abundance) to hold, which was not the case in Oklahoma. We also evaluated harvest rates relative to the self-limitation hypotheses to determine whether rates varied with

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quail abundance. We evaluated data from areas with declining quail populations and from areas with nontrending populations to assess the generality of our findings. The study required that we develop mathematical logic relating quail populations, hunter behavior, and harvest to deduce information on the efficiency of hunters and harvest rates as quail populations vary. Finally, we discuss whether fixed, liberal regulations applied at large scales have converged on state-of-the-art management, unimportance, or both.

METHODS

Data Sources

We obtained time series with indices of quail population abundance, hunter-days of effort, and total quail harvest from state wildlife agencies in Kansas (1966–2001), Missouri (1983–2001), Oklahoma (1990–2001), north (Rolling Plains) and south Texas (1986–2001), and Arizona (1982–1999), USA. Data were on Gambel's and scaled quail in Arizona and bobwhites in other states. Although hunting regulations within states varied slightly among years, these regulations generally were consistent among years and were liberal (season length 2.5–4 months; daily bag limit 8–15 birds, except for a daily bag of 6 in Missouri during 1984–1985). Regulations were more restrictive in states with declining populations (Kansas, Missouri, Oklahoma; Fig. 1) than in those with stable populations (Arizona, Texas; Fig. 1).

Methods of indexing quail abundance varied among states. For Kansas, we used the October Rural Mail Carrier Survey results (Wells and Sexson 1982). This survey involves 550 mail carriers who drive a total of 400,000 km (Wells and Sexson 1982). The Missouri index was based on counts of quail seen along 112 48-km routes traversed during the first 15 days in August (Dailey 2002). The Oklahoma index was based on counts along 32-km routes in 75 counties (Peoples 1991). The counts were completed in August and October, and we used the mean of these counts as an index of abundance ($n = 164$ or 166 , depending on year). Data from the Texas regions were based on 32-km route counts in August (Peterson and Perez 2000). Regional mean indices were based on 30–44 routes in north Texas and 22–31 in south Texas. The abundance index for Arizona, based on pooled populations of Gambel's and scaled quail, was a composite of statewide data from the North American Breeding Bird Survey (Droege 1990), Christmas Bird Counts (Brennan

1991), and annual state harvests. For each species and each count, we transformed the data to a 0–100 scale to standardize the indices, and we used the average of these 6 transformed counts as the index of annual abundance in any year.

Data on hunter effort and harvest came from questionnaire surveys conducted by each state wildlife agency. Generally, respondents were randomly selected and mailed survey instruments and data were derived based on that subset of respondents who hunted quail. Response rates were estimated at 40% for 9,000 questionnaires in Kansas, 51% for 12,500 surveys in Missouri (Reitz 2003), 33% for 5,729–12,349 questionnaires in Arizona, 58% for 15,000 questionnaires in Texas (Peterson 2001), and an unknown rate for >2,000 questionnaires in Oklahoma. In Oklahoma, respondents were contacted by telephone in later years of the survey. We acknowledge potential nonresponse bias, which might have yielded overestimates of hunter-days and harvest (Peterson 2001).

Logic and Data Analysis

The state or regional index of abundance (I) served as the basis for modeling and associated deductions. We assumed that I was an approximately linear, zero-intercept function of quail abundance. This assumption seems tenable because at local scales, hunting success may be expressed as a linear function of quail abundance (Brown et al. 1978, Guthery 1986:149, Palmer et al. 2002), and at state scales total harvest may be expressed as a linear function of the abundance index we used (Peterson and Perez 2000, DeMaso et al. 2002, Guthery et al. 2004). These findings imply a linear correlation between population size and the abundance index. The zero-intercept condition is tenable because the abundance index would be zero if the quail population was zero (with no quail, the index would be 0).

We further assumed that hunting pressure (P ; hunter-days in a state) is some linear function of abundance (Peterson and Perez 2000), i.e.,

$$P = f(I).$$

From this equation, we may derive relative pressure (P_R ; pressure/index bird) as

$$P_R = P/I.$$

We then defined total annual harvest (H) as

$$H = g(P) = g(f(I))$$

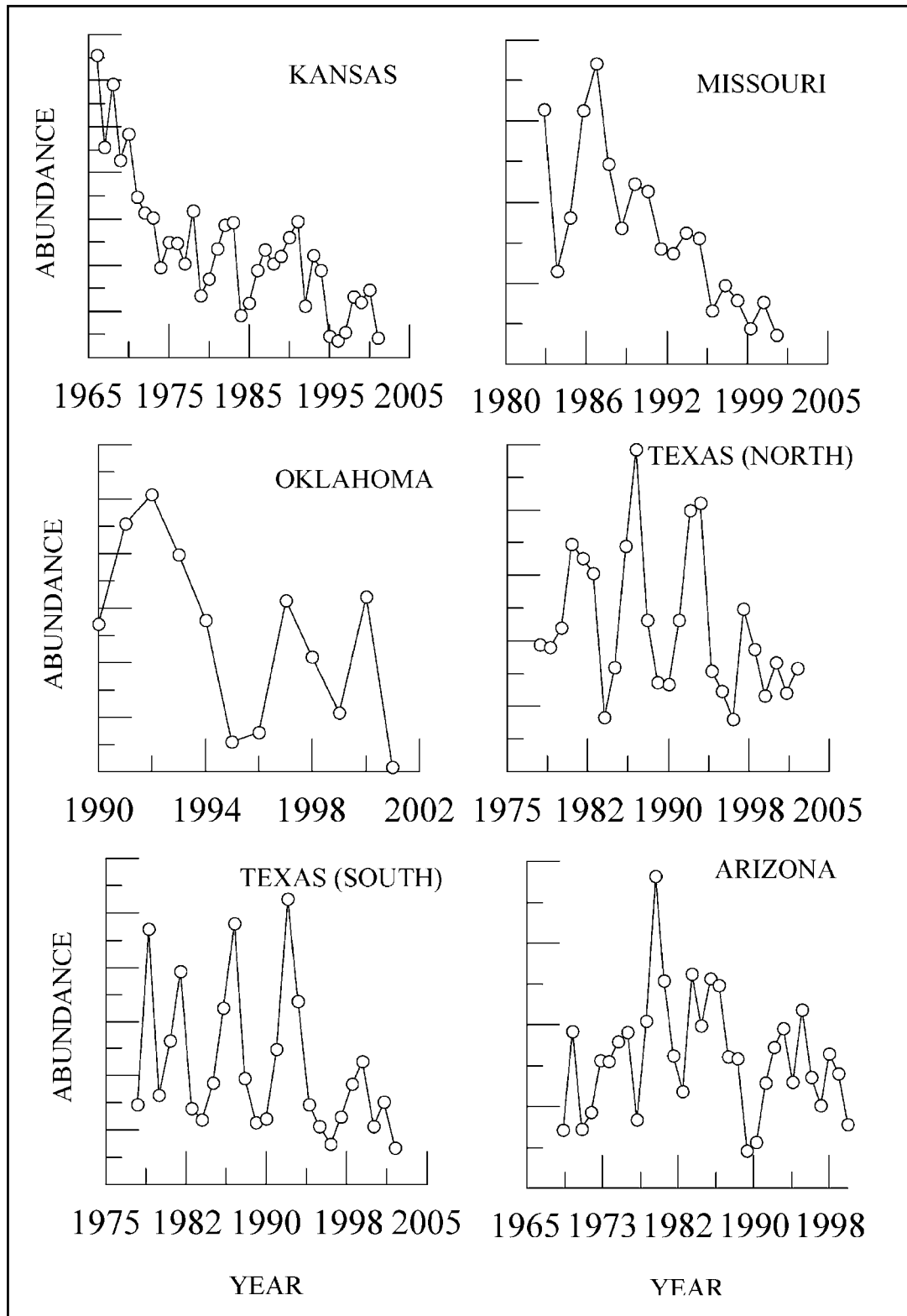


Fig. 1. Recent populations trends of northern bobwhites in Kansas, Missouri, Oklahoma, and Texas, USA, and of Gambel's and scaled quail in Arizona, USA, 1966–2001.

because harvest pressure is a function of the population index. We defined hunter efficiency (S) as

$$S = \frac{(H/P)}{I} = \frac{(H/I)}{P} = \frac{H}{PI}.$$

These definitions are tantamount to “harvest/hunter-day/index bird” or “harvest/index-bird-exposure-day.”

Finally, we defined the relative harvest rate (R ; harvest/index bird) as

$$R = \frac{H}{I}.$$

An interesting outcome is that the relative harvest rate is the product of pressure and efficiency, as defined. The relative harvest rate is a scaled version of the absolute harvest rate (percent of population harvested). We used simple linear regression of hunter-days on the population index and total harvest on hunter-days to estimate $f(I)$ and $g(P)$. Other variables were derived algebraically from these 2 functions. Appendix A provides an example.

RESULTS

For all datasets, hunter-days were linear functions of abundance, and harvest was a linear function of hunter-days (Figs. 2, 3); 95% confidence limits on the intercepts and slopes excluded zero in all regression equations. The existence of nonzero intercepts implied that hunting pressure declined more slowly than quail abundance and harvest declined more slowly than hunting pressure. In other words, the ratio of hunters to quail increased as the quail population declined. For example, the prediction equation for Arizona indicated that an 80% decline in quail abundance (index from 50 to 10) was associated with a 45% decline in hunting pressure. Harvest declined at a slower rate than pressure because the mean daily bag tends to increase with population abundance (Peterson and Perez 2000).

Models for hunter efficiency (harvest/hunter-day/index bird) were curvilinear (hyperbolic) and monotonically decreasing functions of quail abundance for all datasets (Fig. 4), indicating the average hunter at low quail abundance was more efficient than the average hunter at high quail abundance. The magnitude of this effect (efficiency at low populations/efficiency at high populations) ranged from 3.3 in Oklahoma and north Texas to 14.4 in Kansas. Excepting the Kansas estimate, the estimates averaged 3.7 ± 0.25 ($n = 5$). Thus, not only did the ratio of hunters to quail in-

crease as the quail populations declined, but also the efficiency of the average hunter increased.

Likewise, the relative harvest rate tended to decline with quail abundance but, excepting Kansas, in a manner subject to considerable uncertainty (Fig. 5). In Kansas, model predictions indicated the harvest rate declined 89% from low to high populations; the declines were 56% for Arizona, 27% for south Texas, 25% for Oklahoma, 24% for Missouri, and 21% for north Texas. With the exception of Kansas, the generally small modeled effect of quail abundance on harvest rate occurred because the rate was the product of an increasing (hunting pressure) and a decreasing function (hunter efficiency) of quail abundance. That is, the 2 functions tended to cancel each other, especially in Oklahoma and the 2 Texas study regions, resulting in a relatively flat trend for harvest rate as a function of quail abundance.

DISCUSSION

If harvest rate declines as quail populations increase, as our results suggested based on derivations from models of hunting pressure as a function of quail abundance and harvest as a function of hunting pressure (Figs. 2–5), then our results were at variance with previous assertions on the self-limiting nature of quail harvest. Allen (1954:125) presumed that harvest was self-limiting because wariness in quarry populations increased with exposure to hunting pressure. Learned hunter-avoidance behavior would reduce the probability of encountering and flushing a covey as a hunting season progressed (Radomski and Guthery 2000). Likewise, Gallizioli (1965) believed that low populations of Gambel’s quail sustained lighter harvest rates than high populations because low populations consisted of a higher proportion of experienced (more wary) adults and because hunting pressure declined with abundance. Apparently higher vulnerability to harvest of juvenile as compared to adult bobwhites (Shupe et al. 1990, Roseberry and Klimstra 1992) supports Gallizioli’s (1965) conjecture. Finally, a positive correlation between hunting pressure and quail abundance in conjunction with a positive correlation between mean daily bag and quail abundance has been taken as *prima facie* evidence for the self-limiting nature of quail hunting (Peterson and Perez 2000).

All of the above conjectures could hold if efficiency of the average hunter remained constant as quail abundance varied. However, our results suggested that efficiency was a monotonically decreasing function of quail abundance (Guthery et al.

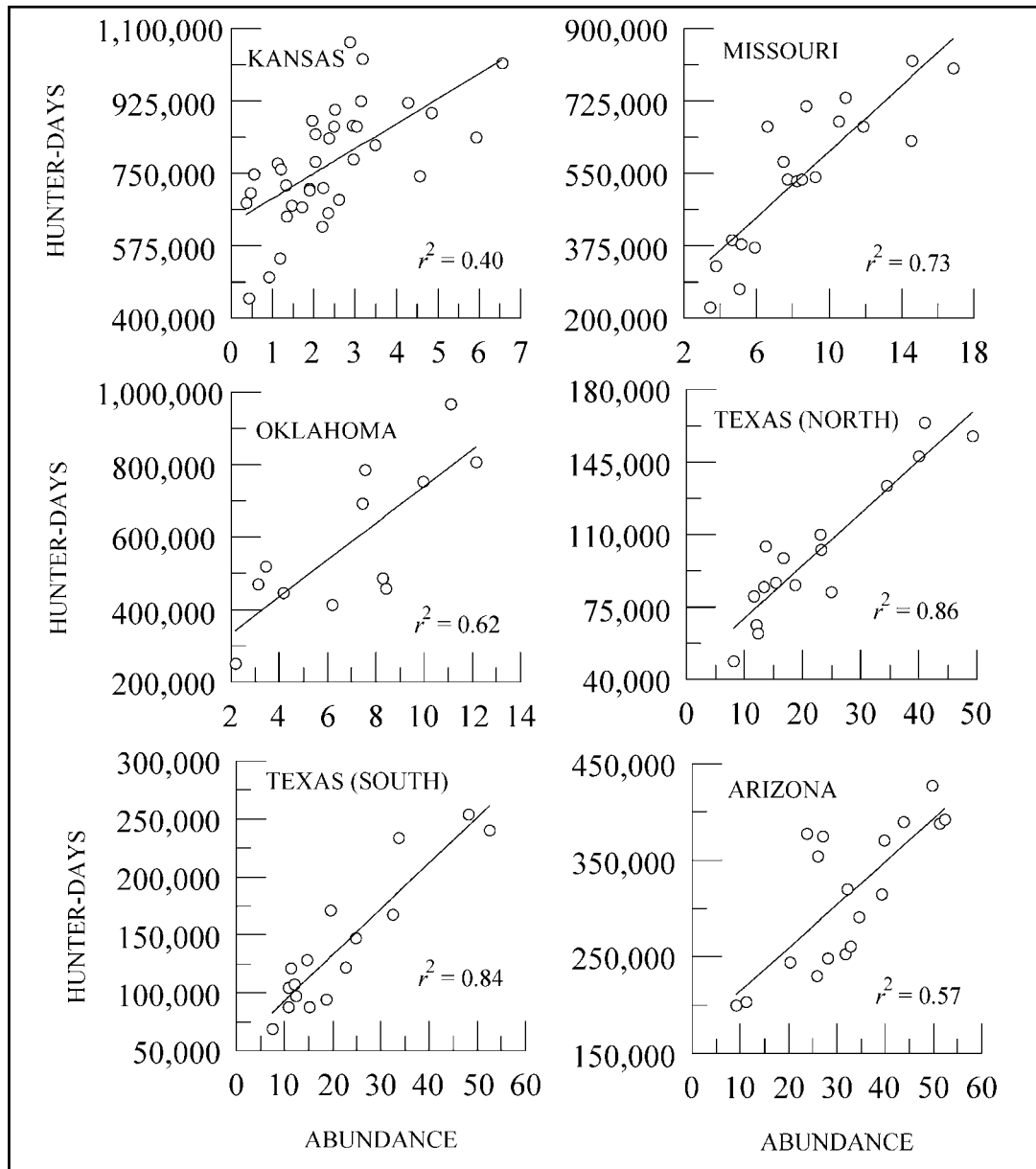


Fig. 2. Hunting pressure as a function of northern bobwhite abundance in Kansas, Missouri, Oklahoma, and Texas, USA, and of Gambel's and scaled quail abundance in Arizona, USA, 1966–2001.

2004; Fig. 4). Efficiency dynamics possibly occurred because hunters in the field during population lows were, on average, more avid and experienced than hunters in the field during population highs. Skilled hunters are known to obtain higher mean daily bags than less-skilled hunters (Hurst and Warren 1982, Peterson 2001). Moreover, hunting pressure per index bird declined with abundance because hunting pressure increased at a slower rate than the index of abundance. At a minimum, vari-

able efficiency in hunter populations and trends in relative pressure draw into question the hypothesis that state-scale quail harvest is self-limiting because hunting pressure tracks quail abundance.

Within the liberal regulation frameworks we examined, quail populations were the primary arbiters of hunting pressure, harvest, hunter efficiency, and perhaps harvest rates (Peterson and Perez 2000; Figs. 2–5). Statewide quail populations seemed to behave independently of the reg-

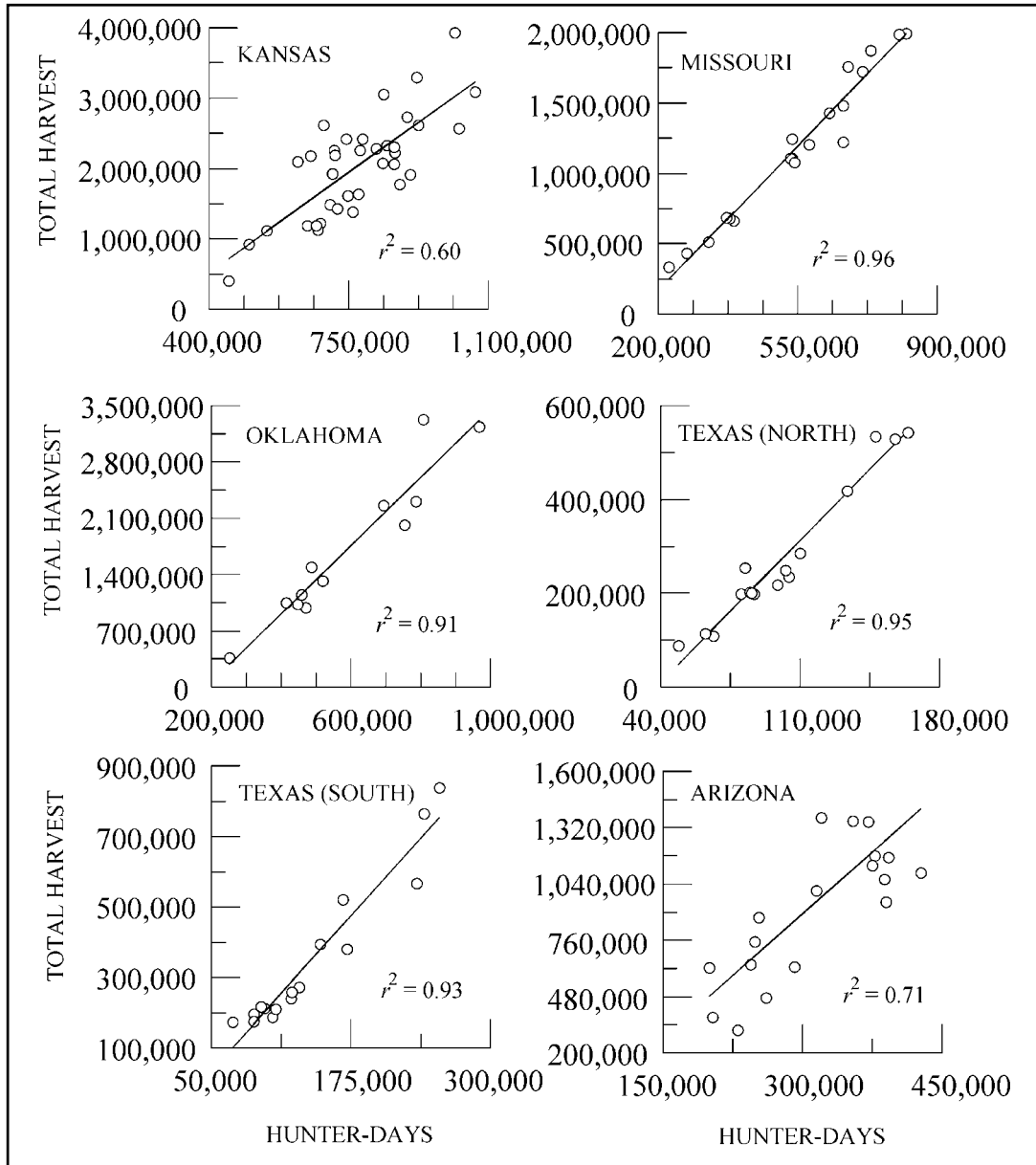


Fig. 3. Total harvest as a function of hunting pressure for northern bobwhites in Kansas, Missouri, Oklahoma, and Texas, USA, and for Gambel's and scaled quail in Arizona, USA, 1966–2001.

ulatory framework. We would need data on absolute harvest rates to feel completely comfortable with this assertion; if the rates were low relative to sustainable rates of 30–55% (Roseberry 1979, Guthery et al. 2000), then the low rates would support the assertion.

We conjecture that state-scale quail harvest regulations have converged on unimportance for state-scale quail abundance; that is, observed relationships between quail and harvest (Figs. 2–5) might

not change if regulations were moderately restricted or liberalized. At first blush, this conjecture seems hypercritical, but in the perspective of history, it seems a natural evolutionary outcome of trial-and-error process customized with research results. In a more positive light, we could also posit that fixed, liberal harvest regulations represent state-of-the-art management, which recognizes the neutral effect of fixed, liberal harvest regulations on statewide quail abundance in the context of sta-

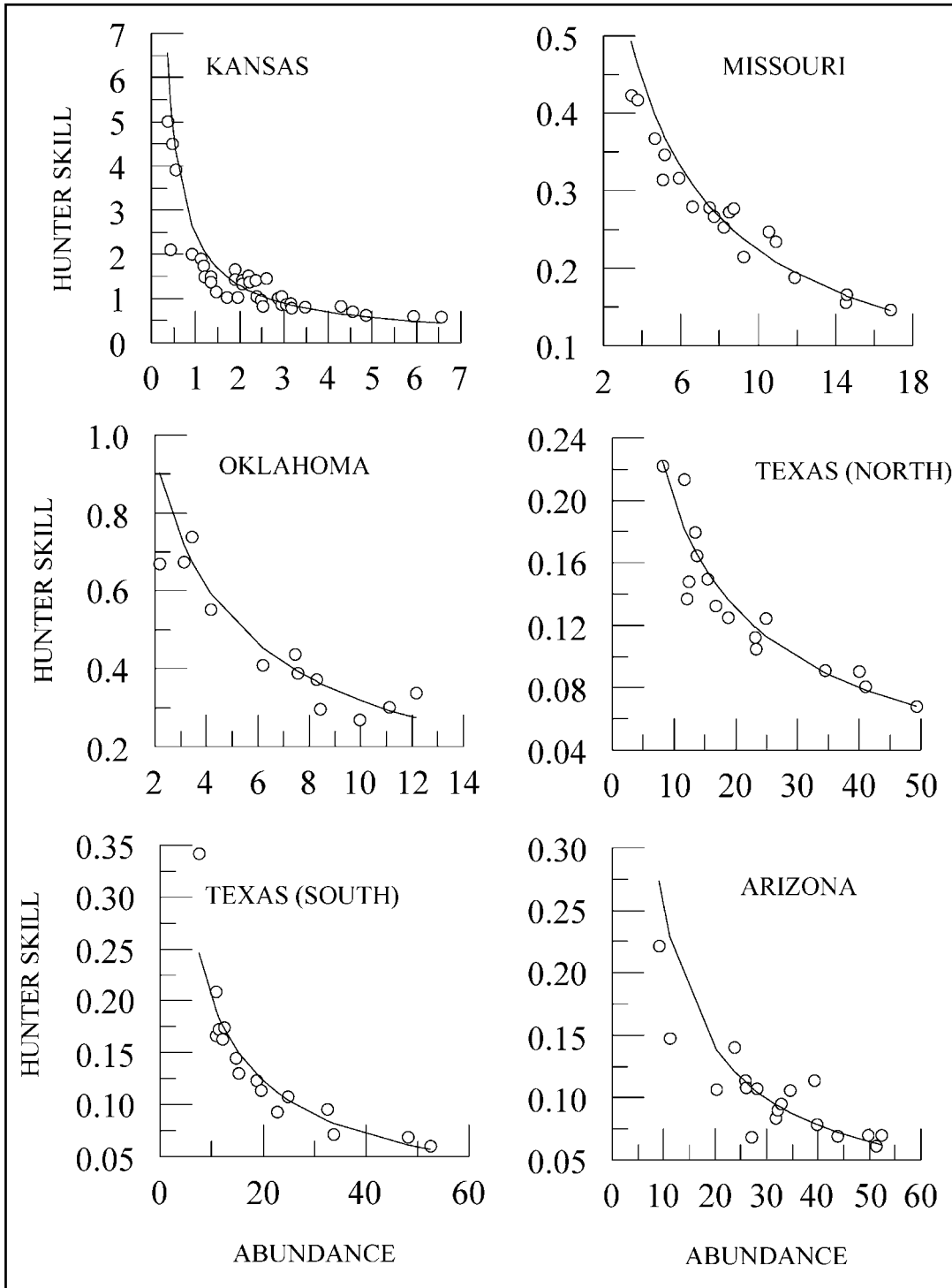


Fig. 4. Hunter efficiency as a function of northern bobwhite abundance in Kansas, Missouri, Oklahoma, and Texas, USA, and of Gambel's and scaled quail abundance in Arizona, USA, 1966–2001.

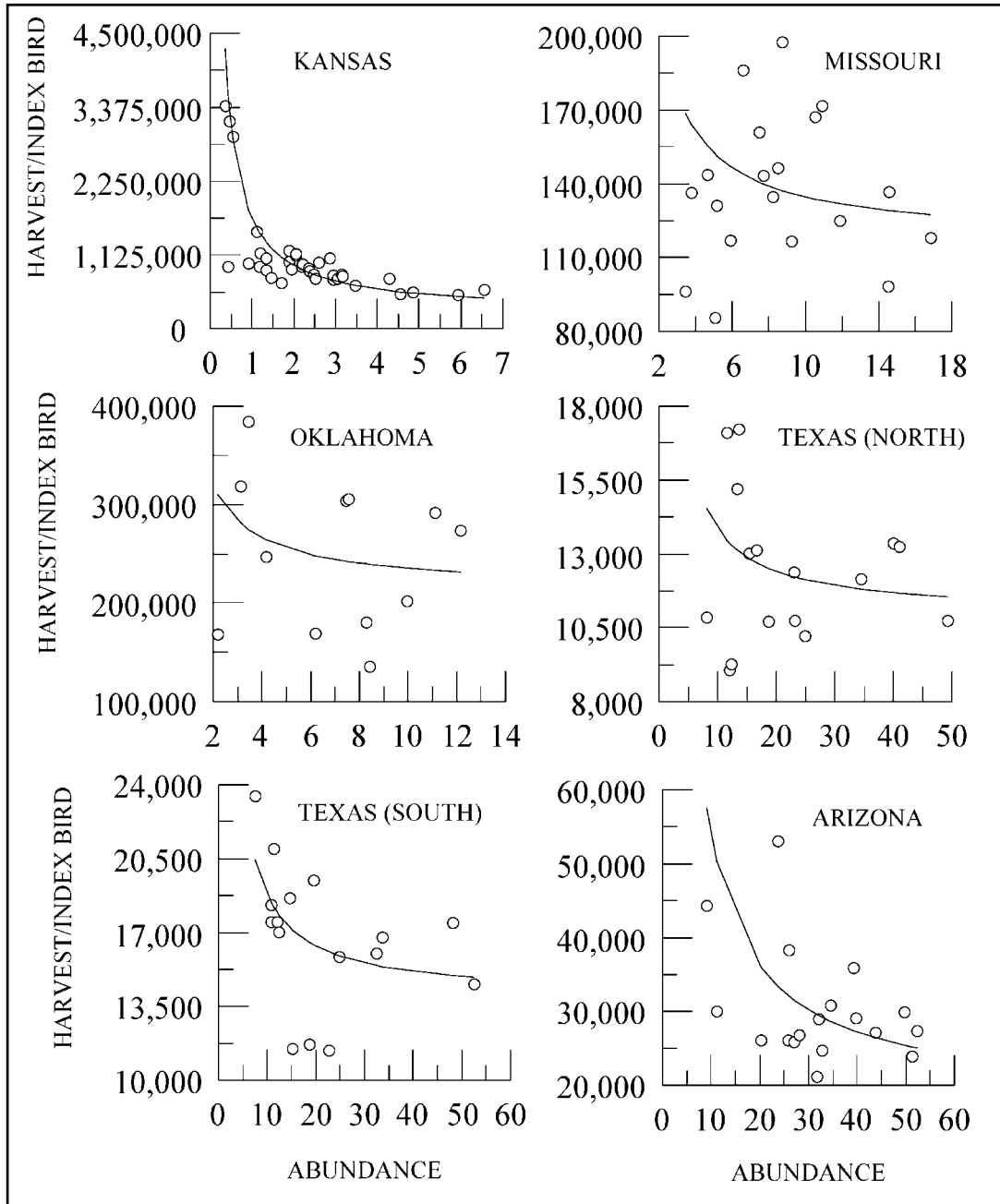


Fig. 5. Relative harvest rate as a function of northern bobwhite abundance in Kansas, Missouri, Oklahoma, and Texas, USA, and of Gambel's and scaled quail abundance in Arizona, USA, 1966–2001.

ble-to-declining quail abundance and declining hunting participation in some states.

We recognize, of course, that hunting regulations are formulated in a context broader than quail population dynamics per se. North American hunting culture is complex and includes ideals for fair chase, distribution of opportunity and harvest among as

many citizens as possible, and other sociological issues (Peterson 2001). In this context, daily limits on quail harvest may be desirable, particularly in an era of widespread quail population declines.

We conclude with a caveat. We do not claim that these results would hold at small spatial scales, such as individual ranches or state wildlife management

areas. Absolute harvest rates on such areas might be high enough to alter the demographics of resident quail populations. For example, Gore et al. (1970) estimated harvest rates of 19.2–42.1% for small areas in Texas. On the 627-ha Carbondale Research Area in Illinois, USA, harvest of northern bobwhites during 1954–1972 averaged 42.5% and ranged between 17.0 and 67.1% (Roseberry and Klimstra 1984:40). These may be examples of small-scale harvest rates considerably higher than harvest rates prevailing in regions and states. However, large-scale harvest rates are unknown.

MANAGEMENT IMPLICATIONS

We addressed the hypothesis that harvest is self-limiting at large scales because hunting pressure tracks quail abundance. The hypothesis presumably implies that harvest rate is independent of quail abundance or declines as quail abundance declines. We observed that hunting pressure tracked quail abundance in all study areas (Fig. 2), in support of the hypothesis. However, upon deeper analysis, we discovered that the ratio of hunters to quail, efficiency of the average hunter, and harvest rate tended to increase as quail abundance declined (Figs. 4, 5). In our datasets, then, harvest tended not to be self-limiting, despite the response of hunting pressure to quail abundance.

In the cases examined, annual variation in quail abundance, not the regulatory framework, appeared to be the primary arbiter of harvest. Thus, fixed, liberal harvest regulations applied at large scales seem to have converged on unimportance, and further liberalization or moderate restriction (reduced season length, bag limit) likely would have limited, if any, impact on regional or state populations of quail.

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APPENDIX A

We illustrate use of the equations given in METHODS with data on northern bobwhites from north Texas during 1986–2001 ($n = 16$). With I = the annual index of abundance, simple linear regression indicated that

$$P = \text{hunter-days} = f(I) = 44,212 + 2,538I; r^2 = 0.86.$$

The above equation implies that harvest pressure per index bird is

$$P_R = \frac{44,212}{I} + 2,538.$$

Thus, P_R declined hyperbolically as bobwhite abundance increased and became asymptotic at the rate of increase in pressure for a unit increase in the bobwhite abundance index.

Regression indicated that

$$H = \text{total harvest} = g(P) = -162,026 + 4.32P; r^2 = 0.95.$$

According to the equations given above, the trend in hunter efficiency as a function of population abundance was estimated as

$$S = \frac{-162,026 + 4.23P}{(44,212 + 2,538I)I}$$

$$= \frac{-162,026 + 4.23(44,212 + 2,538I)}{(44,212 + 2,538I)I}$$

$$= \frac{24,990 + 10,736I}{(44,212 + 2,538I)I}$$

Notice that, given linear functions for $P = f(I)$ and $H = g(P)$, efficiency declines with population abundance because the numerator is positive linear in I , whereas the denominator is positive quadratic in I . At $I = 10$, we obtain $S(10) = 0.190$ quail/hunter-day/index bird, and at $I = 50$, we obtain $S(50) = 0.066$ quail/hunter-day/index bird.

Finally, the relative harvest rate (harvest/index bird) is

$$R = PS = (44,212 + 2,538I) \left(\frac{24,990 + 10,736I}{(44,212 + 2,538I)I} \right)$$

$$= \frac{24,990}{I} + 10,736.$$

In this example, the relative (and absolute) harvest rate declined hyperbolically with bobwhite abundance. For example, $R(10) = 13,235$ bobwhites harvested/index bird, whereas $R(50) = 11,236$ /index bird.